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THE DISTRIBUTIONAL ECOLOGY OF THE CALANOID COPEPOD *PAREUCHAETA ELONGATA* ESTERLY

by

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ABSTRACT

Many field and laboratory studies testing the growth of phytoplankton and the survival of the early developmental stages of zooplankton and benthic organisms have shown that sea waters that are alike in salinity and temperature are nevertheless different in other properties (qualities). These differences in quality may be associated with variations in the concentrations of dissolved trace elements and organics. The concentration of a trace element or organic may have beneficial or harmful effects on marine organisms. Bary (1963) suggested that, in certain areas, these variations in the properties of sea waters may be sufficiently great, and the tolerance of zooplankton sufficiently small, for species to be restricted to various waters. These waters, called water bodies, were described by their temperature and salinity characteristics and the distribution of species was described in relation to these water bodies.

Many of the species Bary (1963) studied were at the northern most or southern most boundaries of their geographic ranges. It was the purpose of this study to investigate whether or not, within the geographic range of an organism, variations in water quality are an important environmental variable in determining a species' abundance and distribution. The study organism was the calanoid copepod Pareuchaeta elongata. Lewis and Ramnarine (1969) had shown that, in the laboratory, the egg and the prefeeding naupliar stages were sensitive to variations in water quality.

The biological portion of this study consists of three parts. The first part is the results of three survey cruises of the waters of the inlets of the British Columbia mainland, the west coast of Vancouver Island, the connecting passages, and the Pacific Ocean. Six groups of water were identified on the basis of the similarity in the temperature-salinity characteristics of their subsurface waters. The results indicate that P. elongata is capable of breeding in all the waters studied, thus suggesting that variations in the species' abundance are unrelated to variations in water quality. Variables which may affect the species' abundance were suggested as being associated with the primary production of that area, and the origin and the residence time of the water in that area.

The one-year laboratory study, testing P. elongata egg clusters in various natural sea waters, indicated that there were differences in the survival among egg clusters from various areas. It was also shown, by testing egg clusters from one area in a number of seawaters of similar salinities, that there were variations in the quality of these waters.

Egg clusters were collected from G.S.-1 (in the Strait of Georgia) and Indian Arm, and were tested in their home water once a month over a 12-month period. Field collections were made at these two stations over a 29-month period. The laboratory data were evaluated in terms of the field data. The number of nauplii in the water was correlated with the number of eggs in the water, and was apparently not significantly affected by variations in the survival of the egg

in its home water (as measured in the laboratory). This lack of any significant effect of variations in survival was probably due to the very large effect of variations in egg production. There was a high mortality from the hatched nauplius to the adult (approximately 97%), indicating that the mortality of the egg due to its interaction with the water had a small role in determining the final population size. The data suggested that variables, such as prey availability, and predation, are probably the most effective variables in regulating the abundance of the species in these two areas.

In conclusion, while the data showed that the species was more abundant in some areas than others, these differences could be explained by considering the primary production of the area, and the origin and residence time of the water. Although seawaters within the study area may vary in quality, these variations probably do not significantly affect the abundance and distribution of the species.

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INTRODUCTION

A planktonic organism is carried by the water in which it lives from one area to another, and is incapable of swimming against this current. Because the range of such organisms is, by necessity, dependent upon currents, descriptions of a species' range have frequently been made in terms of some of the physical characteristics of the water in which it lives. These physical characteristics have been described from measurements of temperature and salinity, and definition has been given to water masses, domains, and the various mechanisms which transport water from one area to another.

Species may be associated with particular water masses (Bieri 1959; Kriss 1960; Kriss et al. 1960a, 1960b; McGowan 1960; Brinton 1962; Fager and McGowan 1963; Johnson and Brinton 1963). They may also be associated with smaller volumes of water, and the currents adjacent to coasts (Russell 1935, 1936, 1937, 1939; Fraser 1937, 1939, 1952; Marumo 1957; Sheard 1965).

Marine organisms possess a range of tolerances for temperature and salinity (Kinne 1963, 1964). Within the oceanic environment, salinity is probably not limiting to oceanic plankton (Hopper 1960), although it may be limiting in estuaries (Gunter 1961). Temperature may limit the viability or fecundity of zooplankton (Hutchins 1947), and is limiting to certain species carried from warm tropical waters into the colder temperate and polar regions (Somme 1929; Berner and Reid 1961; Woodhouse 1971). However, while temperature and salinity may limit a planktonic species at the boundaries of its range, it is

less likely that temperature and salinity variations, per se, are significant variables in determining a species' abundance within its range.

(i) The concept of variations in the 'quality' of sea waters

Sea waters of similar salinities may have different concentrations of the minor elements, although the eleven major elements, which account for 99.9% (by weight) of the salt in oceanic waters, occur in constant proportions (Sverdrup et al., 1942). Many of these minor elements are involved in the more important inorganic and biochemical reactions in the marine environment (Goldberg 1965). These reactions may be important in determining the concentrations of these dissolved elements. The concentrations of dissolved nitrogen and phosphorous in the euphotic zone are largely dependent upon these reactions, and largely independent of variations in salinity. The concentrations of dissolved copper (Atkins 1953), silicone (Armstrong 1954), iron (Armstrong 1959), and dissolved organic carbon, nitrogen and phosphorous (Duursma 1961) vary seasonally in certain waters.

Many of the elements present in sea water are concentrated by marine organisms (Goldberg 1957; Bowen 1966), and have known functions (Lehninger 1950; Williams 1953). Nitrogen and phosphorous are the general limiting factors to growth in the sea (Redfield 1958), and have been studied at various levels in the marine ecosystem (Clowes 1938; Marshall and Orr 1927; King and Demond 1953; Sette 1955; Holmes et al. 1957; Steeman and Jensen 1957; Bogorov 1958; Heinrich 1962;

Reid 1962). However, in certain areas, other trace elements may limit phytoplankton growth, both in lakes (Lund 1950; Goldman 1960, 1961) and in the marine environment (Harvey 1947; Ryther and Guillard 1959; Johnston 1963). The concentration of dissolved copper may be important to the setting of oyster larvae (Prytherch 1934). Dissolved organics may have several effects upon the biota within the marine environment (Lucas 1938, 1947, 1949, 1961), being toxic (Bainbridge 1953; Gunter et al., 1948; Procter 1957) or beneficial (Chu 1946, Collier et al., 1953; Rodhe 1955; Provasoli 1963; Stephen et al., 1961; Barber and Ryther 1969).

Johnston (1963, 1964) indicated that sea waters of similar salinities (and temperatures) may vary in quality, this quality being associated with the availability of dissolved trace elements. He determined these variations in quality by examining the growth of phytoplankton in several sea waters collected from different areas and at different times. Wilson (1951) and Wilson and Armstrong (1952, 1954, 1958, 1961) also indicated that there were variations in the quality of sea waters collected from different areas. However, they were unable to determine the source of variation. Gilfillan (1970) showed that the zooplankter Euphausia pacifica collected from two areas, exhibited different respiration rates in waters of similar temperatures and salinities. Few studies have, however, investigated the role of variations in the quality of natural sea waters in the distributional ecology of zooplankton; a notable exception has been the work of Bary (1963).

Bary (1963) surveyed the surface waters around Great Britain, and subdivided them into 'water bodies' on the basis of their temperature-salinity characteristics. Certain species of zooplankton were associated with particular water bodies, e.g., Pareuchaeta norvegica was associated with the Cold (Northern)-Transitional water bodies but not with the Warm (Southern) water body. Species have been shown to be associated with particular waters many times in the literature, and from these associations arose the concept of indicator species. However, very little of the work on indicator species has attempted to explain why an organism is associated with one water and not another.

Bary (1963) stated that zooplankton-water body associations were due, not to variations in the temperature and salinity of the water bodies, but to variations in the other properties of the waters. A species such as Pareuchaeta norvegica survived in its native water body because it was tolerant of the properties of that water. Conversely, it was not associated with the other water bodies because it was intolerant of the properties of that water. The earlier work of Wilson and Armstrong had shown that variations did occur in the quality of these waters, and the later work of Johnston confirmed this. Bary's contribution was to hypothesize that these variations were sufficiently great, and the tolerances of zooplankton sufficiently small, for the species to be limited to certain waters.

Several criticisms may be made of Bary's work (1963). Many of the species he examined were at the northern-most or southern-

most boundaries of their geographic ranges; at these boundaries temperature may have been limiting. Bary believed that this was not the variable limiting zooplankton to their native water bodies, because, over the year, the species experienced fluctuations in temperature and salinity which were greater than the variations between water bodies. As the native water body varied seasonally in temperature and salinity, the zooplankton associated with these waters must have had a wide temperature and salinity tolerance over the year. However, Gilfillan (1970) showed that the temperature and salinity tolerances of the zooplankter Euphausia pacifica varied through the year, with the result that the tolerances over the year were greater than the tolerances in any one month. An alternative explanation of Bary's data is that although the zooplankton species he examined were able to tolerate changes in temperature and salinity during the year, this ability to tolerate changes was not the same at all times of the year. Because of this, temperature and salinity variations between water bodies could have been limiting, either because the variations were lethal to the species, or because the species avoided the surface layer and remained deeper in the water column.

Another criticism of Bary's work was that he examined only one depth in the water column and, by this, failed to describe adequately the dimensions of the water bodies, the events occurring in the zone of mixing between water bodies, and the vertical distribution of the species within the water bodies. Therefore, while his data

are open to the interpretation that species are associated with certain water bodies because of their tolerances to the properties of these waters, the data are inconclusive. Also, as his studies were not conducted well within the geographic range of most of the species he studied, he failed to give a good evidence that a species is affected by variations in the properties or quality of the water within its range.

The purpose of this study is to test Bary's hypothesis by investigating whether or not the calanoid copepod Pareuchaeta elongata is affected by temporal and spatial variations in the properties of water bodies. This species is an ideal study organism for many reasons. Lewis and Ramnarine (1969) showed that the egg cluster was sensitive to variations in water quality. These clusters were reared in their native water, and experiments conducted once a month over a 12-month period indicated that there were temporal variations in the survival of the eggs. This suggested that there were temporal variations in the quality of sea water. Survival could be enhanced at certain times of the year by the addition of trace elements or the synthetic chelator EDTA to the sea water.

Unlike Euphausia pacifica, which Gilfillan (1970) showed to be sensitive to water quality, Pareuchaeta elongata breeds all year round. It is possible to collect all the developmental stages each month, and to observe changes in their distribution. Although P. elongata has been captured in many areas in the open and coastal North Pacific, it has generally been captured in very low numbers;

conversely, the species occurred in large numbers in the Strait of Georgia. This suggested that P. elongata survives best in water bodies such as those associated with the Strait of Georgia, and is less able to survive in water bodies with a closer geographic and oceanographic connection with the open waters of the Pacific Ocean.

(ii) The distribution and biology of P. elongata

Very little is known about the biology of P. elongata. Most of the field work has consisted of stating its occurrence in various areas, and most of the descriptions have been in oceanographic rather than geographic terms. Few studies have described the vertical distribution of the species and the temperature and salinity of the water in which the species was found.

The species has been described by various authors as Pareuchaeta elongata, P. japonica, Euchaeta elongata, and E. japonica. A literature search was made to determine the basis for the generic and species names, and, from this, it is decided that the name Pareuchaeta elongata is correct. The results of this literaturessearch are reported in the appendix.

P. elongata has been captured from the Bering Sea, the Sea of Okhotsk (Brosky 1950), the Sea of Japan (Marukawa, 1921), the Izu region of Japan (Tanaka and Omori 1968), the subarctic Pacific Ocean, with smaller numbers in the transition zone between the subarctic and subtropical North Pacific Ocean (Morris 1970), the Alaskan Peninsula

(Davis 1949), the Queen Charlotte Island region (Cameron 1957), the Strait of Georgia (Campbell 1929, 1934) and Howe Sound (Pandyan 1971) which lies east of the strait, and the San Diego region (Esterly 1913).

The life history of P. elongata consists of an egg (retained in a cluster of 8 to 24 eggs; Lewis and Ramnarine 1969), six naupliar stages, and six copepodite stages. The first two naupliar stages are nonfeeding, and the remaining four are herbivorous. The copepodites are primarily carnivorous, with the exception of the adult male, which is herbivorous (Pandyan 1971). The morphology of the developmental stages has been described by Campbell (1934).

This thesis presents the results of four studies. These are:

1) Two physical oceanography studies. The first consisted of three survey cruises of a number of stations in the waters of the west coast of Vancouver Island the British Columbia mainland, the connecting passages, and the Pacific Ocean. The second was a two-year study at Juan de Fuca Strait, Haro Strait, Boundary Passage, G.S.-1 (in the Strait of Georgia), and Indian Arm.

2) The study of the temperature-salinity associations of the developmental stages of P. elongata as determined by the three survey cruises.

3) A 1-year laboratory study of the responses of P. elongata egg clusters collected from G.S.-1 and Indian Arm to various natural sea waters, and five shorter studies using egg clusters collected from other areas.

4) A study of the temporal fluctuations in the distribution of the developmental stages of P. elongata at G.S.-1 and Indian Arm, and an evaluation of this in terms of the laboratory data and the temperature-salinity data.

In order to maintain clarity and to better illustrate trends, the four sections are presented separately with an introduction, a materials and methods section, a results section, and a discussion or summary.

CHAPTER I

(1) PHYSICAL OCEANOGRAPHY OF THE STUDY AREA

INTRODUCTION

A prerequisite for a successful study of the temperature-salinity associations of an organism is the examination of a comprehensive range of waters with different temperatures and salinities. The area consisting of the inlets, and the inside passage between Vancouver Island and the British Columbia mainland, and the Pacific Ocean is ideal for such a study. The waters within this area possess distinct temperature-salinity characteristics and are, on this basis, divisible into a number of groups and domains (Pickard 1961, 1963; Dodimead et al. 1963; Herlinveaux and Giovando (1969). This area is also ideal because there is a continual exchange of water between the inshore and offshore environments, so that a study conducted over a 1-year period should reveal whether or not a species is limited to a particular water. This would be indicated if the species were associated with one water, and disappeared as this water was transported into another area.

Within the study area, the dominant process by which oceanic water is transported to the inshore environment and fresh water to the offshore environment is estuarine circulation. Estuarine circulation consists of a 3-layered system with a surface layer of fresh and low-salinity water moving out towards the ocean, and a deeper, high-

salinity layer moving inshore. Between the surface and deep layers, is an intermediate layer where the deeper, high-salinity water is mixed upwards into the lower-salinity water and carried seaward. The lower limit of the halocline represents the point of no net transfer (Tully 1958).

A second process by which subsurface Pacific Ocean water is transferred to the inshore environment is upwelling. Upwelled water is moved inshore, generally in the summer, by estuarine circulation and tidal currents (Tully 1958; Tully and Barber 1960; Lane 1962, 1963).

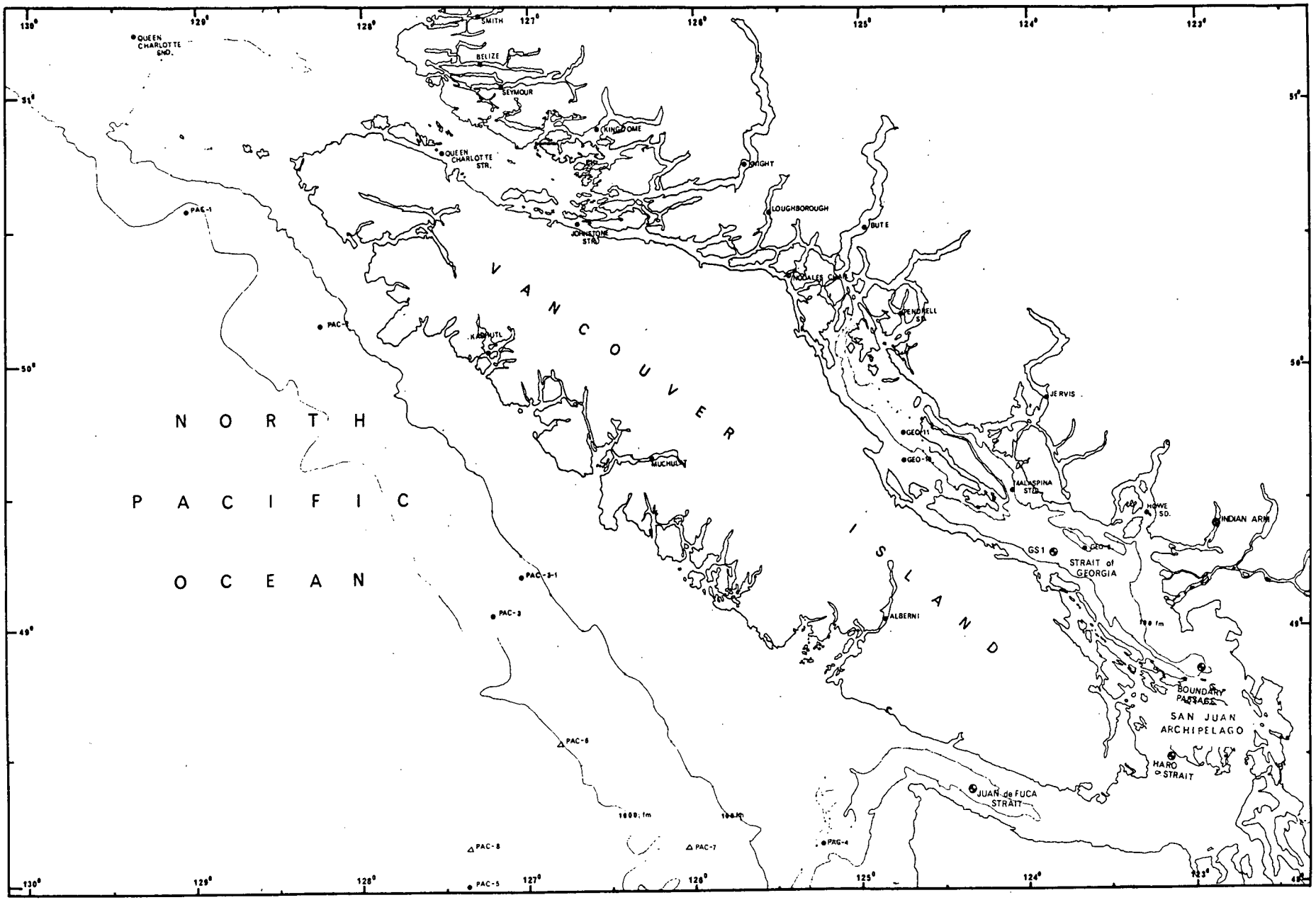
Materials and Methods

(i) Survey Cruises

The three survey cruises were conducted in May and July 1970, and in February 1971, where 22, 26 and 18 stations respectively were examined; Figure 1 shows the positions of the stations. Not all the stations were occupied during each cruise either due to the design of the cruise or to the weather. Table 1 lists the stations occupied during each cruise, the depth of the water column, and the greatest depth to which plankton and water samples were made. The data, including the co-ordinates of the stations and the time of sampling, are reported in the Institute of Oceanography Data Reports (1971, 1972).

Measurements of temperature and the collection of water samples for salinity analysis were made by using NIO bottles equipped with reversing thermometers. A surface sample was collected with a bucket.

Figure 1. The study area and the position of the stations occupied during the three survey cruises ●, the two year study ◓, and two short cruises in the Pacific Ocean △.



NORTH PACIFIC OCEAN
VANCOUVER ISLAND
QUEEN CHARLOTTE SND.
SMITH
BELIZE
SEYMOUR
KINGCOME
QUEEN CHARLOTTE STR.
KNIGHT
LOUGHBOROUGH
BUTE
JOHNSTONE STR.
NODALES CHAN.
PENDRELL SD.
JERVIS
KASHUTL
MUCHULAT
GEO-11
GEO-10
MALASPINA STR.
HOWE SD.
INDIAN ARM
GS1
STRAIT of GEORGIA
ALBERNI
BOUNDARY PASSAGE
SAN JUAN ARCHIPELAGO
HARO STRAIT
JUAN de FUCA STRAIT
PAC-1
PAC-2
PAC-3-1
PAC-3
PAC-6
PAC-8
PAC-7
PAC-5
PAG-4
1000 fm
100 fm
130°
129°
128°
127°
126°
125°
124°
123°
51°
50°
49°

TABLE 1. The depth of the water column, the depth of the deepest sample, and the month of sampling for the stations occupied during the three survey cruises.

Station	Depth of Water Column (meters)	Depth of Deepest Sample (meters)	Months Sampled
Howe Sound (How)	248	225	M J F
Georgia 6 (Geo 6)	132	100	J
Malaspina Strait (Mal)	402	340	M J F
Georgia 10 (Geo 10)	143	100	J
Georgia 11 (Geo 11)	358	325	M J F
Jervis Inlet (Je)	677	600	M J F
Pendrell Sound (Pe)	431	400	M J F
Bute Inlet (Bu)	658	600	M J F
Nodales Channel (Nod)	333	275	M J
Loughborough Inlet (Lo)	256	220	M J F
Johnstone Strait (Jo)	483	450	M J F
Knight Inlet (Knight)	527	475	J F
Kingcome Inlet (Kin)	475	450	M J F
Seymour Inlet (Se)	490	450	M J
Belize Inlet (Be)	388	375	M J
Smith Inlet (Sm)	358	340	M J F
Queen Charlotte Strait (QC Str)	373	340	M J
Queen Sound (QC snd.)	298	250	M J F
Kashutl Inlet (KAS)	256	200	M J F
Muchulat Inlet (MUC)	358	340	M J F
Alberni Inlet (ALB)	311	275	M J F
Pac 1	1,902	1,000	M J
Pac 2	1,390	1,000	M J F
Pac 3	1,792	1,000	M J F
Pac 3-1	227	150	M J F
Pac 4	274	250	M J F
Pac 5	2,578	1,000	F

M = May; J = July; F = February

Temperature was read at sea with an accuracy of ±0.01°C. Samples for salinity analysis were drawn from the NIO bottles, and the salinity was estimated in the laboratory by using the Model 601 MK3 Auto-Lab Inductively Coupled Salinometer (Extended Range Model). For salinities above 28‰, the salinometer has a reported accuracy of ±0.003‰ (Institute of Oceanography Data Report, 1970).

A bathythermograph was used before the bottle cast at all the stations occupied during the three survey cruises, and at all the five stations occupied during the second year of sampling (October 1970 to October 1971) of the 2-year study. Also, additional samples were drawn from the water bottles, and the dissolved oxygen concentration was measured, at sea, by using the Winkler method as modified by Carritt and Carpenter (1966).

(ii) The 2-Year Study

Five stations were studied from October 1969 to October 1971 inclusive, with each station being occupied once a month. These stations were in Juan de Fuca Strait, Haro Strait, Boundary Passage, the Strait of Georgia (G.S.-1), and Indian Arm; Figure 1 shows the positions of the stations. The data are reported in the Institute of Oceanography Data Reports (1970, 1971, and 1972). The methods used at each station are as described above for the survey cruises.

The station (48° 23'N, 124° 21'W) in Juan de Fuca Strait was located in the coastal seaways domain (Herlinveaux and Giovando 1969), in a trough approximately 230 m deep communicating with Juan de Fuca

canyon which runs across the continental shelf. The physical oceanography of this strait has been described by Herlinveaux and Tully (1961). The station in Haro Strait (48° 29'N, 123° 9'W) was located in a narrow depression approximately 300 m deep. The Boundary Passage station (48° 50'N, 122° 59'W) was located at the junction of Boundary Passage with the Strait of Georgia, and was over a flat plain approximately 220 m deep. Both the Haro Strait station and the Boundary Passage station were located within the southern homogeneous domain (Herlinveaux and Giovando 1969).

The station in the Strait of Georgia (49° 17'N, 123° 51'W) was located in the center of a Y-shaped trough; the water column was approximately 420 m deep. The physical oceanography of the Strait of Georgia has been described by Waldichuk (1957). The Indian Arm station (49° 24'N, 122° 53'W) was located in the middle of the inlet; the water column was approximately 220 m deep. The physical oceanography of this inlet has previously been described by Gilmartin (1962).

Results

(i) Survey Cruises

Although the temperature and salinity of the upper 150 m of water at the stations were different during the three times they were studied, the deep waters were similar in these characteristics. Secondly, the relative abundance of the developmental stages of *Pareuchaeta elongata* among the stations was similar during the three cruises.

Because of these observations, the results of only one survey cruise are presented. The July 1970 survey cruise was chosen for representation because it was the most extensive.

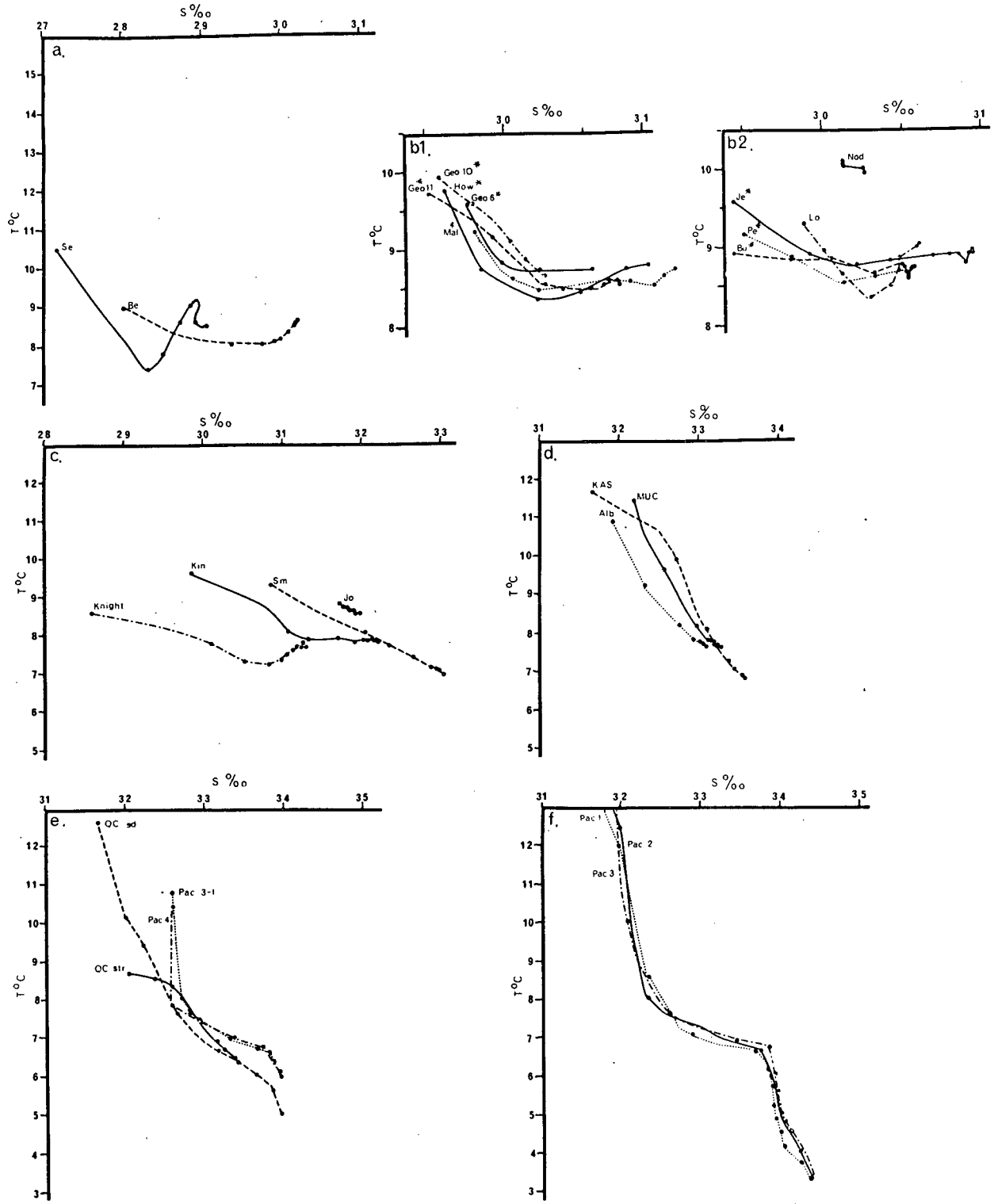
The stations were divided into six groups on the basis of the temperature-salinity characteristics of their subsurface waters. The classifications of Pickard (1961, 1963) for the inlets, Herlinveaux and Giovando (1969) for the waters of the inside passage, and Dodimead et al., (1963) for the sub-arctic Pacific Ocean were referred to, and with slight modifications, used. The groups are: (i) low-salinity 'southern' waters, (ii) southern waters, (iii) intermediate and northern waters, (iv) west coast inlets, (v) coastal seaway waters, and (vi) sub-arctic Pacific Ocean waters.

Figure 2 shows the temperature-salinity curves for the six groups of stations studied during the July 1970 survey cruise. In the summer, surface waters are generally warmer and lower in salinity than deep water; therefore, the upper left portion of each curve represents the near-surface water, and the lower right portion represents the deep water. All the temperature-salinity data collected from 10-m to the deepest water sample were used in drawing the curves; temperature-salinity points where horizontal plankton samples were collected are indicated by symbols on each curve.

The temperature-salinity curves confirm the differences in the deep water characteristics as discussed by Pickard (1961, 1963), Herlinveaux and Giovando (1969), and Dodimead et al., (1963). There was a gradient of salinity and temperature from the warm, low-salinity

Figure 2. The temperature-salinity curves for the six groups of stations studied during the July 1970 cruise (with the exclusion of the 0-meter data). (a) low salinity 'southern' waters, (b-1,2) southern waters, (c) intermediate and northern waters, (d) west coast inlets waters, (e) coastal seaway waters, (f) sub-arctic Pacific Ocean waters (abbreviations as in Table 1). The missing 10-m (*) data for the southern inlets are:

Inlet	Temperature °C	Salinity ‰
Howe	13.6	27.0
Mal	15.2	26.8
Geo 6	12.7	28.2
Geo 10	15.7	26.9
Geo 11	15.9	27.1
Je	15.0	26.3
Pe	13.7	28.1
Bu	9.5	28.5


a.
b1.
b2.
c.
d.
e.
f.
S‰
T°C
Se
Be
Geo 11
Geo 10
How
Geo 6
Mal
Nod
Je
Lo
Pe
Bu
Kin
Sm
Jo
Knight
KAS
MUC
Alb
OC sd
Pac 3-1
Pac 4
OC str
Pac 1
Pac 2
Pac 3

southern waters through to the cold, high-salinity west coast inlet waters. The coastal seaway waters were higher in salinity and cooler indicating less dilution of oceanic water by the warm, low-salinity surface waters from the inlets and the inner straits.

(ii) The 2-Year Study

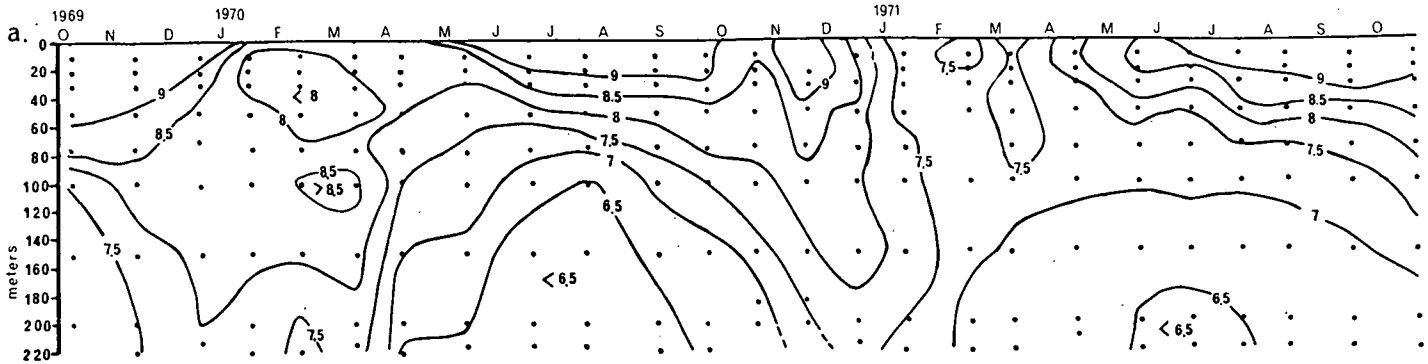
Figure 3 shows the fluctuations in temperature, salinity, and dissolved oxygen concentration which occurred during the 2-year study period at Juan de Fuca Strait, Haro Strait, Boundary Passage, the Strait of Georgia (G.S.-1), and Indian Arm. The data for the period November 1971 to February 1972 for Indian Arm and G.S.-1 are from Mr. G. Gardner (pers. comm.). Broken lines on the figures indicate uncertain data points. The sampling depths are indicated on each graph; horizontal plankton samples were collected from the same depths with the exclusion of 0 and 20 meters.

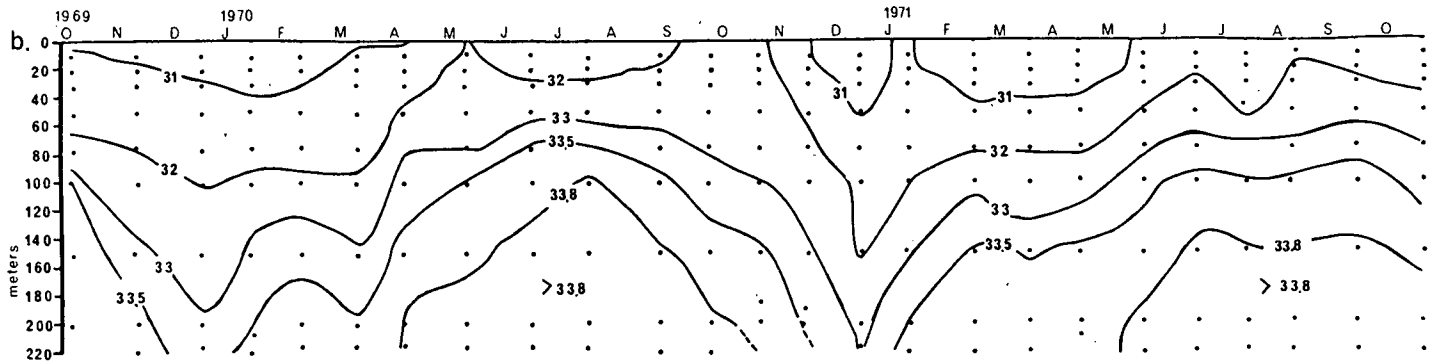
Temperatures of the surface waters at all five stations were lowest in the winter and early spring, and highest in the late summer and autumn. The lowest salinities occurred from the late spring to the late summer associated with the increased discharge of rivers such as the Fraser (Water Survey of Canada 1971, unpublished data for 1971). A second period of low salinity occurred in the late winter, and was associated with the period in which direct precipitation was greatest. The dissolved oxygen concentrations of the near-surface waters were high in the early spring and winter, and low from the late summer to October or November.

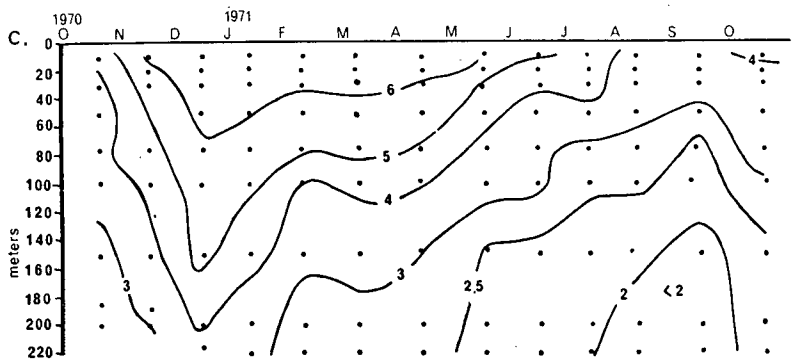
The deep water in Juan de Fuca Strait was coldest and most saline from April to October or November. This was because upwelled subsurface Pacific Ocean water was present in the strait at this time. During the late summer, when upwelling ceased, this oceanic water was gradually mixed into the overlying warmer, less-saline waters. This mixing continued through the autumn and winter, at which time the deep waters reached their lowest salinities and highest temperatures. Similarly, the dissolved oxygen concentrations were low from the spring to the late summer when the undiluted, low-oxygen Pacific Ocean subsurface water was present in the strait, and increased through the autumn and winter as this water was mixed with the overlying, higher-oxygen water.

The deep water in Haro Strait was most saline from the spring to the late autumn. In 1970, the deep water reached its maximum salinity and lowest temperature in September although, in Juan de Fuca Strait, the maximum salinity and minimum temperature were reached in July. From this it is estimated that the deep water in Juan de Fuca Strait takes one to two months to reach Haro Strait. The dissolved oxygen concentration of the deep water in Haro Strait was lowest in the late summer and early autumn, when the low-oxygen subsurface Pacific Ocean water was mixed into the waters of the San Juan Archipelago. Values were higher during the rest of the year, being greatest in the winter when intensive mixing of the water column occurred as evidenced by the water being almost completely isothermal and isohaline.

Figure 3. The temperature, salinity, and dissolved oxygen concentrations of the water at (i) Juan de Fuca Strait, (ii) Haro Strait, (iii) Boundary Passage, (iv) G.S.-1 in the Strait of Georgia, and (v) Indian Arm during the study period. Dashed lines indicate uncertain or missing datam points. The depths at which samples were collected are indicated by dots.





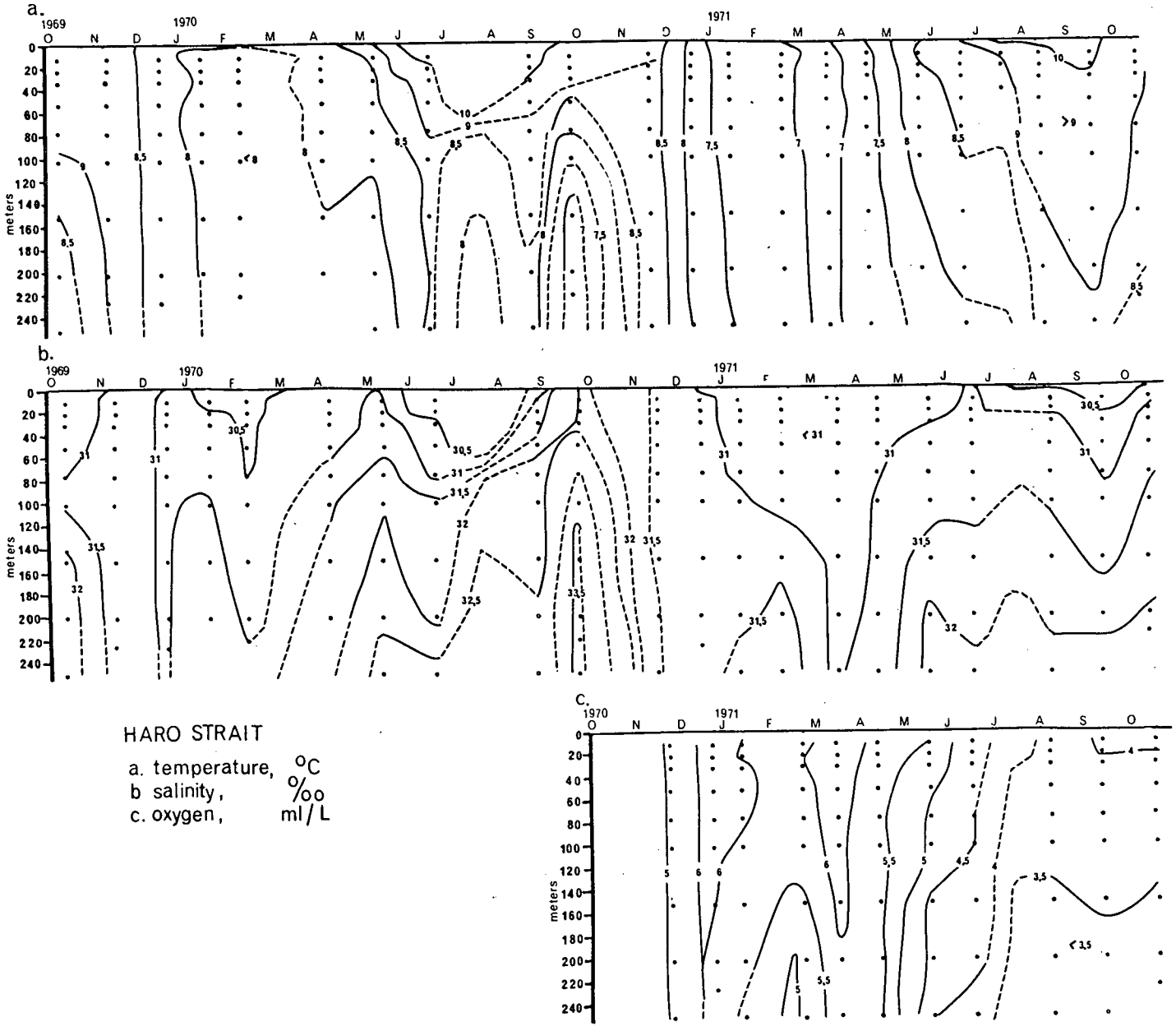


JUAN de FUCA STRAIT

a. temperature, °C

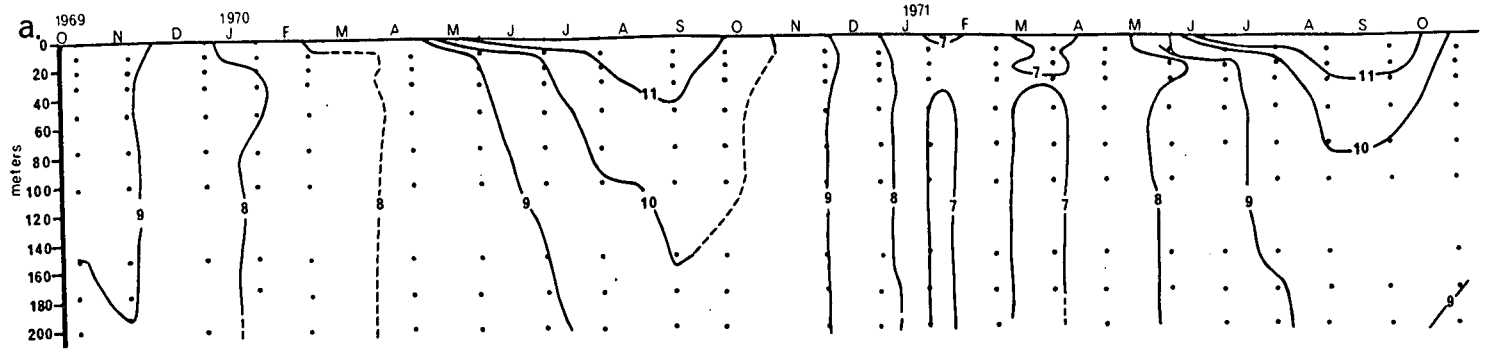
b. salinity, ‰

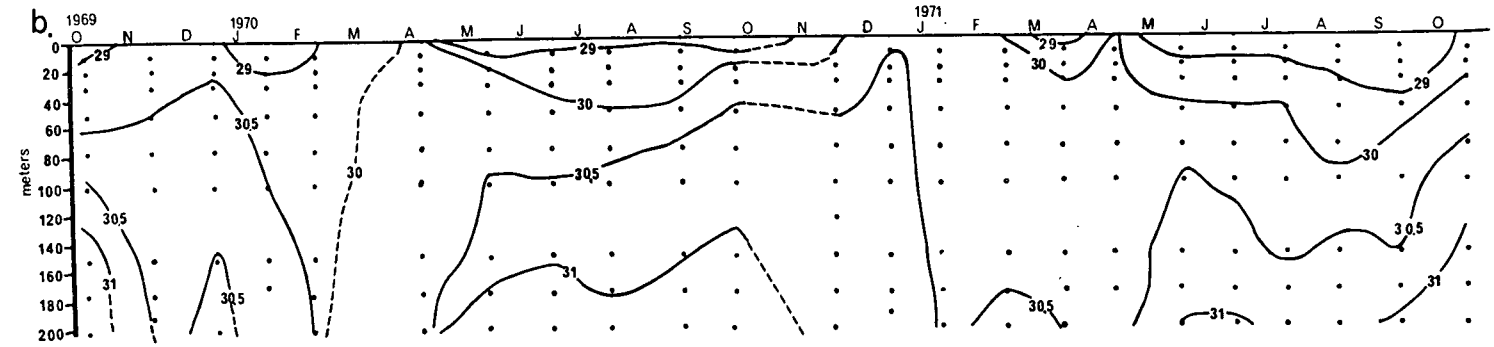
c. oxygen, ml/L



HARO STRAIT

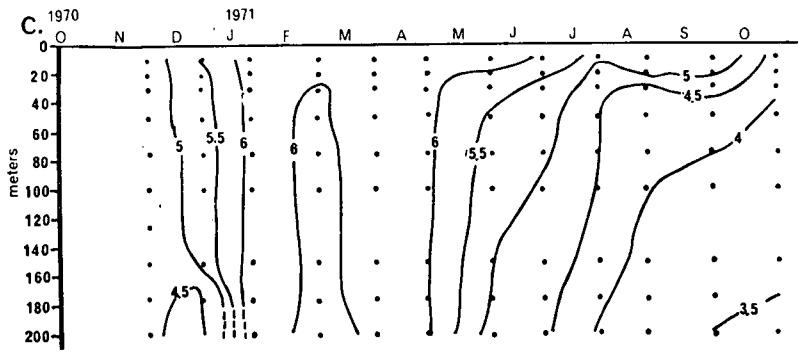
a. temperature, °C
b salinity, ‰
c. oxygen, ml/L

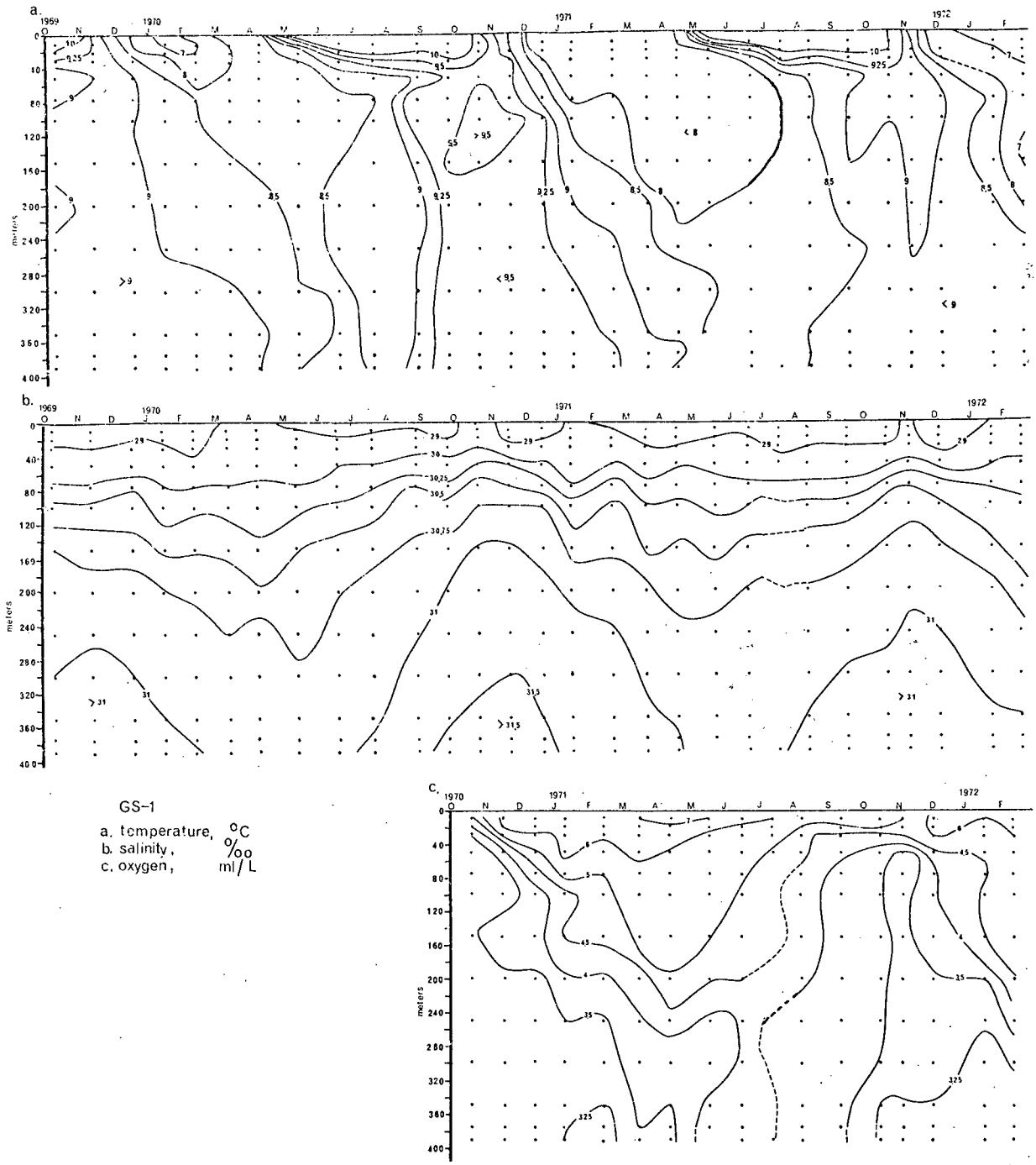




BOUNDARY PASSAGE

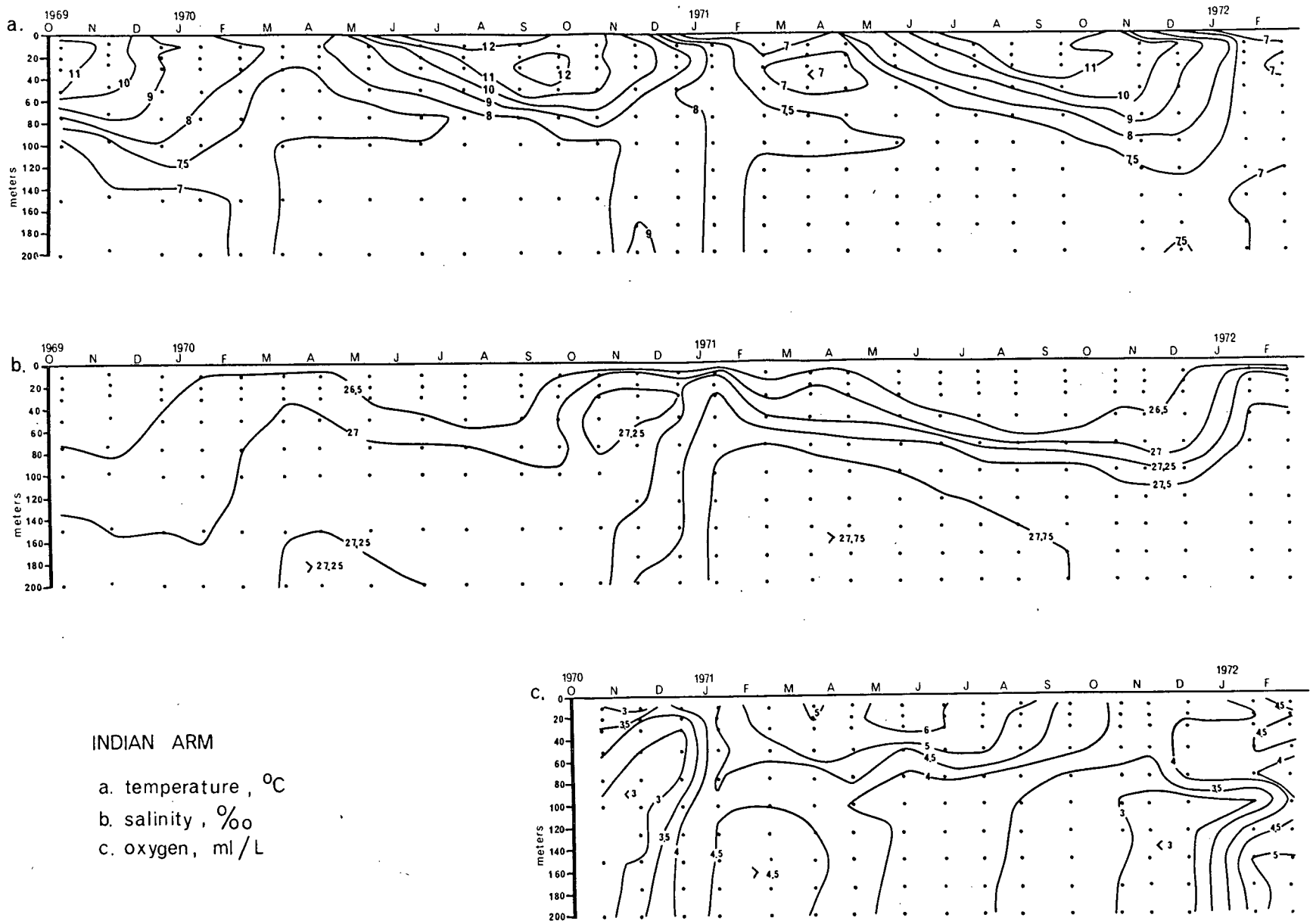
a. temperature, °C
b. salinity, ‰
c. oxygen, ml/L





GS-1

a. temperature, °C
b. salinity, ‰
c. oxygen, ml/L



INDIAN ARM

a. temperature, °C

b. salinity, ‰

c. oxygen, ml/L

The deep water of Boundary Passage was highest in salinity from the late spring to the late autumn. The temperature of the deep water was lowest in the winter. The dissolved oxygen concentrations were low from the late spring to the late autumn, presumably owing to the low-oxygen Pacific Ocean subsurface water being mixed into the waters of Boundary Passage. Values were high during the winter and early spring when there was intensive mixing of the water.

The temperature and salinity of the deep water at G.S.-1 in the Strait of Georgia, were lowest in the early spring and highest in the late autumn. Beginning in the late summer, the bottom water of the Strait of Georgia was replaced by the warmer, higher-salinity water which was formed in the San Juan Archipelago. This water was formed from the mixing of subsurface Juan de Fuca Strait water, and surface water from areas such as the Strait of Georgia and Puget Sound. The replacement of the bottom water of the Strait of Georgia continued until October or November, after which the 'new' water was gradually eroded away and mixed into the overlying colder, less-saline water. The dissolved oxygen concentration of the deep water at G.S.-1 was lowest in the late autumn when the low-oxygen water from the San Juan Archipelago replaced the bottom water. In the winter and spring the values increased as the higher-oxygen water formed in the San Juan Archipelago intruded into the Strait of Georgia at intermediate depths, and eroded away and mixed into the low-oxygen water.

In Indian Arm, the deep water was most saline from the late autumn to the early spring when the water was replaced by an influx of more saline water. This 'new' water was only slightly eroded away and mixed into the overlying, less-saline water during the summer. The deep water was relatively isothermal through the year with changes occurring at the time of deep water replacement. The dissolved oxygen concentration was highest when the deep water was replaced by the higher-oxygen water formed in the vicinity of the sill at the mouth of the inlet. Oxygen values decreased through the late summer and early autumn.

Summary

(1) The three survey cruises of a number of inlets of the British Columbia mainland and the west coast of Vancouver Island, the connecting passages, and the Pacific Ocean examined a wide range of waters with distinct temperature-salinity characteristics. These stations could be subdivided into six groups on the basis of the temperature-salinity characteristics of the subsurface waters.

(2) The survey cruises, because they covered an extensive range of waters with distinct temperature-salinity characteristics, were ideal for determining the temperature-salinity associations of Pareuchaeta elongata, and determining whether or not the species was restricted to various waters.

(3) The 2-year study at Juan de Fuca Strait, Haro Strait, Boundary Passage, G.S.-1 (in the Strait of Georgia), and Indian Arm observed the transfer of subsurface Pacific Ocean water inshore, and the transfer of fresh and low salinity water to the offshore environment.

(4) The 2-year study, while covering a less extensive range of waters than the three survey cruises, was ideal for showing whether or not temporal variations in the distribution of P. elongata in an area were associated with changes in the water of that area.

CHAPTER II

P. ELONGATA TEMPERATURE-SALINITY ASSOCIATIONS AS DETERMINED BY THE THREE SURVEY CRUISES

INTRODUCTION

Pandyan (1971) showed that, in Howe Sound, the naupliar and first copepodite stages of P. elongata were found in the deep water, while the later stages were found higher up in the water column. Secondly, she indicated that the third to sixth copepodite stages were found nearer the surface at night than during the day, although they were always found throughout a large portion of the water column. This suggests that these stages exhibit diel vertical migration, although the vertical migration is less pronounced than that of zooplankton such as Euphausia pacifica, which are found at more discrete depths during the day and night.

In Howe Sound, the vertical distribution of P. elongata appeared to be a function of the stage of development of the organism, and the variables affecting diel migration. What was not known for Howe Sound or for any other area, was the role of temperature, salinity and the other properties of sea waters in determining the distribution of P. elongata. The purpose of the three survey cruises was to investigate the qualitative and quantitative distribution of the developmental stages of P. elongata in a number of groups of waters with distinct temperature-salinity characteristics. In particular, the following were investigated:

(1) Is P. elongata capable of surviving across the range of waters which constitute the oceanic and coastal environments?

(2) Is P. elongata capable of reproducing across the range of waters which constitute the oceanic and coastal environments?

(3) Is the vertical distribution of P. elongata throughout its range a function of temperature and salinity, or is the vertical distribution similar both in the oceanic and coastal environment?

(4) What other environmental variables might account for populations of P. elongata being relatively small in the Pacific Ocean, and relatively large in areas such as the Strait of Georgia?

Materials and Methods

(i) Field Procedures

Figure 1 shows the positions of the stations occupied during the three survey cruises, and Table 1 shows the stations occupied during each cruise, and the maximum depth of plankton and water sampling. The techniques employed at each station were the same. Horizontal plankton tows were made, and the temperature, salinity, and dissolved oxygen concentration of the water were measured at a number of depths. Plankton samples were made at the same depths as the water samples, with the exclusion of 0 and 20 meters.

Discrete horizontal plankton samples were collected by using the opening and closing Clarke-Bumpus samplers equipped with a number 2 mesh (approximate pore size-360 μ). The samplers had a mouth diameter of 12-cm, and were each mounted with a flowmeter. The samplers

had earlier been calibrated thereby allowing 'quantitative' samples to be collected. Two plankton tows were made at each station, with six samplers being used for the first tow, and a variable number of up to six during the second tow. All samples were preserved in a 10% formalin-sea-water solution buffered with borax.

(ii) Treatment of the P. elongata Field Data

The data collected during the three survey cruises were examined in two ways. There were:

(1) The total number of animals at each stage in a 1-m^2 column of water was estimated for each station. This was accomplished by determining the concentration of animals caught at each depth, calculating the mean between two successive depths, and then multiplying this value by the distance between the two sampling depths. This was done for all sample depths, and the values summed to give the total for the water column.

(2) A second method was to draw the standard temperature-salinity-plankton graphs to show the occurrences of P. elongata with water types. The most common method has been to use various sized symbols to represent the numbers or the concentrations of animals caught at various temperature-salinity values (Bary 1963). There were several disadvantages to using this technique in this study, and so it was modified slightly. The first disadvantage was that unless all the temperature-salinity values were shown on the graph, zero-values for captures did not appear. A second problem occurred because few samples were taken in water in which the temperature and salinity changes with

depth were great (i.e. the upper 30-m), and many samples were taken at depths in which the temperature and salinity varied only slightly. It was difficult to present all the datam points on the temperature-salinity-plankton graphs for those areas in which temperature and salinity varied only slightly. Also, it was felt that presenting the data in this fashion would place a bias on interpreting the results; if the animals were uniformly distributed throughout the water column, the graph would have a tendency to suggest that they were more concentrated in the relatively homogeneous zone simply because more symbols appeared there.

In order to circumvent these problems, the mean concentration of organisms in temperature-salinity areas (0.25 C^{o} X 0.25‰) on the temperature-salinity-plankton graph were calculated. The study stations had earlier (Chapter I) been divided into six groups on the basis of the similarities of the temperature-salinity characteristics of their subsurface waters. For each group, the temperature-salinity graph (Figure 2) was divided into rectangles 0.25 C^{o} X 0.25‰. All the plankton data were examined, and each sample was assigned to its particular temperature-salinity rectangle on a master sheet. When all the data for each stage had been entered onto the master sheet, the mean value for each rectangle was calculated. On the final graph, the temperature-salinity rectangles for which there were plankton samples were drawn, and the mean concentration of organisms for each rectangle was written inside. By referring back to the temperature-

salinity curves (Figure 2) for the six groups of stations, one can determine how many sample points were used to calculate the mean.

Results

(i) The Abundance of P. elongata in the Six Groups of Waters

Tables 2, 3, and 4 show, for each station, the estimated number of P. elongata at each developmental stage (the six naupliar stages are combined), and the estimated mean concentration of animals between 10 m and the deepest horizontal plankton sample. For the purposes of comparison, the calculations for Indian Arm, G.S.-1 (in the Strait of Georgia), Boundary Passage, Haro Strait, and Juan de Fuca Strait are included in the tables.

Although the number at each station varied from one cruise to the next, the relative abundance of P. elongata within the six groups of stations was similar during the three time periods studied. Secondly, there was no consistent pattern for the particular stages to be more numerous during one cruise than during another.

Complete populations of P. elongata, consisting of all the developmental stages, were associated with the low-salinity 'southern' waters, although Seymour and Belize Inlets had relatively small populations in comparison with Indian Arm, and in comparison with the populations in adjacent inlets such as Smith and Kingcome. Complete populations of P. elongata were also associated with southern waters,

TABLE 2. The estimated number of the developmental stages of P. elongata in a column (1-m^2) of water between 10 meters and the deepest plankton sample.* (1) low-salinity 'southern' waters; (2) southern waters, (3) intermediate and northern waters, (4) west coast inlet waters, (5) coastal seaway waters, and (6) sub-arctic Pacific Ocean waters.

May 1970 Cruise

Station and Type*	Maximum Sample Depth (m)	Egg	N	C-1	C-2	C-3	C-4	C-5	C-6	** Total	** Total Depth
Seymour (1)	475	3	75	557	42	3	22	23	13	235	0.49
Belize (1)	240	4	25	40	67	3	5	0	8	148	0.61
Howe (2)	225	10	268	103	103	88	98	84	23	767	3.41
Mal. (2)	340	44	586	375	639	246	112	88	103	2149	6.32
Jervis (2)	600	25	613	1006	1589	472	385	120	109	4294	7.16
Geo-11 (2)	325	50	89	127	478	299	156	53	141	1343	4.13
Pendrell (2)	400	18	815	670	1202	518	60	24	159	3448	8.62
Bute (2)	600	105	870	737	1475	755	263	447	642	5189	8.65
Nodales (2)	275	0	0	0	0	0	0	0	0	0	0.00
Lough. (2)	220	0	5	28	27	48	39	18	27	192	0.87
John. (3)	450	0	0	49	0	0	47	0	0	96	0.21
King. (3)	400	23	152	201	237	138	213	326	86	1354	3.39
Smith (3)	325	36	774	764	697	271	253	175	61	2995	9.22
Kashutl (4)	200	13	49	43	137	71	9	30	30	369	1.85
Much. (4)	340	83	425	413	722	309	133	41	159	2202	6.48
Alb. (4)	275	23	1158	745	1006	481	68	63	124	3645	13.25
Q.C. Str. (5)	340	0	0	0	0	0	7	0	0	7	0.02
Q.C. Snd. (5)	250	0	0	0	44	0	0	0	0	44	0.18
Pac 4 (5)	250	0	13	0	13	23	6	14	15	84	0.34
Pac 1***(6)	750	0	0	0	7	28	7	0	0	42	0.05
Pac 2***(6)	1000	0	12	181	92	54	23	30	4	396	0.40
Pac 3***(6)	1000	0	78	205	117	130	45	45	0	620	0.62
Ind (1)	200	18	1423	530	286	175	32	11	51	2508	12.54
G.S.-1 (2)	390	23	630	588	678	349	198	159	109	2711	6.95
Bound. (2)	200	0	0	0	2	2	1	0	0	5	0.03
Haro (3)	250	0	0	0	0	0	0	0	0	0	0.00
J.F. Str. (5)	215	0	10	0	4	66	55	24	0	159	0.74

** excluding the egg cluster *** shallowest sample was at 25 meters

TABLE 3. The estimated number of the developmental stages of P. elongata in a 1-m^2 column of water between 10 meters and the deepest plankton sample* (1) low-salinity 'southern' waters, (2) southern waters, (3) intermediate and northern waters, (4) west coast inlet waters, (5) coastal seaway waters, and (6) sub-arctic Pacific Ocean waters.

July 1970 Cruise

Station and Type*	Maximum Sample Depth (m)	Egg	N	C-1	C-2	C-3	C-4	C-5	C-6	Total **	Total Depth**
Seymour (1)	450	0	85	59	74	43	24	16	15	316	0.70
Belize (1)	275	3	47	72	77	30	53	36	3	318	1.16
Howe (2)	225	14	242	99	97	122	190	44	86	880	3.91
Geo-6 (2)	100	0	0	1	29	35	0	0	0	65	0.65
Mal. (2)	340	35	1018	682	459	354	132	37	82	2764	8.13
Jervis (2)	600	5	582	1004	964	396	390	98	93	3527	5.88
Geo-10 (2)	100	0	0	0	12	11	91	229	22	365	3.65
Geo-11 (2)	325	34	366	271	151	191	316	309	142	1746	5.37
Pendrell (2)	400	17	604	1203	1360	566	61	64	23	3881	9.70
Bute (2)	600	38	564	723	1042	1000	72	0	53	3454	5.76
Nodales (2)	255	0	0	0	2	2	2	0	0	6	0.02
Lough. (2)	220	0	99	52	48	32	6	27	6	270	1.23
John. (3)	450	0	0	0	0	0	0	0	0	0	0.00
Knight (3)	475	13	80	88	144	72	140	1076	157	1757	3.70
King. (3)	450	27	341	160	187	175	91	212	98	1264	2.81
Smith (3)	340	16	370	178	123	98	226	194	86	1275	3.75
Kashutl (4)	200	39	468	349	578	836	460	1339	122	3152	15.76
Much. (4)	340	14	466	346	336	273	363	193	52	2029	5.70
Alb. (4)	275	10	884	1175	758	315	458	309	55	3954	14.38
Q.C. Str. (5)	340	0	0	0	0	0	0	8	0	8	0.02
Q.C. Snd. (5)	250	3	0	0	3	13	14	16	3	46	0.18
Pac 3-1 (5)	150	0	0	0	51	29	14	6	3	103	0.69
Pac 4 (5)	250	0	0	5	12	38	18	5	0	78	0.31
Pac 1***(6)	1000	0	9	9	86	90	18	15	2	229	0.23
Pac 2***(6)	1000	0	26	22	173	100	43	20	39	422	0.42
Pac 3***(6)	250	1	0	0	129	68	18	4	6	225	0.90
Ind (1)	200	8	163	148	148	120	76	160	109	870	4.35
G.S.-1 (2)	390	25	626	535	476	402	132	50	92	2313	5.35
Bound. (2)	200	3	0	0	0	0	4	15	8	35	0.18
Haro (3)	250	0	8	0	0	9	27	29	0	73	0.29
J.F. Str. (5)	215	0	1	0	16	76	72	17	0	192	0.89

** excluding the egg cluster

*** shallowest sample was at 25 meters. Pac 3 is the result of only one tow as the second malfunctioned.

TABLE 4. The estimated number of the developmental stages of P. elongata in a 1-m^2 column of water between 10 meters and the deepest plankton sample* (1) low-salinity 'southern' waters, (2) southern waters, (3) intermediate and northern waters, (4) west coast inlet waters, (5) coastal seaway waters, and (6) sub-arctic Pacific Ocean waters.

February 1971 Cruise

Station and Type*	Maximum Sample Depth (m)	Egg	N	C-1	C-2	C-3	C-4	C-5	C-6	Total **	Total Depth**
Howe (2)	200	3	26	10	7	30	9	37	14	133	0.67
Mal. (2)	340	17	229	59	82	28	36	60	55	549	1.61
Jervis (2)	150****	0	4	0	26	19	16	8	3	76	0.51
Geo-11 (2)	325	17	86	47	103	40	25	119	91	511	1.57
Pendrell (2)	375	44	239	110	64	54	111	113	94	785	2.09
Bute (2)	600	94	828	830	674	548	139	40	220	3279	5.47
Lough. (2)	220	7	368	169	65	32	0	13	40	687	3.12
John. (3)	450	0	53	16	7	0	4	7	0	87	0.19
Knight (3)	475	15	466	386	672	89	7	42	75	1737	3.65
King. (3)	450	3	234	265	176	39	11	9	26	760	1.69
Smith (3)	330	106	176	51	128	5	11	0	126	497	1.51
Kashutl (4)	200	27	137	107	291	115	207	982	263	2104	10.52
Much. (4)	340	11	209	116	251	26	21	270	165	1058	3.11
Alb. (4)	275	46	338	191	333	70	139	590	223	1884	6.85
Q.C. Str.(5)	340	0	21	18	16	7	14	0	0	76	0.22
Pac 4 (5)	225	0	8	0	15	23	5	10	0	61	0.27
Pac 3***(6)	1000	0	27	38	91	10	1	0	1	166	0.17
Pac 5***(6)	1000	0	0	112	56	0	0	0	0	168	0.17
Ind. (1)	200	8	348	225	75	5	0	0	33	611	3.06
G.S.-1 (2)	390	48	338	128	177	148	88	101	203	1183	3.03
Bound. (2)	200	0	0	2	3	6	3	0	3	17	0.09
Haro (3)	250	0	0	0	0	0	5	8	0	13	0.05
J.F. Str.(5)	220	0	0	5	4	4	16	17	10	56	0.25

** Excluding egg cluster
*** Shallowest sample was at 25 meters
**** One tow only as the second malfunctioned.

intermediate and northern waters, and west coast inlet waters with four exceptions; these were Georgia 6, Georgia 10, Nodales Channel, and Johnstone Strait.

Georgia 6 and Georgia 10 were located in shallow areas adjacent to deeper areas (Howe Sound and Georgia 11, respectively) with the purpose of comparing the distribution of P. elongata in deep and shallow areas. The naupliar and first copepodite stages were absent from the two shallow areas, while they were present in the two adjacent deep areas. This absence from the shallow areas could be due to the fact that these stages were not transported, by currents, from the adjacent deep areas to the more shallow banks. A second possibility is that these stages could not survive in the waters associated with these shallow areas.

Nodales Channel and Johnstone Strait form part of the northern homogeneous domain (Herlinveaux and Giovando, 1969) and, during the three times studied, had only relatively small populations of P. elongata. Similarly, Haro Strait and Boundary Passage, which form part of the southern homogeneous domain (Herlinveaux and Giovando, 1969), had small populations of P. elongata; this was consistently observed during the 2-year study period. The largest estimated population at Haro Strait, in a 1-m^2 column of water, was 74 organisms and, at Boundary Passage, was 122 organisms. However, because all the developmental stages have been captured in the two homogeneous domains, the species is probably capable of completing its development in these waters.

Relatively small populations of P. elongata were associated with the northern coastal seaway waters and Juan de Fuca Strait. These low numbers were consistent during the 2-year study period, with the largest estimated population in a 1-m^2 column of water of Juan de Fuca Strait being 232 organisms. As all the developmental stages have been captured in coastal seaways waters, the species is probably capable of completing its development in these waters.

Complete populations of P. elongata were generally associated with the waters of the eastern sub-arctic Pacific Ocean, although the concentration of animals was low. All the developmental stages have been captured in these waters, which indicates that P. elongata is capable of completing its life cycle in sub-arctic Pacific Ocean water.

Loughborough Inlet had high dissolved oxygen concentrations (5 ml/l) throughout the water column in May 1970. These values were comparable to those for Johnstone Strait and Nodales Channel, which suggests that the inlet had been flushed at some earlier interval. As the salinity of the deep water was intermediate to the high-salinity water of Johnstone Strait and the lower-salinity water of Nodales Channel, this 'new' water probably originated from Johnstone Strait. In May 1970, the population of P. elongata was relatively small and was comparable in size to those associated with the homogeneous domains. In July 1970, the population was larger, and reached its largest size in February 1971. Associated with this, was a decrease in the dissolved oxygen concentration of the deep water, which suggests that the deep water, which had been brought into the inlet during the spring influx (1970), remained in the inlet with little replacement.

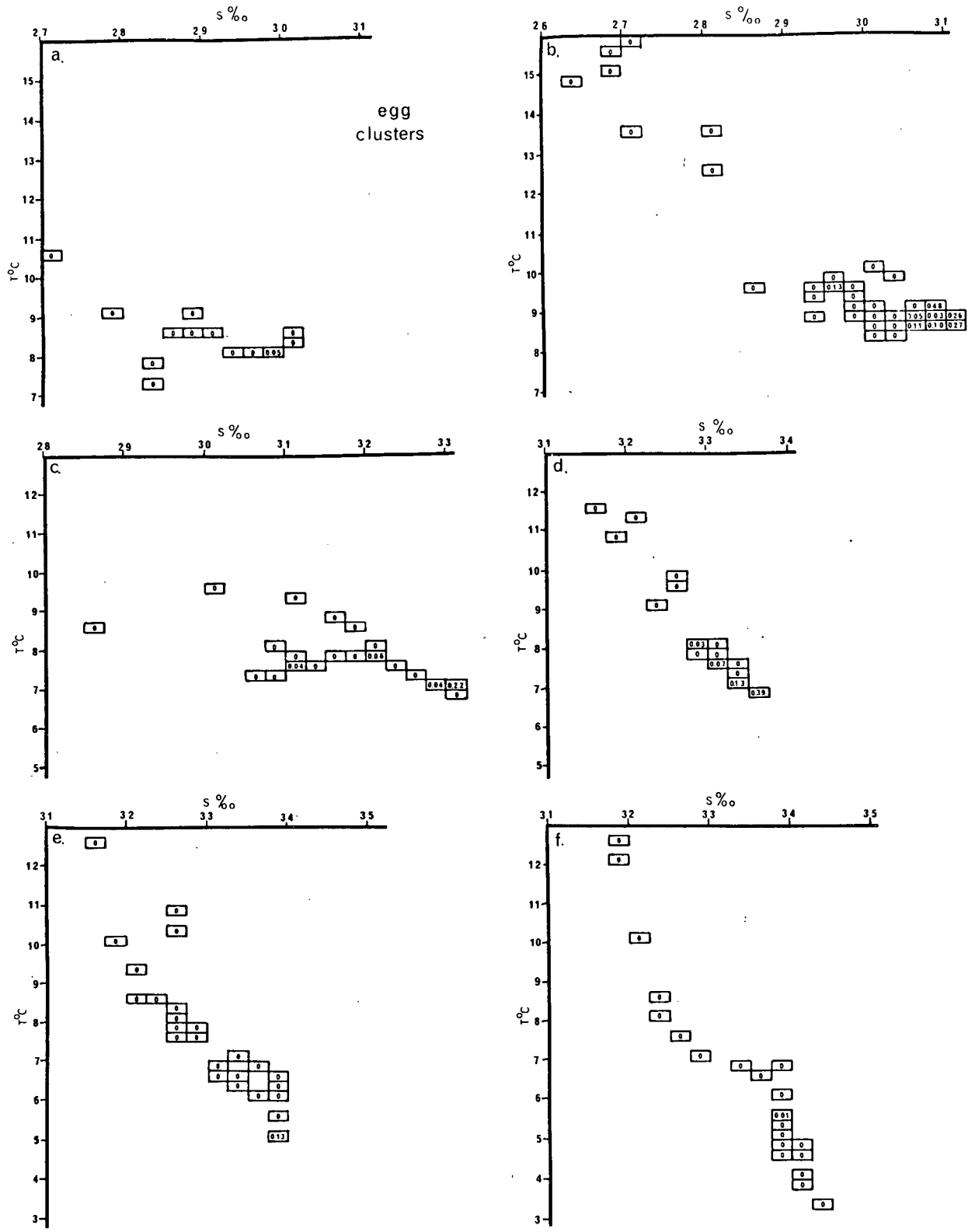
(ii) The temperature-salinity associations of the developmental stages of P. elongata (July 1970).

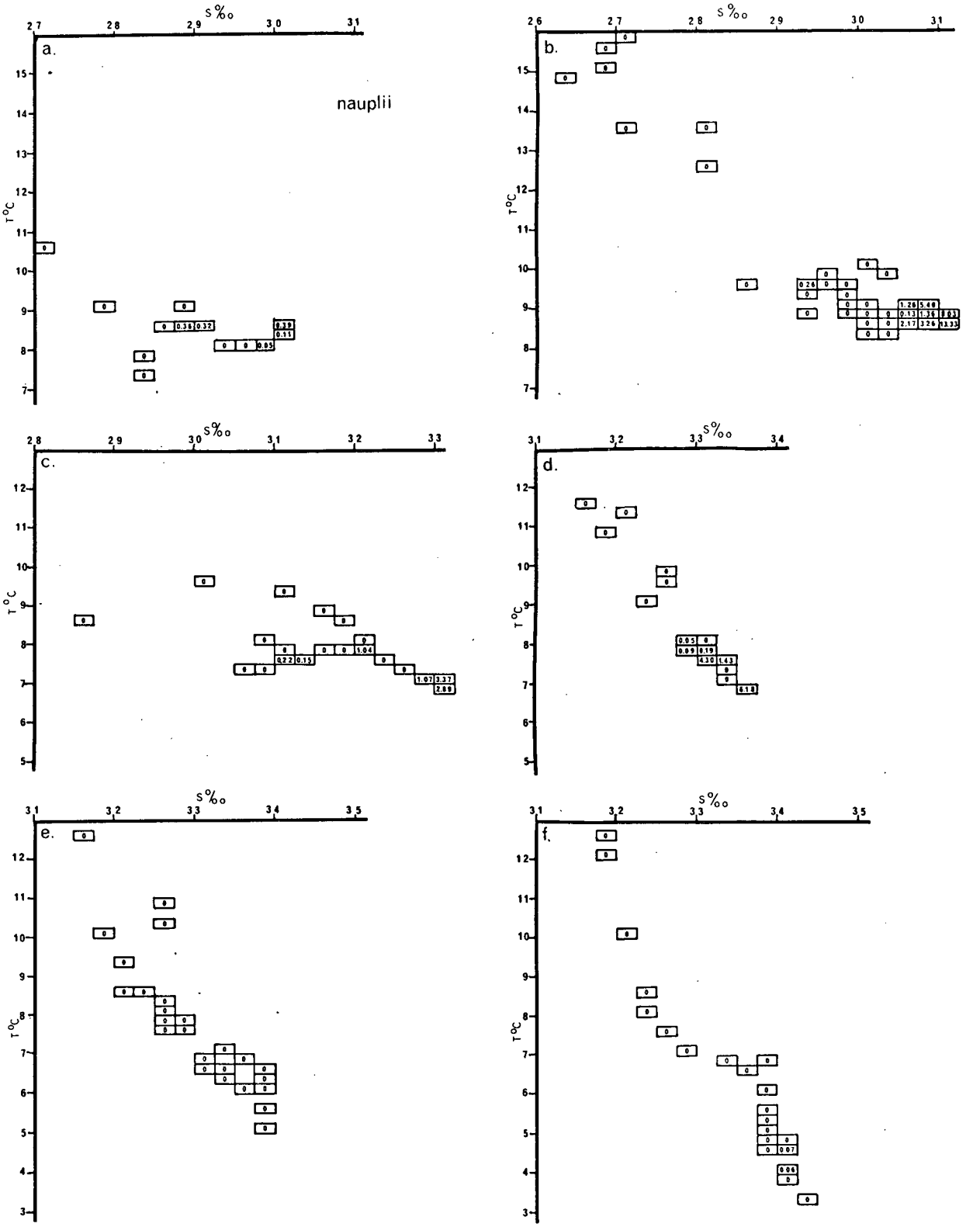
Figure 4 shows the temperature-salinity associations of the egg, the combined (six) naupliar stages, and the six copepodite stages of P. elongata. These graphs, with the exception of that for the southern waters, were drawn on the same scale as the temperature-salinity curves (Figure 2) for the six groups of waters. On these curves, the points at which plankton samples were taken are indicated by symbols.

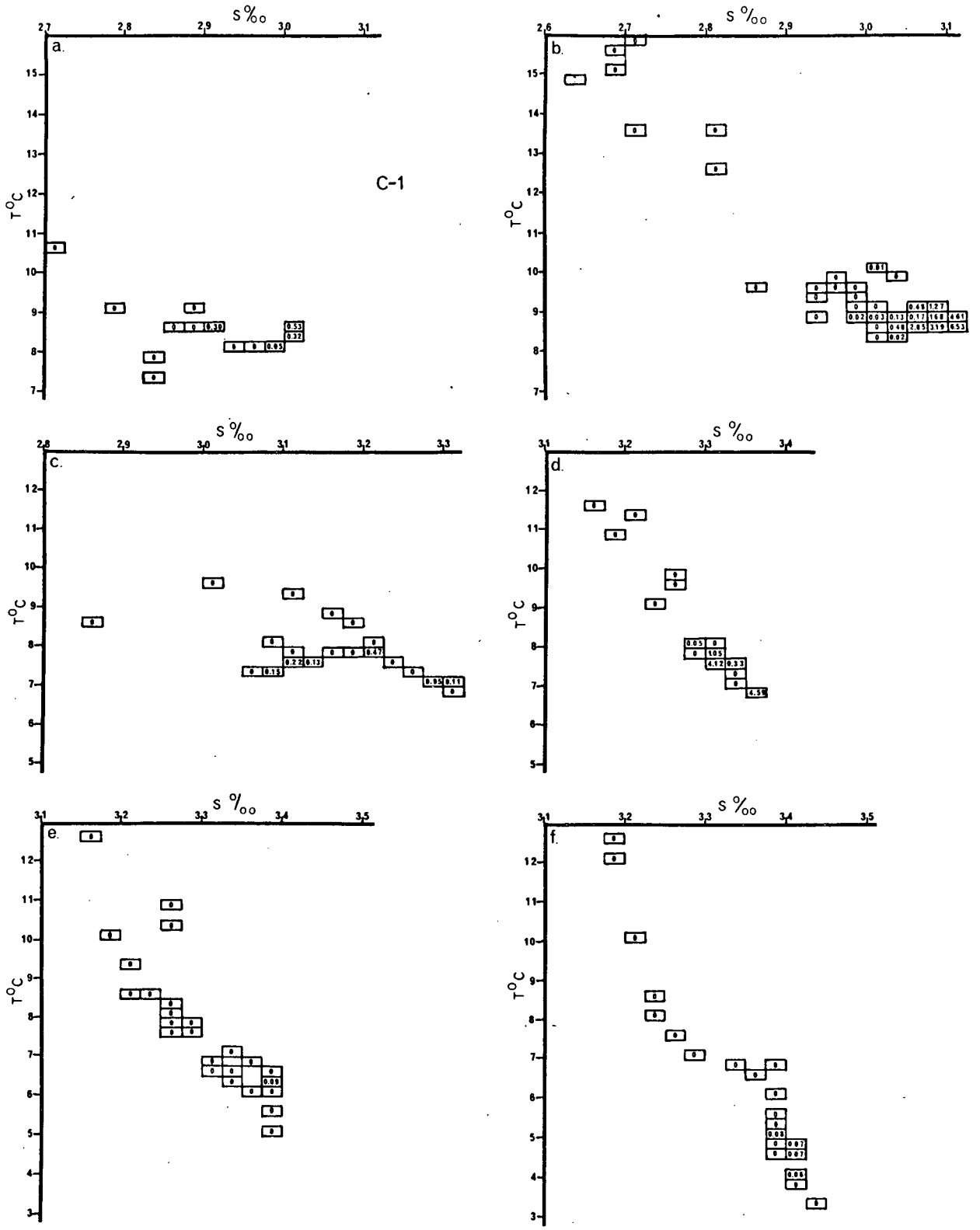
Generally, the egg cluster was associated with the deep water of the various stations, although occasional egg clusters were found higher up in the water column. The temperature-salinity associations of the naupliar stages were similar to that of the egg cluster, in that the strongest associations were with the deep water. In the southern waters group, a few nauplii were captured in near-surface waters (30 m). During the 2-year field study, nauplii were usually found below 100 m, although occasional samples collected as shallow as 10 or 30 m had a small number of nauplii. This, along with the observation that egg clusters were occasionally found in near-surface water suggests that, although egg clusters normally hatched in deep waters, they were capable of hatching in near-surface waters.

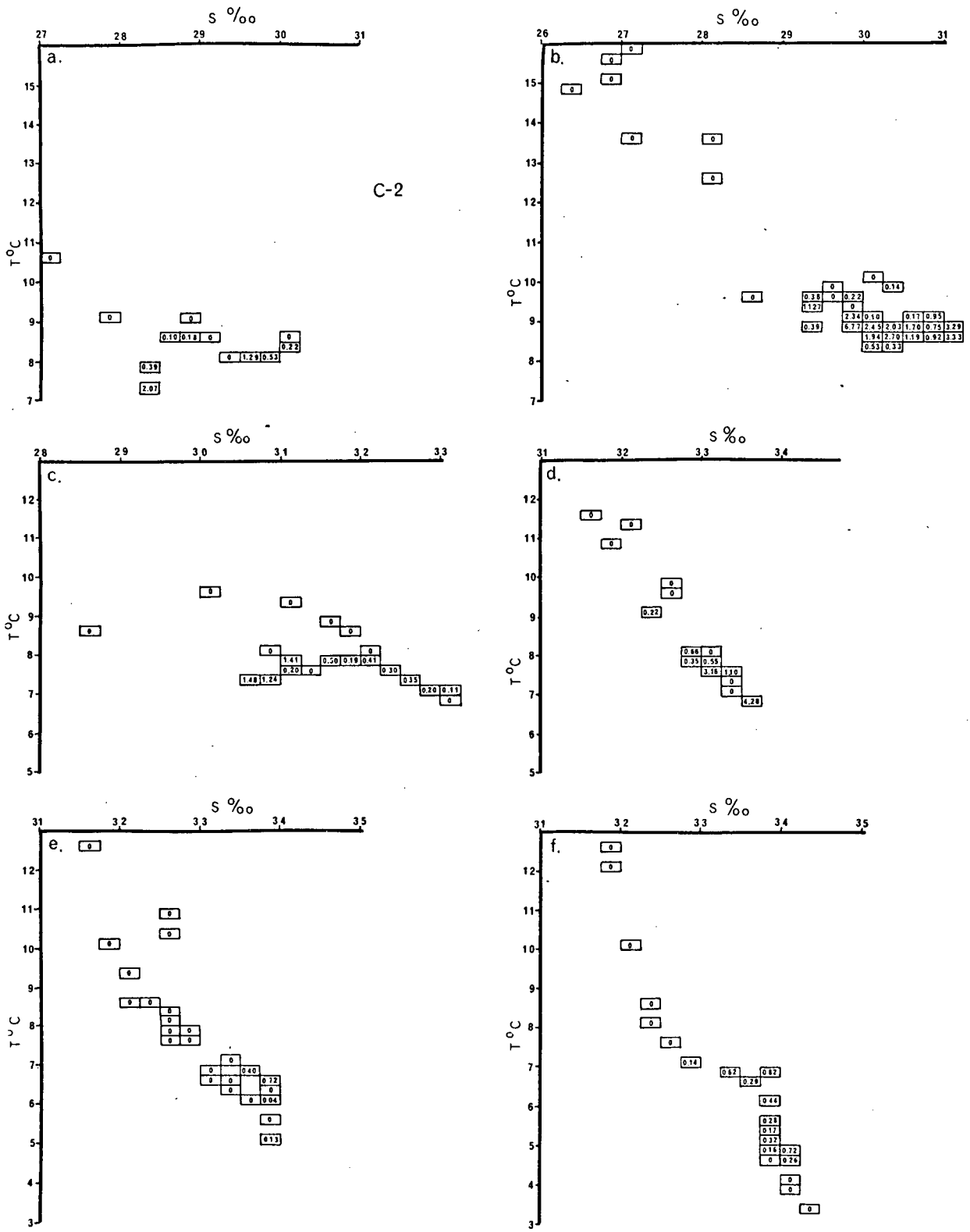
Plankton samples were collected as deep as 1,000 m in the Pacific Ocean. There, the nauplii were associated with Pacific Ocean subsurface water and were most abundant between 500 and 750 meters.

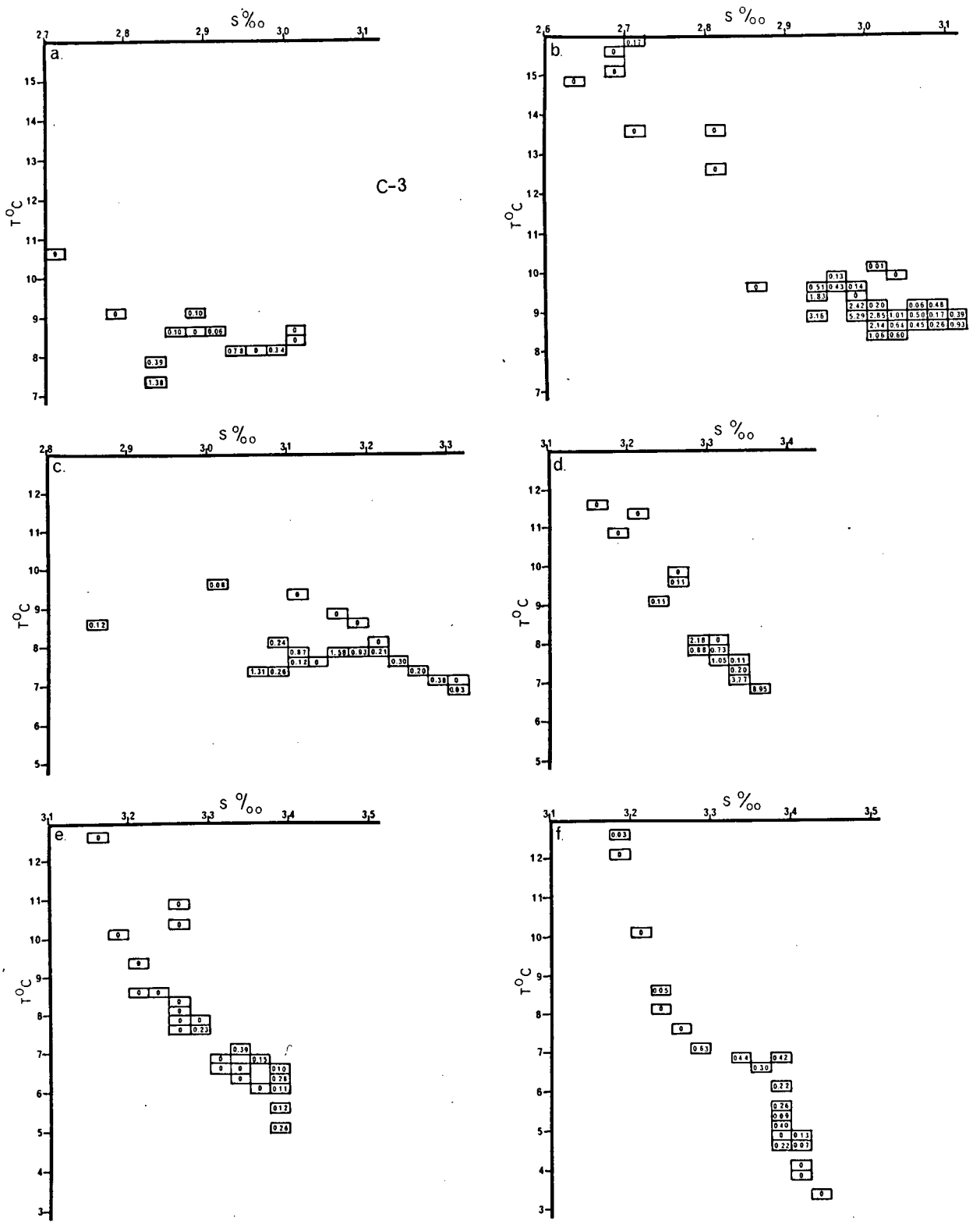
Figure 4. The temperature-salinity associations of the egg cluster, nauplius, and the six copepodite stages of P. elongata in (a) low-salinity 'southern' waters, (b) southern waters, (c) intermediate and northern waters, (d) west coast inlet waters, (e) coastal seaway waters, and (f) the sub-arctic Pacific Ocean. The value inside each temperature-salinity rectangle is the mean concentration of specimens (numbers/m^3) associated with that rectangle. The data are from the July 1970 survey cruise.

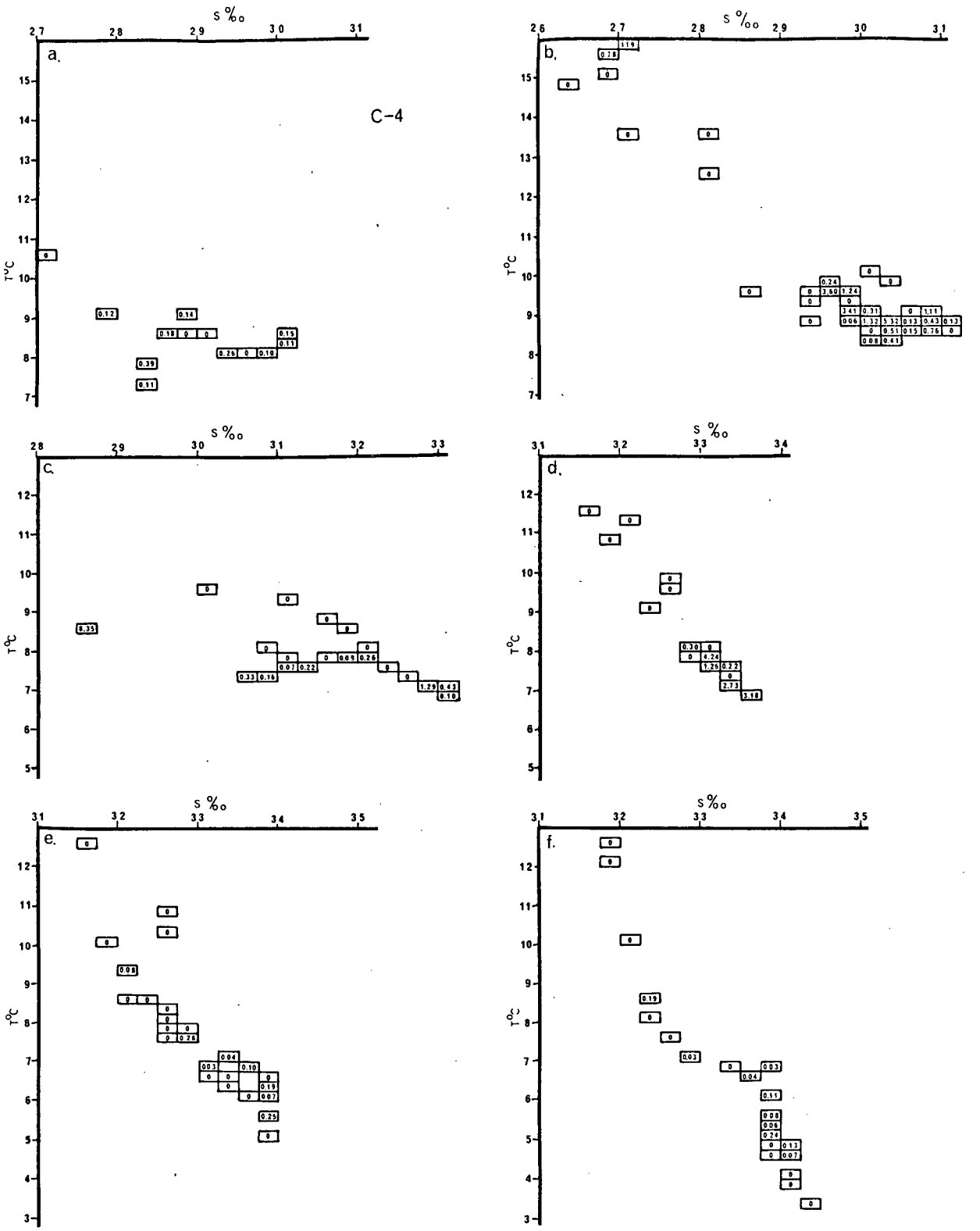

a.
egg
clusters
b.
c.
d.
e.
f.
S ‰
T°C

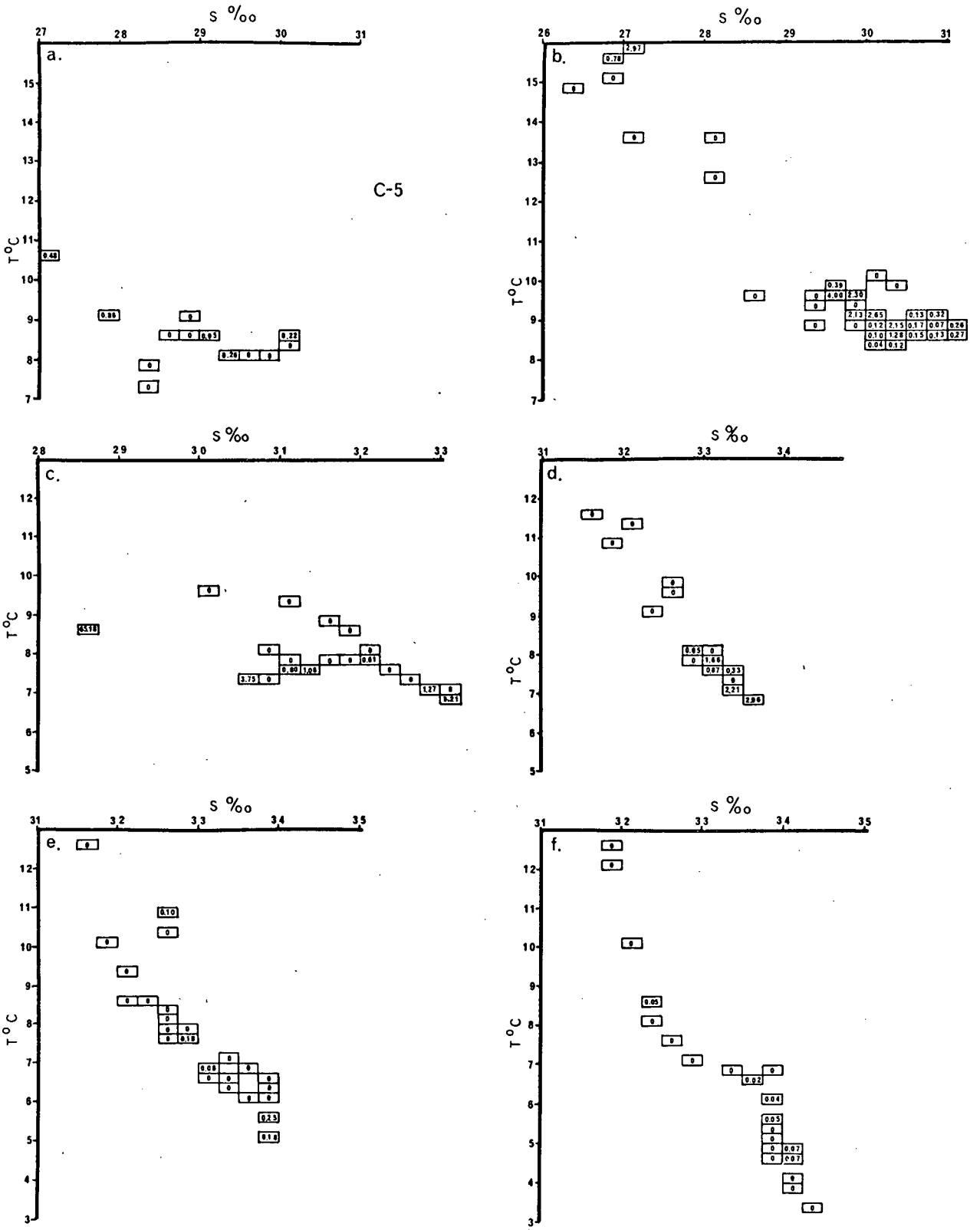

a.
nauplii
b.
c.
d.
e.
f.
S‰
T°C

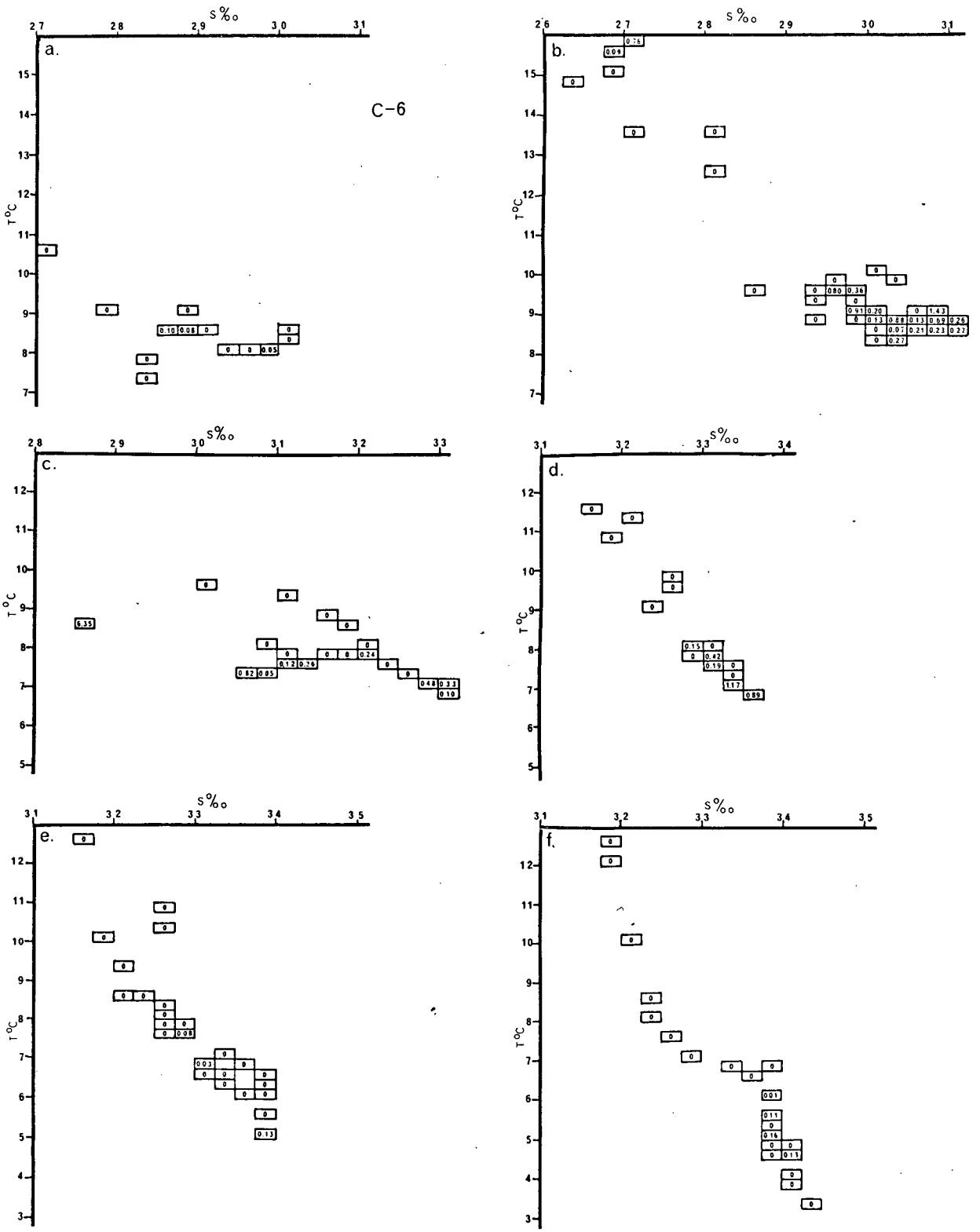

a.
b.
c.
d.
e.
f.
C-1
T°C
S ‰


C-2
a.
b.
c.
d.
e.
f.
S ‰
T°C


a.
b.
c.
d.
e.
f.
C-3
S ‰
T °C


a.
C-4
b.
c.
d.
e.
f.
S ‰
T°C


C-5
a.
b.
c.
d.
e.
f.
S ‰
T °C


a.
C-6
b.
c.
d.
e.
f.
S‰
T°C

The temperature-salinity association of the first copepodite was similar to that of the naupliar stages in that they both tended to be associated with deep water. The second copepodite was less restricted to deep water, being found higher up in the water column.

The temperature-salinity associations of the third to the sixth copepodite were similar. These stages were found throughout the water column although they occurred in higher concentrations in the near-surface waters. No apparent difference was noted in the distribution of males and females (which can be distinguished beginning with the fourth copepodite), and so the sexes were not plotted separately.

Although it is not well indicated by the graphs, it was observed that the third to sixth copepodites were found nearer to the surface in those stations occupied at night, than those stations occupied during the day. For example, the particularly high value for the fifth copepodite (65.18 animals/m^3) was from a sample collected in Knight Inlet at 0010-0025 PDT, July 24, 1970 at 10 m depth.

There was an obvious discrepancy between the distribution of the adult female and the egg cluster. Although adult females were found throughout the water column, the egg clusters were generally restricted to the deep water. As egg clusters were always captured with at least as many females, females bearing egg clusters must have been associated with the deep water. Females without egg clusters must have been associated both with deep and near-surface water.

Discussion

The results of the three survey cruises indicate that P. elongata was restricted neither to the oceanic nor to the neritic water within the study area. Throughout this area, the vertical distribution remained similar with the egg, nauplius, and early copepodite stages being associated with the deep water of all six groups of waters studied, and the later stages being found in deep and near-surface waters. As the six groups of waters had different temperature-salinity characteristics, the vertical distribution of the species throughout the study area could not be associated with temperature and salinity, per se. However, there may be temperatures and salinities of the surface waters (0 to 20 meters), which the species avoids. As the species is capable of breeding in all the waters studied, variables other than water quality may account for the differences in the relative abundances of the species within the study area.

Although there are few estimates available for the primary production in the areas studied, the available data indicate that there is a good correlation between the total primary production of some areas, and the relative abundance of P. elongata in those areas. Low concentrations of P. elongata were associated with the eastern Pacific Ocean sub-arctic waters. However, this area is characterized by low primary production (43 to 78 gC/m^2 year; Anderson 1964). The Strait of Georgia had higher concentrations of P. elongata, and higher primary production

(120 gC/m^2 year; Parsons et al., 1970). Indian Arm had, on the average, higher concentrations of P. elongata than the Strait of Georgia, and higher primary production (609 gC/m^2 year; Gilmartin 1964).

The coastal seaways domains have low concentrations of P. elongata probably because the waters in these areas are continuous with surface and subsurface Pacific Ocean water which also has low concentrations of P. elongata. As the subsurface water in Juan de Fuca Strait and Queen Charlotte Strait moves further inshore, it mixes with the low-salinity waters from the inlets and the Strait of Georgia in the regions of turbulent mixing in the two homogeneous domains. Here also, the populations of P. elongata are small. One of the reasons for this is that the two waters which contribute to the resultant water both have comparatively small populations of P. elongata. The subsurface Pacific Ocean water has small populations of P. elongata probably because of the low production of the oceanic environment. The surface waters from the inlets and the Strait of Georgia have low populations because of the characteristics of the species' diel vertical migration and the estuarine circulation of these areas.

In the British Columbia inlets and the Strait of Georgia, the surface layer usually extends only as deep as 20 m (Pickard 1961, 1963; Waldichuk 1957). P. elongata has only been found to be associated with this layer from the third to the sixth copepodite, and then only during the night; during this time they are carried seaward. However, during the day, these stages are associated with the subsurface layer and so are carried back towards the head of the inlet or back into the Strait

of Georgia. Because of this pattern of diel vertical migration in relation to the estuarine circulation of these areas, P. elongata is 'conserved' within the inlets and the Strait of Georgia. This conservation mechanism has previously been proposed for the plankton in inlets (LeBrasseur 1955), and estuaries (Rogers 1940). Therefore, because of this conservation mechanism, areas such as Haro Strait, Boundary Passage, Nodales Channel, and Johnstone Strait receive a relatively small number of immigrants from the inlets and the Strait of Georgia.

In order for a population to increase in size in an area through reproduction, the residence time of the population in the area must be longer than the time required to complete the life cycle. In the inlets, the bottom water is replaced at intervals of one year or greater (Pickard 1961, 1963), and it is probably only rarely that the major portion of the inlet water is replaced by new water. It is estimated that P. elongata requires a minimum of six to eight months to complete its life cycle (pers. obser.). Because of the long residence time of the deep water in the inlets relative to the time required for P. elongata to complete its life cycle, it is possible for the population to increase through reproduction.

Whether or not a population of P. elongata will increase in size by reproduction in an inlet or the Strait of Georgia will depend upon several variables. Considering only the replacement of the deep water, two variables are the rate of replacement and the origin of the deep water. The west coast, northern and intermediate inlets, and Seymour, Belize, and Loughborough Inlets all open almost directly onto

the Pacific Ocean or to the waters in the northern homogeneous domain. These latter areas have relatively small populations of P. elongata so that an intrusion of water from these regions into an inlet might dilute the relatively large resident population. Whether it does should depend on the rate of influx; if it is so rapid that the species cannot retain its vertical distribution within the inlet, and is carried out with the older water, then there will be a reduction in the size of the population. Such an event may have occurred in Loughborough Inlet in the spring of 1970. However, if the rate of intrusion is low, and P. elongata can retain its vertical position in the water column, then the population should not be appreciably reduced. The southern inlets, with deep sills which open onto the Strait of Georgia, are less likely to have their populations reduced by an influx of new water, since this water originates in the Strait of Georgia. This latter area generally has comparatively large populations of P. elongata all year around.

The waters in the areas of turbulent mixing have a very short residence time, with water passing through areas such as the San Juan Archipelago in one or two months. The currents in this area are turbulent currents, and P. elongata is probably transported through these areas at much the same rate as the water in which it lives. Because it takes only one or two months for the species to pass through such an area, while it requires a minimum of six to eight months to complete its life cycle, it is highly unlikely that populations of P. elongata will increase significantly in numbers in these turbulent areas

through reproduction. The loss of the later developmental stages from the inlets, the Strait of Georgia, and the Pacific Ocean may be more important in determining the size of the populations of P. elongata in the regions of turbulent mixing in the homogeneous domains.

Conclusions

(1) Breeding populations of P. elongata are associated with all six groups of waters studied, i.e. low-salinity 'southern' waters, southern waters, intermediate and northern waters, west coast inlet waters, coastal seaways waters, and sub-arctic Pacific Ocean waters.

(2) The vertical distribution of the developmental stages throughout the study area is independent of the temperature and salinity of the subsurface water, but dependent upon the stage of development of the organism, and possibly upon the factors which affect diel vertical migration.

(3) Populations of P. elongata in the Pacific Ocean are probably small because of the low production of this environment.

(4) Populations of P. elongata in the coastal seaways are probably small because this area is simply an extension of the oceanic environment.

(5) The homogeneous domains are characterized by small populations of P. elongata. The populations are small because (i) the two waters which contribute to the formation of the water in the homogeneous

domains both contain small populations of P. elongata, and (ii) the short residence time of the water in the homogeneous domains relative to the time required for P. elongata to complete its life cycle prevents a significant increase in the size of the population through breeding.

(6) The relatively large size of the populations of P. elongata associated with the inlets and the Strait of Georgia is probably due to several factors. Three of these are (i) the high primary production of these areas, (ii) the long residence time of the deep water relative to the time required for P. elongata to complete its life cycle, and (iii) the vertical distribution of the developmental stages in relation to the characteristics of the estuarine circulation in these areas.

CHAPTER III

THE LABORATORY STUDY-AN EXAMINATION OF THE HATCHING SUCCESS OF P. ELONGATA EGG CLUSTERS IN VARIOUS NATURAL SEAWATERS

INTRODUCTION

It was shown in the preceding section that breeding populations of P. elongata are restricted neither to the oceanic nor to the neritic water within the study area. This implies that the species either has a wide range of tolerances for temperature, salinity, and the other properties of the waters of its range, or else is able to adapt to its environment. Physiological variations within a species in different parts of its range have been demonstrated for responses to temperature (Moore 1949, 1950; Stauber 1950; Loosanoff and Nemejko 1951; Vernberg 1962; Gilfillan 1970), to salinity (Prosser 1955, Guillard and Ryther 1962; Gilfillan 1970), and to the 'other' properties of sea water (Gilfillan 1970).

Although P. elongata has been shown to be restricted neither to oceanic nor to neritic water within the study area this does not imply that variations in temperature, salinity, and the other properties of the water within the species' range do not affect the organisms. Subpopulations of the species may possess a narrow range of tolerances for temperature, salinity, and other properties of sea waters. However, if the species can adapt to its environment, then it will have a wider range than would be inferred from determining the tolerances of a subpopulation collected from one area.

This chapter presents the results of two investigations:

(1) A study was conducted to determine whether or not sea waters with similar salinities and temperatures have different other properties. The properties which were measured were the concentrations of dissolved zinc, copper, nickel, and manganese. Lewis and Ramnarine (1969) indicated that the survival of P. elongata egg clusters collected from G.S.-1 (in the Strait of Georgia) was affected by the addition of trace elements to the sea water.

(2) A study was conducted to determine whether or not P. elongata egg clusters collected from different areas and at different times, from waters of similar temperatures and salinities, were distinct in their ability to survive in various natural sea waters of similar salinity. Experiments were also conducted to determine whether or not P. elongata egg clusters collected from various areas with large differences in salinity were distinct in their ability to survive in waters with large differences in salinity.

The egg cluster was tested because this stage is frequently the most sensitive stage in the life history of an organism. It was thought that testing this stage would have a greater probability of indicating differences between waters than testing one of the more hardy stages.

Materials and Methods

Water for experiments was collected with a 96-L fibreglass and lucite water sampler. The water was passed through two thicknesses of

a number-20 mesh net (approximate pore size-64μ), and placed in 5-gallon Nalgene carboys. A portion of the water was further filtered through a 0.45u-millipore filter for dissolved trace element analysis. This was done only for the water collected from Indian Arm, G.S.-1 and Juan de Fuca Strait. In the laboratory, all sea water was stored in a non-illuminated cold-room at 8°C. Water collected from the Pacific Ocean was stored at 4°C.

Egg clusters were collected with a 1-m ring net (approximate pore size-700u). The plankton sample was placed in plastic trays, along with water collected by the water sampler. Egg clusters and egg-cluster bearing females were examined, and young, undamaged clusters (and females) were transferred with a large bore pipette to a cooled 4-L isotherm containing sea water.

In the laboratory, the egg clusters were sorted under a binocular microscope, and only young egg clusters were set aside for use in experiments. Young egg clusters are a uniform blue in colour, while in older egg clusters, the individual eggs are polarized, with one pole being blue and the other white.

Egg clusters were individually reared in 1,000-ml Nalgene Erlenmeyerr flasks. These flasks were rinsed three times with a total of 400 ml of sea water, and then 600 ml of sea water was added. The number of eggs in a cluster were counted, and the egg cluster added to a flask. The mouth of the flask was then covered with a piece of Parafilm (American Can Company, Marathon Products) to reduce evaporation.

Flasks were maintained in the dark at 8°C in a Psycrotherm incubator (New Brunswick Scientific Company), and were horizontally rotated at 40 rpm. In supplementary experiments, flasks were maintained in the dark in a cold-room; flasks maintained in the cold-room were not rotated.

Every three days, the contents of each flask was placed in a large fingerbowl, the number of organisms at each stage were counted, and dead organisms were removed. Each flask was again rinsed with a total of 400-ml of sea water, and 600 ml of sea water was added. The remaining living organisms were replaced, and the flask was returned to the incubating chamber.

Eggs were reared through to the first copepodite. However, only the hatching success of the egg was used because (i) most of the mortality between the egg and the first copepodite occurred in the egg and the first two naupliar stages (Lewis and Ramnarine 1969), (ii) 90% of the eggs hatch directly into the second nauplius (Borgmann 1971), and (iii) the mortality of the hatched first and second nauplius was low, being less than 5% (Whitfield, pers. comm.; pers. obser.).

Tests

Of the five stations studied over the 2-year period, only Indian Arm and G.S.-1 had large, breeding populations of P. elongata; therefore, the laboratory work was largely restricted to these two populations. The specific procedures were:

(1) Egg clusters were collected from Indian Arm and G.S.-1

once a month, from March 1971 to February 1972. These egg clusters were tested in three waters, i.e. (i) Indian Arm 200-m water, (ii) G.S.-1 350-m water, and (iii) Juan de Fuca 200-m water until October 1971. After this time, tests were made using only Indian Arm and G.S.-1 water. Five replicates were used for each test, and all tests were run in the Pyscrotherm incubator.

(2) Egg clusters from Indian Arm were collected and tested in a second series of Indian Arm 200-m water, and Juan de Fuca 200-m water (April 1971). A third water was made by diluting the Juan de Fuca water with distilled water, so that its salinity was the same as the Indian Arm 200-m water. Five replicates were used for each test, and these tests were run in an 8°C cold-room.

(3) Egg clusters were collected from Pac-6 (Figure 1) in May 1971, and tested in Pac-6 750-m water, Juan de Fuca 200-m water, G.S.-1 350-m water, and Indian Arm 200-m water; the salinities of these waters were 34.4‰, 33.8‰, 30.9‰, and 27.8‰ respectively. Five replicates were made for each test, except for Indian Arm where only 3 replicates were made. All tests were run in a 4°C cold-room.

(4) Egg clusters were collected from Pac-8 (Figure 1), in July 1971, and tested in Pac-8 750-m water, Juan de Fuca 200-m water, G.S.-1 350-m water, and Indian Arm 200-m water; the salinities of these waters were 34.2‰, 33.9‰, 30.9‰, and 27.8‰ respectively. Five replicates were used for each test, and the tests were run in a 4°C cold-room.

(5) Egg clusters were collected from Bute Inlet in June 1971, and tested in Bute 600-m water (salinity - 31.1‰) and G.S.-1 350-m

water (salinity - 30.8‰). Nine replicates were used for each test, and the tests were run in an 8°C cold-room.

(6) Egg clusters were collected from Seymour Inlet, in August 1971, and tested in Seymour 450-m water (salinity - 28.9‰) and Indian Arm 200-m water (salinity - 27.8‰); five replicates were used for each test. Egg clusters were also collected from Indian Arm and tested in the two waters using four replicates for each test. The tests were run in an 8°C cold-room.

(7) Egg clusters were collected from Alberni Inlet, in September 1971, and reared in Alberni 250-m water (salinity - 32.8‰) and in Juan de Fuca 200-m water (salinity - 33.9‰). Five replicates were used for each test, and the tests were run in an 8°C cold-room.

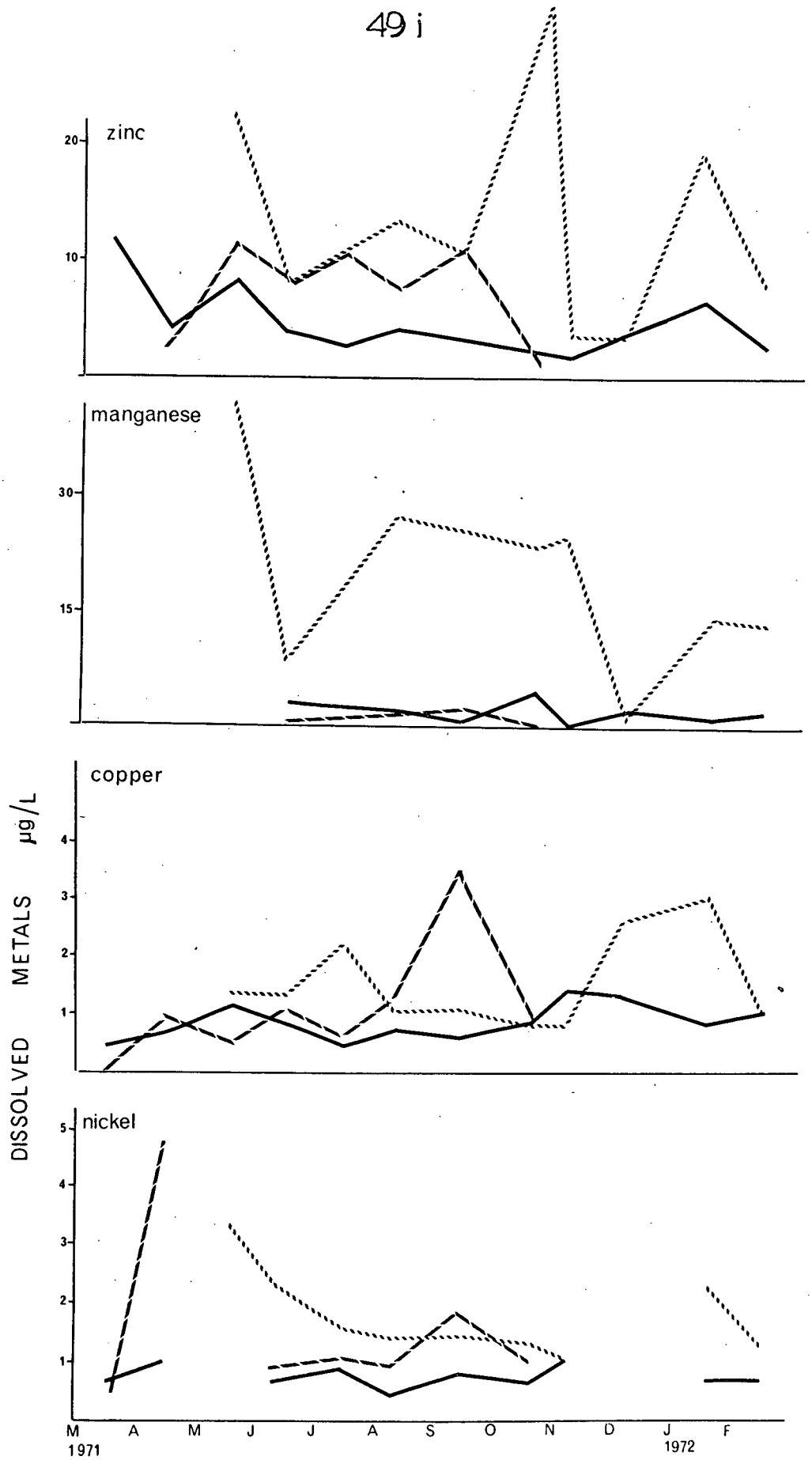
(8) Egg clusters were collected from Indian Arm and G.S.-1, and reared in G.S.-1 20-m water (salinity - 29.6‰) in January 1972. Five replicates were used for each test, and the tests were run in the Psycrotherm incubator.

Results

(i) Variations in the Concentrations of Dissolved Zinc, Manganese, Copper and Nickel

Figure 5 shows the concentrations of the four measured trace elements during the study period at the three stations. These values are higher than values previously determined from other studies, and some contamination may have been introduced either during the collecting or the filtering of the water (E. Grill, pers. comm.). The data were

Figure 5. The concentrations of dissolved zinc, manganese, copper, and nickel in Juan de Fuca 200-m water (———), G.S.-1 350-m water (_____), and Indian Arm 200-m water (••••••). The data for dissolved nickel are incomplete as analyses were not made every month.


zinc
20
10
manganese
30
15
copper
4
3
2
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nickel
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DISSOLVED METALS µg/L
M A M J J A S O N D J F
1971
1972

interpreted by assuming that they were qualitatively correct.

Figure 5 shows the fluctuations in the concentrations of dissolved zinc in Indian Arm 200-m water, G.S.-1 350-m water, and Juan de Fuca 200-m water during the period of the laboratory study. Concentrations were generally greatest in Indian Arm water, intermediate in Juan de Fuca water, and lowest in G.S.-1 350-m water. Therefore, the concentration of dissolved zinc was not directly related to the salinity of the water. Secondly, while the concentrations of dissolved zinc at the three stations fluctuated with time, there was no apparent association with changes in the deep water as measured by temperature and salinity (Figure 3).

Figure 5 shows the fluctuations in the concentrations of dissolved manganese, copper, and nickel at the three stations. Concentrations were generally highest at Indian Arm, and lowest at G.S.-1. Again, there was no apparent relationship between fluctuations in the concentration of an element and changes in the temperature and salinity of the deep water. While the concentrations of the four elements at each station varied with time, there was little similarity in their fluctuations. This implies that different processes regulate the concentration of each element, rather than one process regulating all four. These processes were probably chemical and biological, and other physical processes not adequately described by temperature and salinity measurements.

(ii) Fluctuations in the Survival of Indian Arm and G.S.-1 Egg Clusters in Indian Arm, G.S.-1, and Juan de Fuca deep Waters

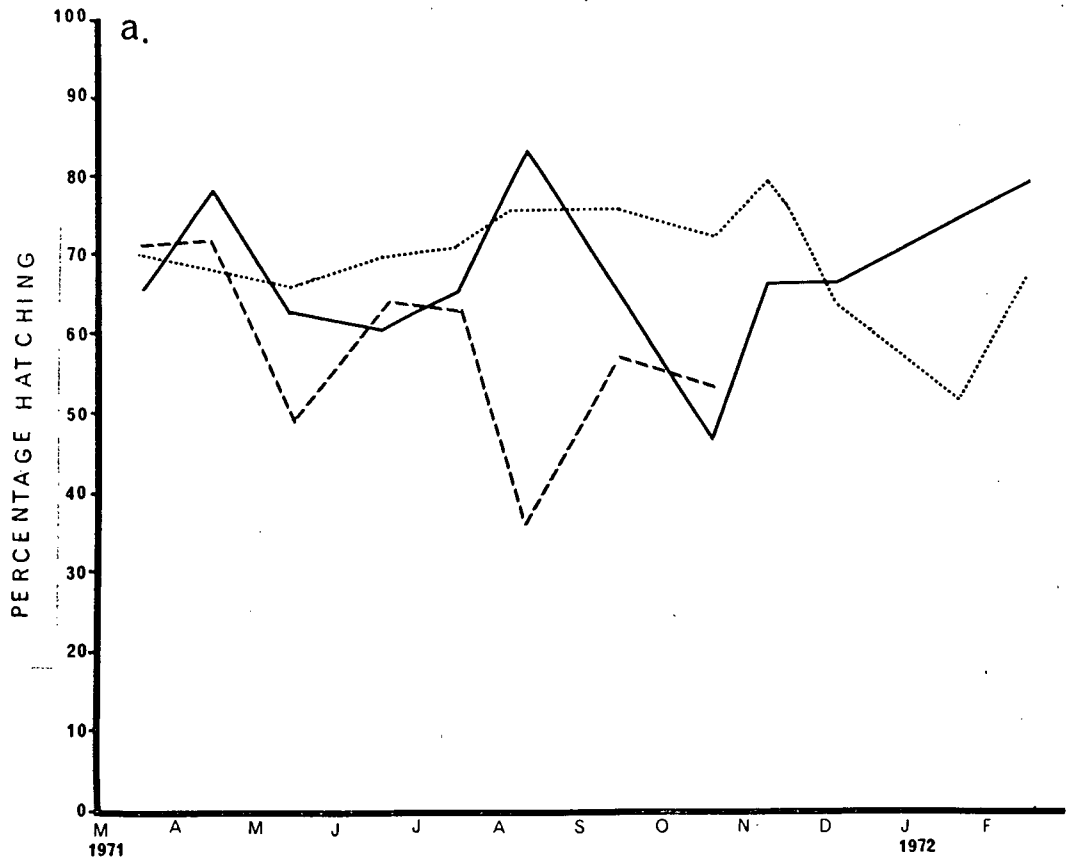
Figure 6a shows the fluctuations in the percentage hatching of G.S.-1 egg clusters in the three waters. With five replicates, one standard deviation was 10 to 30%, and the standard error was 5 to 15%. Although there were large differences in the salinities of the three waters, survival was generally good, usually being above 60%.

Survival of G.S.-1 egg clusters in Indian Arm water was significantly correlated with the concentration of dissolved copper ($r = .8$; $p = .004$), and in G.S.-1 water with the concentration of dissolved manganese ($r = -.68$; $p = .04$). Survival did not appear to be associated with changes in the temperature and salinity of the deep water, although survival was lowest in Indian Arm water in December, January, and February, when the deep water was replaced (Figure 3).

Figure 6b shows the fluctuations in the percentage hatching of Indian Arm egg clusters in the three waters. These fluctuations were distinct from those of G.S.-1 egg clusters. Survival was generally highest in Indian Arm water, and lowest in Juan de Fuca water.

Table 5 presents the results of the experiments using Juan de Fuca water, diluted Juan de Fuca water, and Indian Arm water as a rearing medium for Indian Arm egg clusters. These results suggest that the high salinity of the Juan de Fuca water was probably the causal factor in preventing the hatching of Indian Arm egg clusters. The

Figure 6. The mean percentage hatching of (a) G.S.-1 egg clusters, and (b) Indian Arm egg clusters in Juan de Fuca 200-m water (------), G.S.-1 350-m water (_____), and Indian Arm 200-m water (.....).


a.
PERCENTAGE HATCHING
100
90
80
70
60
50
40
30
20
10
0
M
A
M
J
J
A
S
O
N
D
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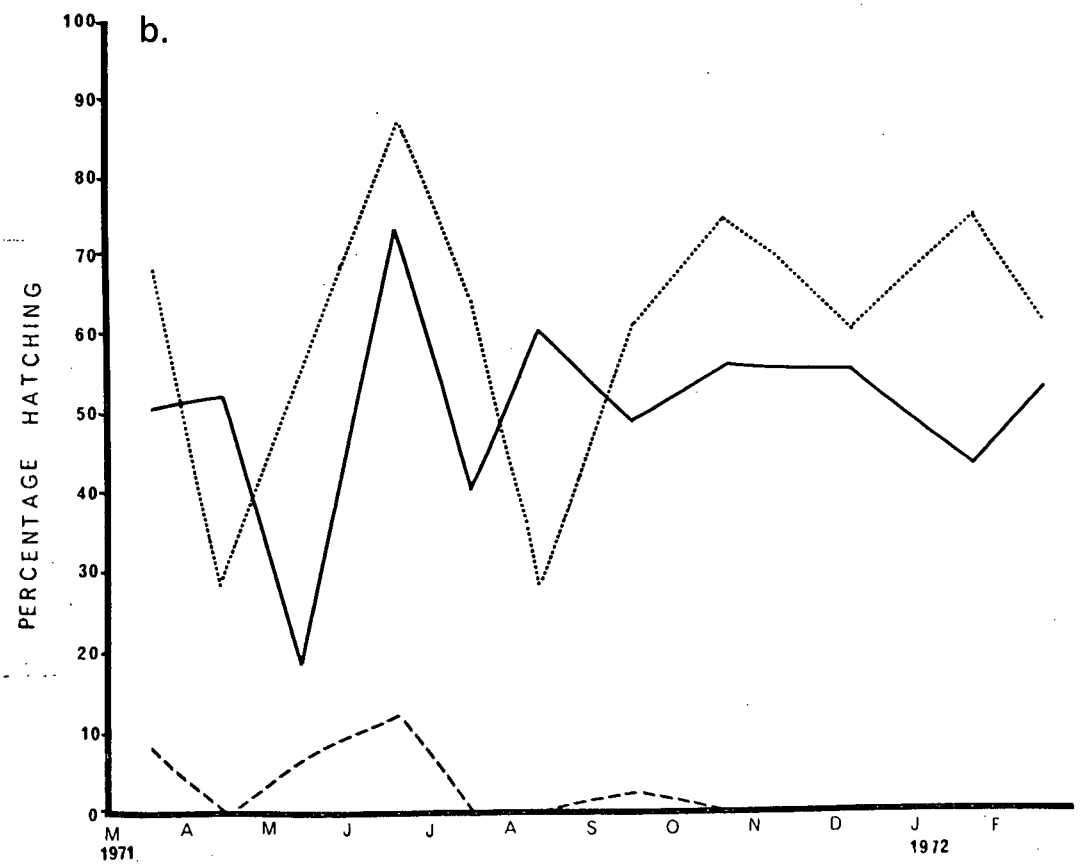
1972


b.
PERCENTAGE HATCHING
100
90
80
70
60
50
40
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1972

TABLE 5. Results and the analysis of variance of the survival of Indian Arm egg clusters in Indian Arm 200-m water, Juan de Fuca 200-m water, and diluted Juan de Fuca 200-m water.

	Percentage Survival		
	Indian Arm Water 200-m	Juan de Fuca Water 200-m	Diluted Juan de Fuca Water 200-m
Replicate 1	61.5	59.0	78.5
Replicate 2	61.5	5.2	100
Replicate 3	64.7	30.7	61.5
Replicate 4	62.5	5.2	69.2
Replicate 5	71.4	64.2	68.4
Mean Survival	64.3	32.8	75.5

	Sum of Squares	Degrees of Freedom	Mean sum of Squares	F-ratio
Category means	0.489	2	0.245	
Within means	0.416	12	0.035	7.00
Total	0.905	14		

A significant difference in the means at the 99% confidence level.

actual factor may have been associated with the ability of the eggs to osmoregulate in high-salinity water. Secondly, survival in the diluted Juan de Fuca water was higher than in Indian Arm water indicating that there were differences in the properties of these two waters.

The survival of Indian Arm egg clusters in Indian Arm water and Juan de Fuca water in the cold-room was higher than in the duplicate series run in the Psycrotherm incubator. This was noted several times during the study when duplicate series were run; the reason for these differences is not known.

Survival of Indian Arm eggclusters in the three waters was not significantly correlated with the concentration of dissolved zinc, manganese, copper, or nickel. Similarly, changes in survival did not appear to be associated with changes in the temperature and salinity of the deep water (Figure 3). The smallest fluctuations in survival of Indian Arm egg clusters in Indian Arm and G.S.-1 waters occurred from September 1971 to February 1972, and it was during this period that the deep water of these two areas was replaced.

An analysis of variance was made by using the method outlined in Steel and Torrie (1960) for factorial experiments with three variables. The data analyzed were the survival of Indian Arm and G.S.-1 egg clusters in Indian Arm 200-m water and G.S.-1 350-m water. Survival in Juan de Fuca 200-m water was excluded because it was believed that the failure of Indian Arm egg clusters to hatch in this water was probably due to an osmotic stress imposed on the eggs by the relatively

high salinity of the water. Since the purpose of this series of tests was to examine differences in water other than salinity, it was decided to exclude the Juan de Fuca data from this analysis.

Table 6 presents the results of the analysis of variance. Over the 12-month period, there was a statistically significant difference in the properties of Indian Arm and G.S.-1 waters, and in the survival of Indian Arm and G.S.-1 egg clusters. Survival of the egg clusters in the two waters varied over the 12-month period, as did the properties of the waters from these two areas. There was no significant interaction over the 12-month period.

The data were further analyzed to determine the source of variation. Three analyses of variance were made, testing (i) the survival of Indian Arm egg clusters in the two waters over the 12-month period, (ii) the survival of G.S.-1 egg clusters in the two waters over the 12-month period, and (iii) the survival of G.S.-1 egg clusters in Indian Arm, G.S.-1 and Juan de Fuca water over the 8-month test period. The analysis was made by using the method described in Dixon and Massey (1957) for two variables of classification and repeated measurements.

Table 7 shows the results for Indian Arm egg clusters; there was a significant difference in the response of the egg clusters to the two waters tested, and a significant difference in the response over the 12-month period. Conversely, there was no significant difference in the response of G.S.-1 egg clusters to the two waters tested

TABLE 6. Results of the analysis of variance of the percentage hatching of Indian Arm and G.S.-1 egg clusters in Indian Arm 200-m water and G.S.-1 350-m water (March 1971-February 1972).

Source	df	SS	MS	F ratio	Probability
Blocks	4	0.399	0.099	2.475	$>.05$
A (Population)	1	0.510	0.510	12.750	$<.005$
B (Water)	1	0.323	0.323	8.075	$<.005$
C (Time)	11	0.739	0.067	1.675	$>.05$
AB	1	0.491	0.491	12.275	$<.005$
AC	11	1.401	0.127	3.175	$<.005$
BC	11	0.870	0.079	1.975	$<.05$
ABC	11	0.410	0.037	0.925	$>.05$
Error	188	7.650	0.040		

TABLE 7. Analysis of variance of (a) the survival of Indian Arm egg clusters in Indian Arm 200-m water and G.S.-1 200-m water (12 months), (b) the survival of G.S.-1 egg clusters in G.S.-1 350-m water and Indian Arm 200-m water (12 months), (c) the survival of G.S.-1 egg clusters in Indian Arm 200-m water, G.S.-1 350-m water, and Juan de Fuca 200-m water (8 months).

	Sum of Squares	Degrees of Freedom	Mean Sum of Squares	F-ratio	p
A)					
Row means	0.322	1	0.322	5.919	< 0.025
Column means	1.465	11	0.132	2.430	< 0.025
Interaction	1.122	11	0.102	1.873	> 0.05
Subtotal	2.909	23	0.126		
Within groups	5.226	96	0.054		
Total	8.135	119			
B)					
Row means	0.004	1	0.004	0.144	> 0.05
Column means	0.331	11	0.030	0.984	> 0.05
Interaction	0.466	11	0.042	1.382	> 0.05
Subtotal	0.801	23	0.035		
Within groups	2.938	96	0.031		
Total	3.739	119			
C)					
Row means	0.327	2	0.164	4.810	< 0.001
Column means	0.247	7	0.035	1.035	> 0.05
Interaction	0.708	14	0.051	1.481	> 0.05
Subtotal	1.283	23	0.037		
Within groups	3.280	96	0.034		
Total	4.562	119			

(Table 7b), nor in the responses over the 12-month period. Therefore whether or not there are significant differences in the 'quality' of the Indian Arm or G.S.-1 water tested depends on whether or not Indian Arm or G.S.-1 egg clusters are used as a bioassay. Table 7c shows the results of the analysis of G.S.-1 egg clusters in the three waters. In this case there were significant differences in the response to the three waters, although there were no significant temporal variations. Over the 8-month test period, Juan de Fuca water was a less satisfactory rearing medium for G.S.-1 egg clusters (and Indian Arm egg clusters) than G.S.-1 water, giving a mean survival of 57.9% vs. 65.6%.

(iii) Survival of Pacific Ocean Egg Clusters in Four Natural Sea Waters of Different Salinities

Table 8 presents the results of the Pac-6 experiments. Survival was good in all four waters, although it was lower in Indian Arm water (43.8%). This indicates that Pac-6 egg clusters were tolerant of large variations in salinity, and of the other properties associated with these waters. It also suggests that the populations of P. elongata in the Pacific Ocean are not relatively small because the properties of the water are unfavourable for the survival of the species. Because the station was close to the coast (50 miles), it is possible that a significant percentage of P. elongata originated from the neritic environment. This could account for the tolerance for low salinities.

Table 9 presents the results of the Pac-8 experiments. Survival was highest in Pac-8 water, higher in Juan de Fuca water, high

TABLE 8. Results and the analysis of variance of the hatching success of Pac-6 egg clusters in four different sea waters.

	Percentage Hatching			
	Pac-6 750-m Water	J.F. 200-m Water	G.S.-1 350-m Water	Ind. Arm 200-m Water
Replicate 1	89.4	52.9	82.3	20.0
Replicate 2	31.8	76.1	47.3	50.0
Replicate 3	83.3	65.4	75.0	65.2
Replicate 4	23.5	94.4	31.1	
Replicate 5	57.1	83.3	55.5	
Mean Survival	57.0	74.4	58.3	43.8

	Sum of Squares	Degrees of Freedom	Mean Sum of Squares	F-ratio
Category means	0.175	3	0.058	1.137
Within means	0.724	14	0.051	
Total	0.899	17		

No significant difference at the 95% confidence level.

TABLE 9. Results and the analysis of variance of the survival of Pac-8 Egg clusters in four different sea waters.

	Percentage Hatching			
	Pac-8 750-m Water	J.F. 200-m Water	G.S.-1 350-m Water	Ind. Arm 200-m Water
Replicate 1	63.6	90.0	9.5	0
Replicate 2	88.8	65.0	47.8	40.0
Replicate 3	85.7	65.0	57.1	36.8
Replicate 4	85.0	66.6	56.5	42.1
Replicate 5	70.0	76.1	38.0	0
Mean survival	78.6	72.5	41.8	23.8

	Sum of Squares	Degrees of Freedom	Mean Sum of Squares	F-ratio
Category means	1.005	3	0.335	12.41
Within means	0.437	16	0.027	
Total	1.442	19		

A significant difference in the means at the 99.95% confidence level.

in G.S.-1 water, and low in Indian Arm water. There was a statistically significant difference in the means at the 99.95% confidence level. However, it is questionable whether this difference was due to differences in the salinity of the four waters which exerted an osmotic stress on the eggs, or due to the other properties of the waters. The salinity factor, per se, was probably more important, just as this factor was more important in causing the low survival of Indian Arm eggs in Juan de Fuca deep water. Pac-8 egg clusters may have been less tolerant of low-salinity water than Pac-6 egg clusters because the P. elongata in the former region were more isolated from the neritic environment (80 miles from the coast), and had fewer immigrants from the coastal region. Correspondingly, there may have been a larger percentage of the P. elongata population which had spent several generations in the oceanic environment.

(iv) Bute, Alberni, and Seymour Experiments

Table 10 presents the results of the series testing Bute egg clusters in Bute water and G.S.-1 water; there were no significant differences in the survival in the two waters. Table 11 presents the results of the series testing Alberni egg clusters in Alberni water and Juan de Fuca water; again there were no statistically significant differences in the results. Table 12 presents the results of the series testing Seymour and Indian Arm egg clusters in waters from the two areas. Indian Arm egg clusters survived equally well in the two

TABLE 10. Results and the analysis of variance of the survival of Bute Inlet egg clusters in Bute Inlet water and G.S.-1 water.

	Precentage Hatching	
	Bute 600-m Water	G.S.-1 350-m Water
Replicate 1	60.0	66.6
Replicate 2	88.8	53.3
Replicate 3	37.5	76.9
Replicate 4	90.9	76.9
Replicate 5	43.7	76.9
Replicate 6	76.4	52.9
Replicate 7	58.8	81.2
Replicate 8	86.6	66.6
Replicate 9	66.6	75.0
Mean Survival	67.7	69.2

	Sum of Squares	Degrees of Freedom	Mean Sum of Squares	F-ratio
Category means	0.001	1	0.001	0.042
Within means	0.338	16	0.024	
Total	0.039	17		

No statistically significant difference in the means at the 95% confidence level.

TABLE 11. Results and the analysis of variance of the survival of Alberni egg clusters in Alberni water and Juan de Fuca water.

	Percentage Hatching	
	Alberni 250-m Water	Juan de Fuca 200-m Water
Replicate 1	75.0	64.7
Replicate 2	83.3	82.3
Replicate 3	100	72.2
Replicate 4	93.7	94.1
Replicate 5	60.0	73.3
Mean Survival	70.4	77.3

	Sum of Squares	Degrees of Freedom	Mean Sum of Squares	F-ratio
Category means	0.012	1	0.012	0.090
Within means	1.063	8	0.132	
Total	1.075			

No significant difference in the means at the 95% confidence level.

TABLE 12. Results and the analysis of variance of the hatching success of Seymour egg clusters and Indian Arm egg clusters in water collected from the two inlets.

Percentage Hatching

	Seymour egg cl.		Indian Arm egg cl.	
	Seymour 450-m	Ind. Arm 200-m	Seymour 450-m	Ind. Arm 200-m
Replicate 1	84.2	61.9	94.4	61.1
Replicate 2	78.9	55.5	80.9	95.0
Replicate 3	63.1	50.0	71.4	57.8
Replicate 4	5.2	0	35.2	78.9
Replicate 5	72.2	28.5		
Mean survival	60.7	39.2	70.7	73.2

	Sum of Squares	Degrees of Freedom	Mean Sum of Squares	F-ratio
Category mean	0.329	3	0.109	1.626
Within means	0.942	14	0.067	
Total	1.271	17		

No significant difference in the means at the 95% confidence level.

waters. Seymour egg clusters had lower survival in Seymour water than Indian Arm egg clusters, and very low survival in Indian Arm water. This suggests that there were differences in the egg clusters from the two areas, and that for Seymour egg clusters, the two waters were qualitatively different. However, there were no statistically significant differences in the results.

(v) G.S.-1 20-m Water

Table 13 presents the results of the series testing G.S.-1 and Indian Arm egg clusters in G.S.-1 20-m water. Survival of these egg clusters in G.S.-1 350-m water and Indian Arm 200-m water is shown on Figure 6. Survival of Indian Arm egg clusters in G.S.-1 20-m water was slightly higher than in G.S.-1 350-m water while the reverse was true for G.S.-1 egg clusters. There is, from this experiment, no evidence to suggest that egg clusters are incapable of developing in the near-surface water. This supports the hypothesis that one of the reasons nauplii are usually found only in deep water is that the females, which carry the egg clusters until the nauplii hatch, normally remain in deep water.

Summary

The analysis of the concentrations of dissolved zinc, manganese, copper, and nickel in Indian Arm 200-m water, G.S.-1 350-m water, and Juan de Fuca 200-m water, indicated that the values associated with

TABLE 13. Results of the survival of Indian Arm and G.S.-1 egg clusters in G.S.-1 near surface (20-m) and deep (350-m) water.

	Percentage Hatching			
	Indian Arm egg clusters		G.S.-1 egg clusters	
	G.S.-1 20-m	G.S.-1 350-m	G.S.-1 20-m	G.S.-1 350 m
Replicate 1	50.0	50.0	50.0	76.9
Replicate 2	50.0	54.5	28.5	90.9
Replicate 3	71.4	12.5	76.9	92.3
Replicate 4	58.3	75.0	45.4	54.5
Replicate 5	72.7	26.6	64.2	53.8
Mean survival	60.4	43.7	53.0	73.6

each water were not a function of salinity. G.S.-1 deep water generally had the lowest concentrations of dissolved trace elements, and yet was intermediate in salinity to the deep waters of Juan de Fuca Strait and Indian Arm. There were, at each of the three stations, temporal variations in the concentrations of the four measured trace elements. While the salinity of the water also varied, there was no apparent relationship between the fluctuations in the salinity (and temperature) of the waters, and fluctuations in the concentrations of the dissolved trace elements. This suggests that unmeasured biological and chemical processes, and physical processes not adequately described by measurements of temperature and salinity, were affecting the concentrations of these trace elements. Therefore, within each of the three areas studied, measurements of temperature and salinity by themselves would not give a good indication of the concentrations of the trace elements which would be associated with that water.

The laboratory data indicated that the survival of G.S.-1 egg clusters in G.S.-1 water was significantly correlated with the concentration of dissolved manganese, and in Indian Arm water with the concentration of dissolved copper. There were no other significant correlations between the survival of egg clusters in a water and the concentrations of the dissolved trace elements.

The laboratory data also indicated that P. elongata egg clusters collected from different areas may exhibit different responses to a series of sea waters (when tested at the same temperature). The

factor to which the egg responds may be the salinity of the water or its other properties. For example, it was shown that both Indian Arm eggs and Pac-8 eggs reacted differently to a series of waters which had large differences in salinity (28 to 34‰). These differences in response were probably due to the egg responding to the salinity of the test waters per se, rather than to their other properties.

It was also shown that egg clusters may react differently to a series of waters with similar salinities. It was shown that Indian Arm egg clusters reacted differently to Indian Arm and G.S.-1 deep waters, that G.S.-1 egg clusters reacted differently to Juan de Fuca deep water than to Indian Arm and G.S.-1 deep waters, and it was suggested that Seymour Inlet egg clusters may react differently to Indian Arm and Seymour deep waters. As the salinities of these waters were similar, the egg cluster may have been reacting to differences in other properties of these waters.

Many of the tests indicated that egg clusters did not react differently to sea waters with similar salinities. G.S.-1 egg clusters had similar responses to Indian Arm and G.S.-1 water, Alberni Inlet egg clusters had similar survival in Alberni and Juan de Fuca deep waters, Bute Inlet egg clusters had similar survival in Bute and G.S.-1 deep waters, Indian Arm egg clusters had similar survival in Indian Arm and Seymour deep waters, and Pac-6 egg clusters had similar survival in Pac-6, Juan de Fuca, G.S.-1, and Indian Arm deep waters.

This study has therefore shown that sea waters with similar salinities may vary in quality. Whether these differences are

biologically detectable depends largely upon the test organism which is used as a bioassay. Secondly, P. elongata egg clusters collected from different areas may be distinct in their response to salinity, and in their response to the other properties of sea waters. Whether or not P. elongata living in areas such as Indian Arm and G.S.-1 are significantly affected by variations in water quality will be discussed in the final section of this thesis.

There are no data to suggest that areas such as Juan de Fuca Strait and the eastern sub-arctic Pacific Ocean, which consistently had relatively small populations of P. elongata, have waters whose properties are unfavourable for the survival of the egg (collected from or near these areas). This supports the results of the survey cruises (section 3), which indicated that the relatively small populations in these areas were probably associated with low primary production.

CHAPTER IV

AN EVALUATION OF THE ROLE OF THE VARIATION IN WATER QUALITY IN THE DISTRIBUTION OF P. ELONGATA AT INDIAN ARM AND G.S.-1

INTRODUCTION

The data in Chapter II indicated that P. elongata was capable of breeding both in the oceanic and the neritic waters examined by the three survey cruises. This suggests that the species is probably not limited in these areas by variations in the quality of natural sea waters. However, the laboratory data (Chapter III) indicated that within areas such as Indian Arm, the survival of egg clusters in their home water varied over a 12-month period. As the abundance of the species is, in part, dependent upon the survival of the egg clusters, local variations in water quality may affect the abundance of local populations.

Gilfillan (1970) showed that the zooplankter Euphausia pacifica was sensitive to variations in water quality. However, he indicated that variations in water quality were probably not a major limiting factor in the distribution of the species.

Wilson (1951) and Wilson and Armstrong (1952, 1954, 1958, 1961) showed, by using sea urchin larvae collected near Eddystone, that there were variations in the quality of sea waters. While they attempted to determine the sources of the variation within the test waters, they did not attempt to evaluate the significance of this variation in the ecology of sea urchins near Eddystone. Sea water collected from Eddystone gave poor survival over the 12-year study period (1948 to

1960) and yet there was no apparent decline in the size of the adult sea urchin population. Smith (1972) estimated that echinoderm populations turnover at a range of 0.1 to 1.6 per year. An application of this estimate to the sea urchin population near Eddystone indicates that, over the 12-year study period, the population was replaced 1.2 to 9.2 times. As the size of the population did not diminish, variations in the quality of sea water (or larval quality) at Eddystone as determined in the laboratory must have had a minor role in affecting the local abundance of sea urchins.

This section investigates whether or not variations in water quality were a significant factor in determining the abundance of P. elongata in G.S.-1 and Indian Arm. As temperature and salinity have been used to describe water bodies, fluctuations in the temperature and salinity of the water in an area may be indicative of changes in the 'quality' of the water. If the species is affected by variations in the quality of sea water, then there might be some relationship between fluctuations in the species' distribution and fluctuations in the temperature and salinity of the water. This does not imply that temperature and salinity act directly on the species, but rather, that these measurements may be indicative of some fluctuating environmental variable (water quality) that is less easily measured.

This chapter also attempts to determine what other variables might be important in regulating the abundance of P. elongata in G.S.-1 and Indian Arm. It was shown, in Chapter III, that there were no significant differences in the survival of G.S.-1 egg clusters in G.S.-1 350-m water over the 12-month study period. However, the field data

indicated that there were pronounced fluctuations in the number of nauplii in the water. This suggests that variables other than water quality may be more important in regulating the abundance of nauplii at this station.

Materials and Methods

The methods for the collection of the field data have been described earlier (Chapters I and II), as have been the techniques for estimating the abundance and vertical distribution of the developmental stages (Chapter II). The field data were examined in the following ways:

(1) The vertical distribution of the developmental stages were examined, and were subjectively compared with the changes in the temperature and salinity of the water.

(2) The variation in the abundance of the developmental stages were examined over the 29-month study period to determine whether or not the species was more abundant at some times than others.

(3) The correlation coefficient between the number of nauplii in the water and (i) the survival of the egg in its home water as determined in the laboratory, and (ii) the number of eggs in the water was calculated. The estimate of the number of eggs was obtained by multiplying the number of egg clusters in a 1-m^2 column of water (Clarke-Bumpus sampler data) by the mean number of eggs per cluster (laboratory data).

(4) The mean percentage mortality of the developmental stages was calculated by estimating the mean concentration of each stage over the 29-month study period, and comparing these estimates with the mean number expected. The mean number expected was calculated by estimating the proportion of the population each stage should represent simply on the basis of the time spent in that stage relative to the total time of the life cycle. The data for the development time of the egg and the six naupliar stages are from Borgmann (1971). The first and second copepodites require three to four weeks to complete development (Ramnarine, pers. comm.; pers. obser.), and an estimate of three to four weeks can be used for the other three copepodite stages. The average time spent in each of these stages is shown in Table 14. The laboratory studies indicate that the adult male and female can survive for at least three months (Ramnarine, pers. comm.; pers. obser.). From these data, the mortality between stages, and the cumulative mortality from the egg to the adult can be calculated. The number of nauplii and successive stages expected were also recalculated with the assumption that 30.5% of the G.S.-1 eggs and 38.5% of the Indian Arm eggs failed to hatch owing to their interaction with their home water. This estimated mean mortality was obtained from the laboratory study (Chapter III). The recalculation of these data allows the cumulative mortality from the egg to the adult to be estimated with an allowance being made for the mortality due to the interaction between the egg and the water. These calculated mortalities are therefore due to other environmental stresses such as food limitation and predation.

TABLE 14. The estimated mean time spent in each of the developmental stages of P. elongata, the percent of the total spent in each stage, and the time spent in each stage relative to the time spent in the egg and first nauplius.

Stage	Time (days)	% of Total	Relative to egg + N-1
Egg + N-1	7	2.9	1
N-2 to N-6	19	7.9	2.7
C-1	25	10.4	3.6
C-2	25	10.4	3.6
C-3	25	10.4	3.6
C-4	25	10.4	3.6
C-5	25	10.4	3.6
C-6	90	37.3	
Total	241		

(5) The stability of the measured biological, chemical, and physical variables was estimated. Leigh (1971) states that "a system is stable if it returns to equilibrium when disturbed; the stabler the system, the more quickly equilibrium is restored." Patten (1961, 1962), while not formally defining stability, obtained a quantitative value for the stability of the system where

$$\text{Stability} = \frac{\sum_{j=1}^{n=1} \det P_j}{\sum_{j=1}^{n=1} (s/\bar{x})_j} .$$

s_j is the standard deviation for the jth variable and $\bar{x}$ is the mean of the jth variable,

and $$P_j = \begin{bmatrix} P_{id} & P_{ii} \\ P_{dd} & P_{di} \end{bmatrix}$$ which is the matrix of transition probabilities for the jth of m variables. For a series of measurements,

P_{id} = probability of an increase followed by a decrease

P_{ii} = probability of an increase followed by an increase

P_{dd} = probability of a decrease followed by a decrease

P_{di} = probability of a decrease followed by an increase

and Det $P_j = (P_{id} P_{di} - P_{ii} P_{dd})$.

The biological data used in the analysis were the abundance of the developmental stages of P. elongata at Indian Arm and G.S.-1 over the 29-month study period. The physical data were the temperature, and

salinity of the water at a number of depths. These were 0, 10, 75, 100, 150, and 200 m at Indian Arm and G.S.-1, and 250 and 350 m at G.S.-1. The chemical data were the concentrations of dissolved zinc, manganese, copper, and nickel in Indian Arm 200-m water and G.S.-1 350-m water. The analysis was made by using the IBM 1130 computer.

Results

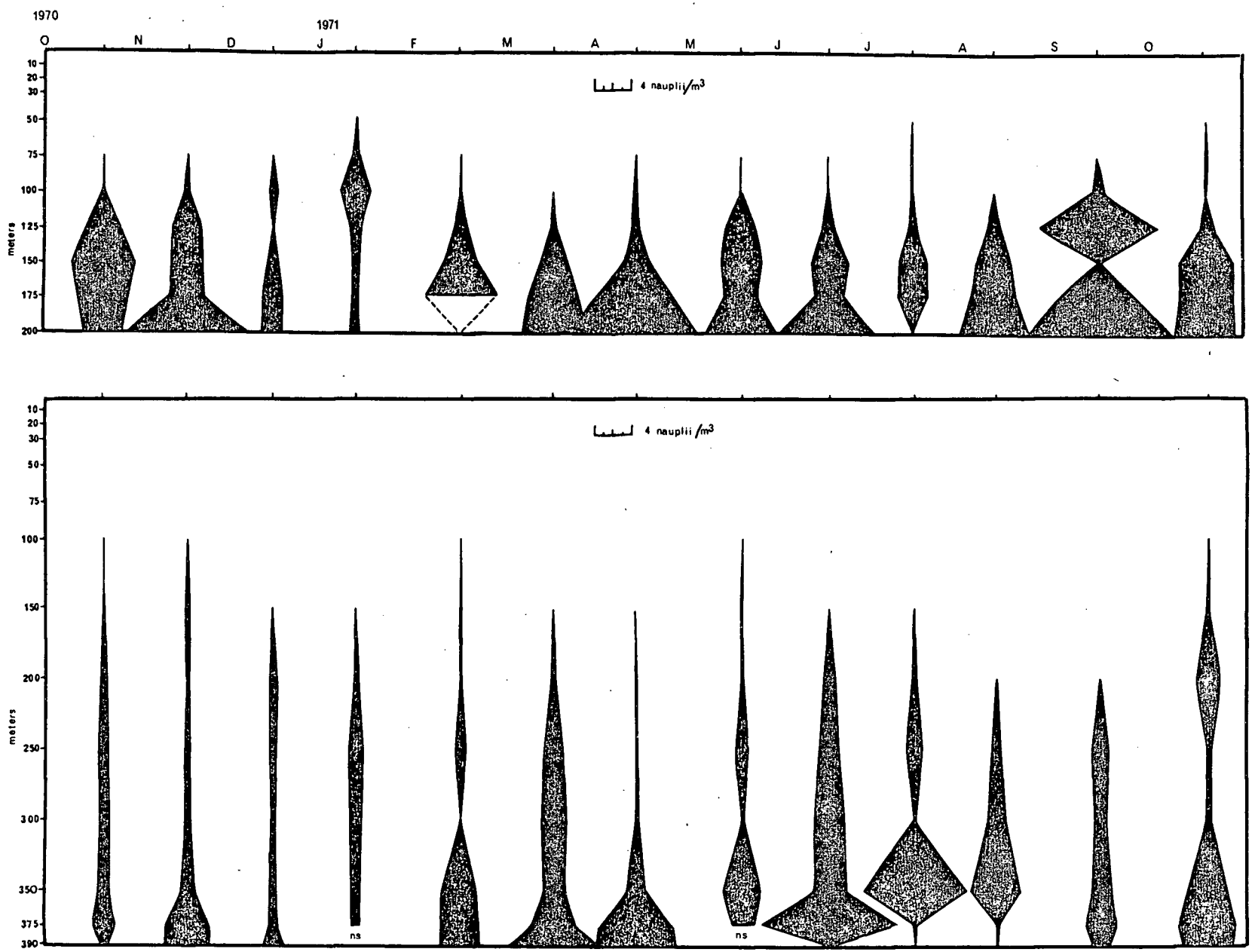
(i) The vertical distribution of the nauplius and the third copepodite at Indian Arm and G.S.-1 from October 1970 to October 1971

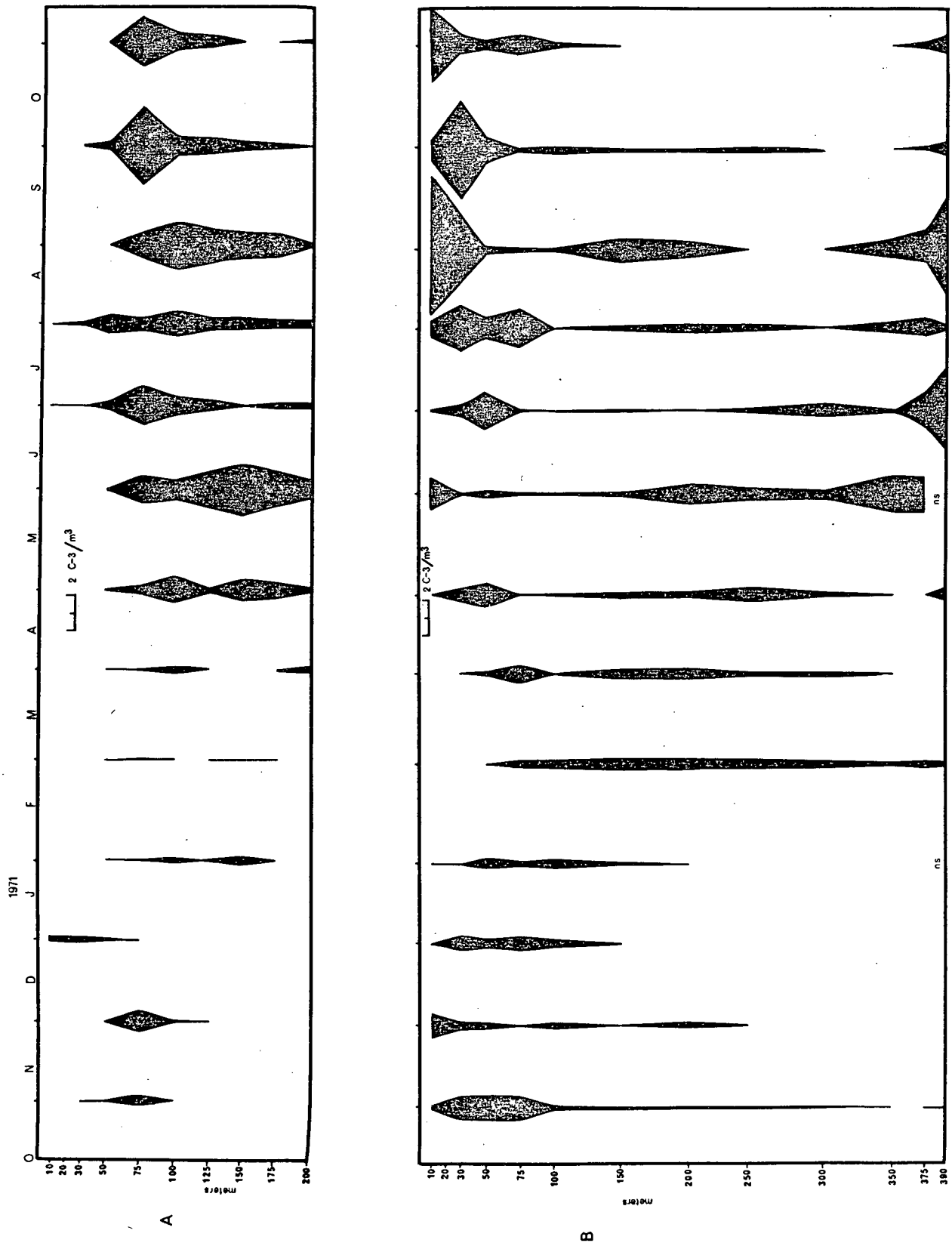
As the vertical distributions of the developmental stages were similar over the study period, only the data for the second year of the study (October 1970 to October 1971) are presented. This year was chosen because of the greater changes which occurred in the temperature and salinity of the deep water than in the preceding year. Only the vertical distribution of the nauplius and the third copepodite are presented as this is sufficient to illustrate the trends.

Figure 7 shows the vertical distribution of the nauplius at G.S.-1 and Indian Arm. At each station, the nauplii were found deep and were seldom above 100 meters. Over the years, the vertical distribution was essentially the same (although the abundance varied), and was not affected by changes in the temperature and salinity of the deep water (Figure 3). Although the deep water at both stations was replaced, the vertical distribution of the nauplius remained unchanged.

The third copepodite was found through a large portion of the water column, although it was found nearer to the surface at G.S.-1

Figure 7. The vertical distribution of the nauplius and the third copepodite at Indian Arm (a) and at G.S.-1 (b). Broken lines indicate an uncertain datum point. (ns) indicates that no sample was collected from that depth.


1970
1971
O
N
D
J
F
M
A
M
J
J
A
S
O
A
B
meters
10
20
30
50
75
100
125
150
175
200
4 nauplii/m³
4 nauplii /m³
100
150
200
250
300
350
375
390
ns
ns


1971
O
N
D
J
F
M
A
M
J
J
A
S
O
2 C-3/m³
meters
10
20
30
50
75
100
125
150
175
200
A
2 C-3/m³
ns
ns
meters
10
20
30
50
75
100
150
200
250
300
350
375
380
B

than at Indian Arm. However, the former station was always occupied during the day, and the latter was always occupied during the night. As the third copepodite may be found nearer to the surface at night than during the day (Pandyan 1971; pers. obser.), these differences may be accounted for by considering the time of sampling. The vertical distribution of the third copepodite was not affected by changes in the temperature and salinity (and other properties) of the water. Nor was the vertical distribution altered at the time of deep water replacement at both stations (Figure 3).

(ii) Temporal variation in the abundance of the developmental stages of P. elongata at G.S.-1 and Indian Arm.

Figure 8 presents the data showing the temporal variations in the total number of P. elongata (excluding the egg) at G.S.-1 and Indian Arm during the study period. The species was abundant during the spring, summer, and autumn, was low in numbers in the winter, and was possibly less abundant in 1971 than in 1970. There is no evidence that the deep water replacement at either G.S.-1 or Indian Arm resulted in a marked reduction in the number of P. elongata.

The 'new' deep water at G.S.-1 was formed in the San Juan Archipelago, and this latter area is characterized by relatively small populations of P. elongata. The 'new' deep water at Indian Arm was formed from surface and near-surface waters in the vicinity of the shallow sill (26 m) at the mouth of the inlet, and this area is probably also characterized by relatively small populations of P. elongata.

The failure of the populations to be reduced at either G.S.-1 or Indian Arm at the time of deep water replacement supports the hypothesis that, within these areas, deep water replacement occurs at a slow enough rate for the species to retain its vertical position in the water column, and so reduces the tendency for the species to be lost from the area with the older deep water.

Nauplii and the first four copepodite-stages were most abundant during the spring, summer, and early autumn, and were less abundant during the late autumn and the winter. There was no apparent seasonal trend in the abundance of the fifth and sixth copepodites at G.S.-1. At Indian Arm, these stages were less abundant in the spring and early summer.

The number of egg clusters varied throughout the year, and were more numerous at G.S.-1 during the spring. Egg clusters were possibly more numerous at Indian Arm during the late summer and autumn.

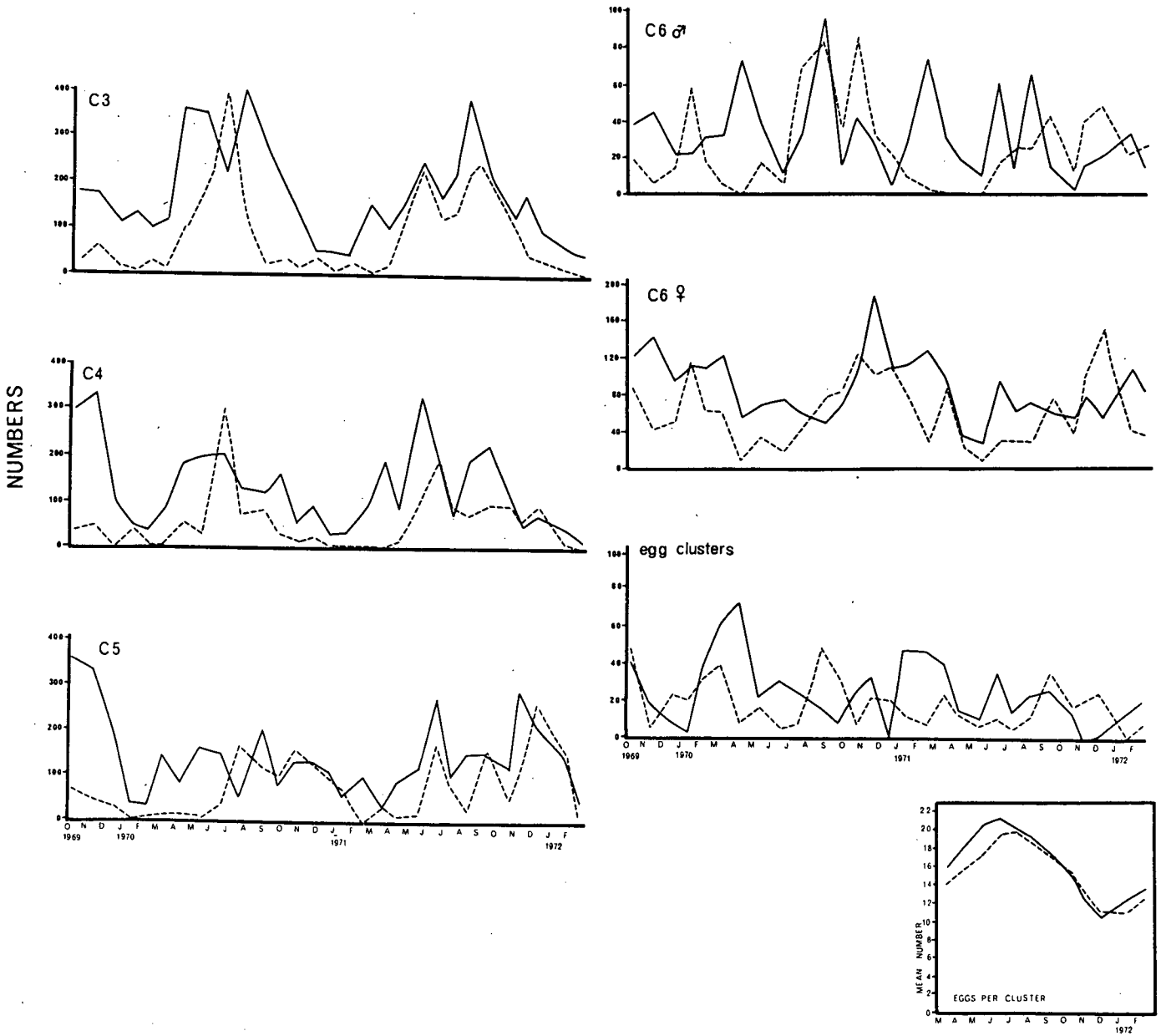
The number of eggs per cluster varied through the year, with clusters containing the fewest eggs in the winter and the most during the summer. Increases in the number of eggs per cluster occurred at the same time at Indian Arm and G.S.-1. However, Indian Arm egg clusters tended to have fewer eggs than G.S.-1 egg clusters.

(iii) Correlation between the number of nauplii and (i) the survival of the egg, and (ii) the number of eggs in the water

The number of nauplii at G.S.-1 was not significantly correlated with the survival of G.S.-1 eggs in G.S.-1 350-m water ($r = .25$;

Figure 8. The estimated number of the developmental stages of P. elongata in the water column at G.S.-1 (10-390m) (_____), and at Indian Arm (10-200m) (.....). The estimate of the total number of P. elongata includes only the naupliar and copepodite stages. The data for the mean number of eggs per cluster were calculated from the laboratory data.

Total
P. elongata
C1
nauplii
C2
NUMBERS
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F
1969
1970
1971
1972


NUMBERS
C3
C4
C5
C6 ♂
C6 ♀
egg clusters
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F
1969
1970
1971
1972
MEAN NUMBER
EGGS PER CLUSTER
M A M J J A S O N D J F
1972

$p > .1$) but was significantly correlated with the number of eggs ($r = .76$; $p < .005$). Similarly, the number of nauplii at Indian Arm was not significantly correlated with the survival of Indian Arm eggs in Indian Arm 200-m water ($r = -.17$; $p > .1$) but was significantly correlated with the number of eggs ($r = .79$; $p < .005$). This indicates that the number of nauplii at G.S.-1 and at Indian Arm were not significantly affected by the interaction between the egg and the native water (as measured in the laboratory), but were affected by processes which affect egg production. This may be because variations in the survival of eggs during the study period were very much smaller than the variations in the numbers of eggs produced during the study period.

(iv) The estimated mean mortalities of the developmental stages of *P. elongata* at G.S.-1 and Indian Arm

Table 15 shows, for G.S.-1 and Indian Arm, (i) the mean number of the developmental stages, (ii) the estimated mean mortality between stages, (iii) the estimated mean cumulative mortality from the egg to the adult, and (iv) the estimated mean cumulative mortality from the egg to the adult excluding the estimated mortality of the egg due to its interaction with the water. High mortality between stages occurred at G.S.-1, between the egg and the first nauplius and the second to sixth nauplius (68.5%), between the second and third copepodites (52.4%), and the fifth and sixth copepodites (76.3%). No valid estimate was made for the mortaility between the first and second copepodites, and

TABLE 15. The mean number of the developmental stages during the 29-month study period in a 1-m^2 column of water at G.S.-1 (10-390m) and at Indian Arm (10-200m), (ii) the estimated mean mortality between successive stages, (iii) the estimated mean cumulative mortality from the egg to the adult, and (iv) the estimated mean cumulative mortality from the egg to the adult excluding the possible mortality due to the interaction between the egg and the water.

Stage	Mean Number	Percentage Mortality		
		Between Stages	Cumulative (iii)	Cumulative (iv)
G.S.-1				
Egg + N-1	408			
N-2 to N-6	357	68.5	68.5	53.2
C-1	308	33.1	78.9	68.7
C-2	363	x	x	x
C-3	173	52.4	88.2	82.4
C-4	129	25.5	90.4	86.9
C-5	140	x	x	x
C-6	120	76.3	97.8	96.7
Indian Arm				
Egg + N-1	292			
N-2 to N-6	385	51.1	51.1	20.2
C-1	213	58.1	79.5	66.5
C-2	155	27.3	85.1	75.6
C-3	80	48.4	92.3	87.5
C-4	55	31.3	94.7	91.4
C-5	78	x	x	x
C-6	88	68.8	97.7	96.2

the fourth and fifth copepodites. The cumulative mortality from the egg to the adult was 97.8% with only 2.2% of the eggs maturing to the adult stage. If the mortality of the egg due to its interaction with the water is removed from this estimate, 3.3% of the eggs which are successful in hatching reach the adult stage.

Table 15 also shows the calculation for Indian Arm. High estimated mortality between stages occurred between the egg and the first nauplius and the second to the sixth nauplius (58.1%), the second and third copepodites (48.4%), and the fifth and sixth copepodites (68.8%). No valid estimate was made for the mortality between the fourth and fifth copepodites, possibly because a longer time is spent in the fifth copepodite than estimated. The cumulative mortality from the egg to the adult stage was 97.7% with only 2.3% of the eggs reaching the adult. This was similar to the estimate for the cumulative mortality from the egg to the adult at G.S.-1. If the mortality of the egg due to the interaction with the water is removed from this estimate, 3.8% of the eggs which are successful in hatching reach the adult stage.

(v) Stability Analysis

Tables 16 and 17 present the determinants, the mean variabilities, and the stability indices for the biological, chemical, and physical variables measured at G.S.-1 and Indian Arm. The physical variables were generally characterized by negative determinants and negative

TABLE 16. The analysis of stability of the biological, chemical, and physical variables measured at G.S.-1

Variable		Determinant	Mean Variability	Stability Index
Egg clusters		-0.03	00773	0.04
Nauplii		0.04	0.69	0.06
C-1		0.34	0.63	0.54
C-2		0.12	0.58	0.21
C-3		0.23	0.60	0.38
C-4		0.11	0.70	0.16
C-5		0.23	0.61	0.38
C-6		0.26	0.38	0.63
Total biological				0.24*
Copper		-0017	0.37	-0046
Nickel		0.27	0.26	1.04
Manganese		0.60	0.58	1.03
Zinc		0.25	0.61	0.41
Total chemical				0.52*
Temperature	0-m	-0.35	0.40	-0.88
Salinity	"	-0.15	0.14	-1.07
Temperature	10-m	-0.38	0.25	-1.52
Salinity	"	0.00	0.06	0.00
Temperature	75-m	-0.15	0.09	-1.67
Salinity	"	0.08	0.01	8.00
Temperature	150-m	-0.14	0.07	-2.00
Salinity	"	-0.03	0.01	-3.00
Temperature	200-m	-0.28	0.05	-5.60
Salinity	"	-0.31	0.004	-77.50
Temperature	250-m	-0.12	0.04	-3.00
Salinity	"	-0.46	0.003	-153.53
Temperature	350-m	-0.07	0.03	-2.33
Salinity	"	-0.58	0.003	-193.33
Total physical				-2.53*

*Obtained by dividing the sum of the determinants by the sum of the mean variabilities (Patten 1963).

An examination of Patten's analysis of stability is presented in the appendix.

TABLE 17. The analysis of the stability of the biological, chemical, and physical variables measured at Indian Arm

Variable		Determinant	Mean Variability	Stability Index
Egg Clusters		0.41	0.69	0.59
Nauplii		0.12	0.72	0.17
C-1		0.16	0.77	0.21
C-2		0.17	0.99	-0.17
C-3		0.12	1.17	0.10
C-4		0.28	1.20	0.23
C-5		0.20	0.84	0.24
C-6		0.04	0.63	0.06
Total biological				0.17*
Copper		0.60	0.51	1.17
Nickel		0.40	0.41	0.98
Manganese		0.50	0.57	0.88
Zinc		0.60	0.64	0.94
Total chemical				0.99*
Temperature	0-m	-0.18	0.43	-0.42
Salinity	"	0.60	0.47	1.28
Temperature	10-m	-0.55	0.18	-3.06
Salinity	"	-0.31	0.04	-7.75
Temperature	75-m	-0.26	0.09	-2.89
Salinity	"	-0.48	0.01	-48.00
Temperature	150-m	-0.18	0.07	-2.57
Salinity	"	-0.10	0.01	-10.00
Temperature	200-m	0.14	0.08	1.75
Salinity	"	-0.21	0.01	-21.00
Total physical				-1.10*

*Obtained by dividing the sum of the determinants by the sum of the mean variabilities (Patten 1963).

stability indices. Conversely, the biological variables were characterized by positive determinants and positive stability indices (with the exception of the number of egg clusters at G.S.-1, and the number of second copepodites at Indian Arm). The overall stability of the measured biological system was greater than that of the measured physical system, suggesting that the biological system was relatively insensitive to the physical system. Patten (1961, 1962) also measured a higher stability of the biological system over that of the physical system.

The chemical variables were (with the exception of copper in G.S.-1 350-m water), characterized by positive determinants and positive stability indices. The overall stability index was higher than that for the physical system, again suggesting that the measured chemical system was relatively insensitive to the measured physical system.

Conclusions

There was no indication that variations in the temperature and salinity of the deep water, and variations in water quality were important in determining the abundance of P. elongata at Indian Arm and G.S.-1. At both stations, the number of nauplii in the water was significantly correlated with the number of eggs present in the water, but not with the survival of the eggs due to their interaction with the water.

The estimated mean mortality from the egg to the adult stage was 97.8% at G.S.-1 and 97.7% at Indian Arm. If the mortality of the

egg due to the interaction between the egg and the water is removed from these estimates, the mortality from the egg to the adult becomes 96.7% at G.S.-1 and 96.2% at Indian Arm. This indicates that there is a large mortality (or loss) of the developmental stages after the nauplius hatches, and again suggests that the interaction between the egg and the water has only a minor role in determining the abundance of P. elongata at Indian Arm and G.S.-1.

The vertical distribution of the nauplius and the third copepodite at Indian Arm and G.S.-1 was similar throughout the study period. This would not be expected if (i) variations in the temperature and salinity of the deep water were associated with variations in the quality of the water, and (ii) these variations in the quality of the water affected the developmental stages.

While the vertical distribution of the developmental stages was similar throughout the study period, there were pronounced fluctuations in their abundance. The species was most abundant during the spring, summer, and early autumn. This is the period in which primary production is highest both at Indian Arm (Gilmartin 1964) and at G.S.-1 (Parsons et al. 1970). This relationship between increases in the number of P. elongata and increases in primary production suggest that environmental variables associated with primary production may be important in regulating the abundance of the species in these two areas. These variables may be associated with the availability of prey organisms and predation.

Many zooplankton breed at those times of the year when primary production is greatest. The increase in the primary production of the surface water in the Strait of Georgia is also associated with an increase in secondary production (Parsons et al. 1970). This increase in secondary production may provide more prey organisms for the carnivorous copepodite stages of P. elongata. Secondly, there may be a reduction of the predation pressure on the nauplii and the copepodites, which are, in the main, found below the surface layer, where the highest primary and secondary production occurs.

In the autumn and winter, there is a reduction in the primary and secondary production in the surface water (Parsons et al. 1970), and at these times the developmental stages may be food limited. Secondly, the predation pressure on these stages may be increased if predators are no longer able to obtain sufficient food in the surface layer. There is also an increase in the concentration of carnivorous zooplankton such as Sagitta elegans and Tomopteris septentrionalis at this time (Stephens et al. 1969), which may also increase the predation pressure on the developmental stages of P. elongata.

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APPENDIX

THE GENERIC NAME AND SPECIES NAME OF THE STUDY ORGANISM

It was apparent from the literature that there is some disagreement over the generic and species name of the study organism. It is the purpose of this appendix to present an unbiased picture of the arguments for and against each name, and then to give the reasons why the final name was chosen. However, only detailed laboratory studies can determine whether or not the genus Pareuchaeta is valid, and whether or not the species elongata and japonica are so genetically distinct as to constitute separate species.

(1) Genus Euchaeta or Pareuchaeta?

The first genus of the family Euchaetidae, Euchaeta marina (Prestandrea), was established by Phillippi in 1882 (Scott 1909). In the following years, the genera Valdivella, Pseudeuchaeta, and Pareuchaeta have been added to the family (Brodsky 1950). There are at least eighty-five species within the family, of which one belongs to the genus Pseudeuchaeta, eight to the genus Valdivella, nineteen to the genus Euchaeta, and fifty-seven to the genus Pareuchaeta.

The genus Pareuchaeta was established by Scott (1909) who used, as distinguishing characteristics, the armature of the second maxilla in the adult female, and the structure of the fifth leg in the male. In Euchaeta, some of the spines on the apex of the second maxilla are equipped with long spinules; in Pareuchaeta, the spines are equipped with short spinules. In the adult male Euchaeta, the

third segment of the exopodite of the left fifth leg is long and spinform; in Pareuchaeta, it is short and rudimentary. Scott (1909) identified twelve species of the genus Pareuchaeta and seven of the genus Euchaeta by using these two characteristics.

Sars (1925, in Sewell 1929) agreed with the establishment of the genus Pareuchaeta, and added a third distinguishing characteristic based on the structure of the accessory setae of the furcal rami. In Euchaeta, these setae are more strongly developed than the other furcal setae; in Pareuchaeta, these setae are quite slender, and form a 'knee-joint' a short distance past their point of origin.

Brodsky (1950) and Tanaka (1958) also accepted the validity of the genus Pareuchaeta although each used only two of the three distinguishing characteristics. Brodsky (1950) used the structure of the left fifth leg in the male, and the caudal rami. Tanaka (1958) used the structure of the left fifth leg in the male, and the second maxilla. While the above used only two of the three distinguishing characteristics, they gave no indication that they considered the third invalid.

Veervoot (1963) did not accept the validity of the species Pareuchaeta. He found that it was equally possible to divide the thirteen Euchaeta-Pareuchaeta species he examined into five groups which would probably not deserve any more than a sub-generic rank. However, three of his groups contain only Euchaeta species, and the remaining two contain only Pareuchaeta species (according to the above who recognize the genus Pareuchaeta). In effect, Veervoot used certain

characteristics to divide the species into two groups which could be further subdivided.

Sewell (1929) also found it possible to further subdivide the genus Euchaeta (into two groups), and the genus Pareuchaeta (into four groups). Secondly, he acknowledged that there was at least one species of those he examined which was intermediate in character to Euchaeta and Pareuchaeta, but he believed that this species was a connecting link between the two genera. It is probable that there are several such intermediates and, that with a thorough study of the morphology of the family Euchaetidae, their role in the phylogeny of the family will be better understood.

Veervoot examined thirteen of the known seventy-six species of Euchaeta and Pareuchaeta and concluded that the separation of the species into two genera was not justified. Conversely, Scott (1909), Sewell (1929), Brodsky (1950), and Tanaka and Omori (1968) examined fifty-nine of the known seventy-six species and concluded that the separation was valid. As the latter group have examined a more representative sample of the family Euchaetidae, it was decided to accept their classification of Euchaetidae. Therefore, the genus Pareuchaeta is accepted as being valid.

Brodsky (1950) and Tanaka and Omori (1968) have both placed the study organism in the genus Pareuchaeta. The structure of the second maxilla (Campbell 1934), the male fifth leg (Campbell 1934), and the caudal furci (pers. obser.) indicate that the study organism belongs to the genus Pareuchaeta, and that it is not an intermediate form.

(2) Species japonica or elongata?

In 1913, Esterly identified a new species, Euchaeta elongata, from the San Diego region. The specimen, an adult female 4.13 mm in length, was characterized by the blunt projection on the side of the last thoracic segment, the asymmetric genital protuberance, and the structure of the first and second pairs of feet.

In 1921, Marukawa described a new species from the Sea of Japan, using the same identifying characteristics as Esterly (1913). However, the adult females was larger, being 8 mm in length. Marukawa named the species japonica.

It is apparent, from the literature, that the species name japonica has been accepted by certain authors over that of elongata, and yet none of the reasons given are satisfactory. Wailes (1929) identified E. japonica from the Strait of Georgia, but was apparently unaware of Esterly's original description of elongata. Campbell (1929) captured E. japonica from Deep Cove, Rocky Bay, Sherington, and Seaside Park. She noted that her specimens differedtslightly in the structure of the second foot from Marukawa's descriptions, and that Vancouver Island region specimens were only 5 to 6.3 mm in length. While she assigned the species name japonica to her specimens, she was aware of Esterly's description and concluded (Esterly (1913) seems to have described the same species (as Marukawa)." In a later paper (1934), Campbell was less certain as to whether or not elongata and japonica were, in fact, two forms of the same species.

Brodsky (1959) noted the occurrence of a species which he called P. japonica in the Sea of Ohkotsk, and the Sea of Japan, the Bering Sea, and the northwest Pacific Ocean. He was aware of Esterly's description and stated "this species (japonica) is identical to P. elongata of Esterly."

Tanaka and Omori (1968) noted the occurence of P. elongata from the Izu region of Japan, and state that Esterly's elongata and Marukawa's japonica are synonomous. Morris (1970) collected E. elongata from the sub-arctic Pacific Ocean, and agrees that elongata and japonica are synonomous species (pers. comm.).

Davis (1949) captured specimens of E. japonica from off the mouth of Juan de Fuca Strait and from the Portland Canal. He concluded that these specimens were distinct from Esterly's elongata because of qualitative differences in the species. His specimens were 5.4 to 6.4 mm in length in comparison to 4.13 mm of Esterly's elongata. There were also qualitative differences in the frontal papilla, and the concavity of the border of the exopod of the first leg.

The validity of Davis' arguments (1949) are hard to accept. First, he believes that his specimens and Esterly's are distinct species because they differ in size. However, his specimens were intermediate in size to Marukawa's japonica and Esterly's elongata, and so were similar to neither holotypes.

It is well documented in the literature that a species can mature to different sizes. Species living in the same area may, for example, exhibit different sizes at maturity. Campbell (1929)

measured adult female E. japonica as being 5.0 to 6.3 mm in length, Fulton (1968) measured adult females as being 6.3 to 6.5 mm in length, and Pandyan (1971) measured adult females as being 4.4 to 5.99 mm in length. These specimens were all captured from the Strait of Georgia or its surrounding waters.

A species may exhibit different sizes at maturity in different parts of its range (Deevy 1966; McLaren 1965). McLaren (1963, 1965) showed that Pseudocalanus minutus living in different areas attained sizes at maturity which could be correlated with the temperature of the water in which the species was living and with possible physiological differences within the species.

Davis (1949) accepted the differences in the structure of the second foot between his specimens and Marukawa's, but did not accept the differences in the structure of the first foot and the frontal papilla between his specimens and Esterly's. In both cases, the differences were qualitative rather than quantitative. There is ample evidence in the literature of morphological variation within a species in different parts of its range. Brinton (1962) observed morphological variations within two species of Euphausiids in different parts of their range. Morphological variation within a species does not mean, a priori, that the variants are distinct species-only extensive studies can resolve this. In the case of elongata-japonica, this kind of study has not been done, and so there is no valid reason for considering the species distinct. As Esterley's (1913) description was

the original, his species name is accepted. It is concluded that the study organism should be called Pareuchaeta elongata.

AN EXAMINATION OF PATTEN'S ANALYSIS OF STABILITY

Patten's (1961, 1962) analysis of stability is of interest as it attempts to quantitize fluctuations in the variables of an ecosystem. Several criticisms can be made of Patten's analysis. The major criticism stems from the fact that 'stability' can be defined in several ways, and so be applied to quite different systems. For the purposes of this discussion, they will be called statistically stable and physically stable systems.

A system in which the measured variable does not fluctuate with time is a static system. A statistically stable system is one in which the measured variable remains, in theory, constant with time, but, due to sampling error, fluctuates in a random direction about the mean value. For example, an experiment could be conducted in which the same coin was tossed one hundred times and the number of 'heads' recorded. This could be repeated several times, and the data plotted with the number of 'heads' recorded at the end of each experiment on the Y-axis, and the experiment number on the X-axis. The data would be described by the line y=50, and the actual data points would be scattered randomly about that line. This system is stable in that the variable 'number of heads' remains statistically constant with time, and the data fluctuates in a random direction about the mean value.

Conversely, a system in which the measured variable fluctuates in a predictable and cyclic direction about the mean with time is physically stable. For example, the swing of a pendulum is

a physically stable system. Therefore, to state that a system is stable is ambiguous unless the type of stability is described.

There is a tendency among ecologists to consider a physically stable system as being ecologically instable, and a statistically stable system as being ecologically stable. For example, Dunbar (1960), in discussing the stability of the marine environment, based his arguments on the premise that " oscillations are bad for any system and that violent oscillations are often lethal." In this paper, he discussed the variables which dampen oscillations (ie increase the trend towards a static or statisticallly stable system), and increase the ecological stability of that ecosystem.

Patten (1961, 1962) failed to describe what he meant be 'stability'. From his 1961 paper, it is suggested that he considered a physically stable system to be ecologically instable, and a system which fluctuates less about the mean over the same time interval to have a greater ecological stability. However, Patten failed to recognize that the system with the highest ecological stability is a statistically stable system and, because of this, made several errors in deriving his index.

Patten (1961) derived the stability index empirically, and the assumption of which he based the index is incorrect. Patten stated " if all the variables of an ecosystem were random variables, randomly sampled, then each variable might be regarded as most stable if and when the probablity for an increase in value when low

and for a decrease in value when high were unity." This is incorrect. In a statistically (and ecologically) stable system, the probability of a low value followed by a high is 0.5, and the probablity of a low value followed by another low is 0.5. Similarly, the probability of a high value followed by another high is 0.5, and the probability of a high value followed by a low is 0.5.

Patten (1961) derived a stability measure, σ, for the determinant of P, where

$$P = \begin{bmatrix} p_{id} & p_{ii} \\ p_{dd} & p_{id} \end{bmatrix} \qquad \text{(as on page 75)}$$

When $\sigma>0$, the system, according to Patten, is stable. The greatest ecological stability is when $\sigma=1$, ie, $p_{id}=p_{di}=1$, and $p_{ii}=p_{dd}=0$. Thus, a system in which an increase is followed by a decrease, and then by an increase, etc, is stable. However, this is a physically stable system in which fluctuations in direction about the mean are cyclic and predicatble. The system does not possess statistical stablity and is therefore ecologically instable.

When $\sigma=0$, the system, according to Patten, has null stability. This value is applicable to three systems. In a static system, $p_{id}= p_{di}= p_{ii}=p_{dd}=0$. In a statistically stable system, $p_{id}=p_{di}=p_{ii}=p_{dd}=0.5$. Patten predicts that both these systems have null stability, and are less stable than the above system in which the variables fluctuate

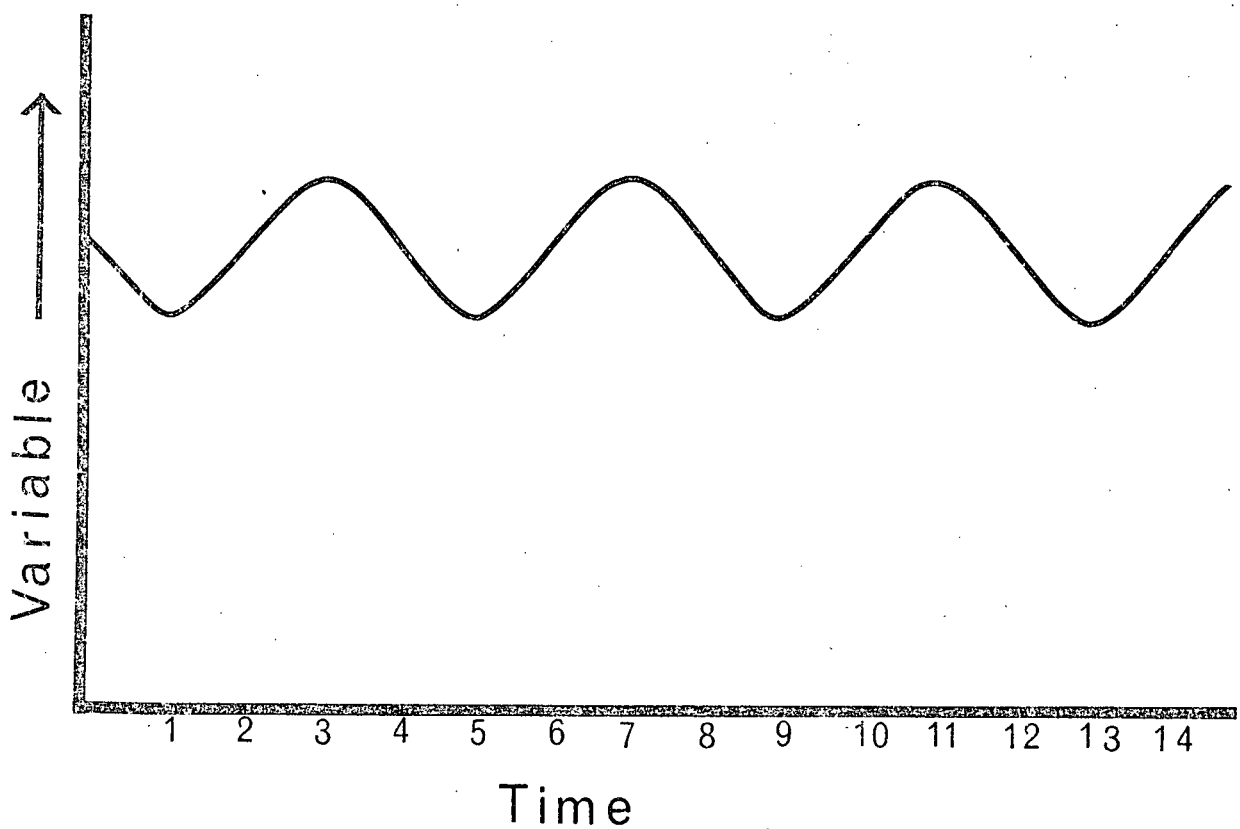
in a less random manner. This is incorrect, as the greatest ecological stability occurs when the measured variable remains constant with time, or else fluctuates in a random manner.

A null stablity is also obtained if the measured variable increases (or decreases) continuously with time, ie, $p_{ii}=1.0$, and $p_{dd}=p_{id}=p_{di}=0$. Thus, Patten's stability index fails to distinguish between a system in which the variable is constant, or varies in a random manner, and between a system in which the variable increases (or decreases) continuously with time. It is also obvious that a variable which does not approach an equilibrium value is instable (both statistically and physically), and does not possess a null stability.

When $\sigma<0$, the system, according to Patten, is instable. The greatest instability occurs when $p_{ii}=p_{dd}\rightarrow 1$, and $p_{id}=p_{di}\rightarrow 0$, and $\sigma\rightarrow -1$. This type of system is a physically stable system in which the variable fluctuates in a cyclic and predicatable direction with time. A critical examination of Patten's analysis indicates that there is no difference in the stability of a system when $\sigma=1$, and $\sigma=-1$ for, in both systems, the fluctuations are cyclic and are predictable in direction, rather than being random.

A second limitation to Patten's anaylsis is that it is sensitive to sampling frequency. Figure 9 shows a system in which an environmental variable fluctuates in a cyclic manner with time, ie the system is physically stable (but ecologically instable).

Figure 9. A hypothetical system in which the measured variable has physical stability.


Variable
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Time

Depending on when the variable is measured, at least three different values of σ can be obtained.

(i) if measurements are made only at t=1,5,9, etc, or t=2,6,10, etc, or t=3,7,11,etc, then $\sigma=0$. According to the analysis, and with the available data, the system has null stability.

(ii) if measurements are made only at t= 1,3,5,7,etc, then $\sigma=1$ as $p_{id}=p_{di}=1$, and $p_{ii}=p_{dd}=0$. According to the analysis, the system is stable (ecologically).

(iii) if many measurements are made during each cycle, then as the sampling frequency increases, $\sigma \to -1$, as $p_{ii}=p_{dd} \to 1$, and $p_{id}=p_{di} \to 0$. According to the analysis, the system in instable ecologically.

These problems could be avoided by choosing the sampling such that it coincided with several stages in the phases of a variaable which varied cyclically. Secondly, it might be better to consider only the absolute value of σ. A stable system would be one in which $\sigma=0$, and a less stable system would be one in which $|\sigma|>0$. Those systems in which variables increased or decreased with time would have to be excluded from the analysis in its present form.

Patten (1962) 'improved' the stability index by dividing σ by the mean variability. Small mean variabilities tend to increase the magnitude of the stability index, and large mean variabilities decrease the magnitude of the stability index. However, it is unlikely that an ecologically instable system with a small mean variability is actually less stable than an ecologically instable system with a large mean variability. Therefore, if Patten's approach to stability analysis is to be retained, it is

probably best to consider only $|\sigma|$.

The data in Tables 16 and 17 were re-examined, and the mean values of $|\sigma|$ for the biological, chemical, and physical variables determined. These were;

	G.S.-1	Indian Arm
Biological	0.17	0.19
Chemical	0.32	0.53
Physical	0.22	0.30

The biological system has a higher ecological stability than either the physical or chemical system. However, the chemical system is less stable ecologically than the physical system while, in the previous analysis, it was more stable.

Patten's stability measure therefore might be modified to give a better index of stability than it its present form. However, this index, like any index, has limited use in describing ecosystem processes. A better approach would be to make use of some of the mathematical techniques used by physicists, meteorologists, and astronomers in time lag studies to describe the dynamics of the interactions between the variables within a system.