ASPECTS OF THE LIFE HISTORY OF
Lycodopsis pacifica (Collett) 1879

by

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Date Oct 21 1967

ERRATA SHEET

P. 9 First line second paragraph read "March" for "march".

P. 22 Fourth line read "viviparous" for "ovoviviparous".

P. 29 First line, first paragraph - read "12" for "10".

P. 67 Thirteenth line read "viviparous" for "ovoviviparous".

ABSTRACT

Aspects of the life history of Lycodopsis pacifica (Collett) 1879 were studied during the period September 1965 to November 1966. Two areas in the Strait of Georgia, British Columbia, were investigated. Trawls were used as sampling devices.

Sexually mature individuals were collected during the period September to January. Lycodopsis pacifica has a remarkably small complement of mature eggs (average complement 30.4). The mature eggs are large, with an average diameter of 5.0 mm. Sexual dimorphism is present. Males start to grow faster than females at approximately 170 mm in length. The older males are larger than females. There is some evidence that parental care is involved in the reproductive behaviour of the species.

Age was estimated by counting the annular rings on otoliths. Both males and females ranged up to five years of age. The age-length relationship for both sexes is presented. The length-weight relationship of the species is described.

The food spectrum of Lycodopsis pacifica was determined. At outer Burrard Inlet, the species feeds primarily on infaunal invertebrates of the Phyla Mollusca and Annelida, and the Subphylum Crustacea. The place of L. pacifica in the bottom community is considered.

The anatomy of structures associated with feeding are described. Visual and "chemical" senses are probably important in food-getting behaviour. The feeding adaptations and food of the species is discussed in relation to sediment type. L.

pacifica is probably not specialized to remove infaunal food items from one type of sediment.

It was assumed that *Lycodopsis pacifica* would aggregate where high concentrations of infaunal organisms suitable as food would be found. At outer Burrard Inlet, high numbers were caught on several sediment types, ranging from silt-sand to silt. At the Cape Lazo area, catches of *L. pacifica* were highest on a silt sediment. The species is likely capable of foraging on a range of sediment types. Some factors affecting the infauna are discussed, and the usefullness of simple mechanical analysis of sediments in benthic ecology is questioned.

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The cooperation and assistance of many persons interested in marine ecological research made this study feasible. Messrs. K. Tanaka and J. Kondo, commercial shrimp fishermen, kindly helped collect in outer Burrard Inlet. Mr. T. H. Butler, Crustacea Investigation, Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C., provided accomodation on the R/V "Investigator No. 1" for studies at the Cape Lazo gully. Dr. R. Sheldon, Atlantic Oceanographic Group, Fisheries Research Board of Canada, Dartmouth, N.S., provided data on the sediments at this site. The encouragement and inspiration of Mr. Butler and Dr. Sheldon is greatly appreciated. Dr. J. Murray and other members of the Geological Oceanography group, Institute of Oceanography, University of B.C., Vancouver, B.C., provided lab space, sediment sampling equipment, and advice on sediment analysis. Dr. N. J. Wilimovsky and the Institute of Fisheries, University of B.C., Vancouver, B.C., provided financial assistance in the operation of the Institute vessel. Messrs. P. Young, D. Hay, and several members of the Institute of Fisheries assisted in field work. Dr. E. W. Fager, Scripps Institute of Oceanography, La Jolla, California, kindly allowed use of the photograph of *Lycodopsis pacifica* taken from a submersible. Mr. S. Gopaul did the drawings of the feeding anatomy of the species. Dr. I. McT Cowan, Dean of the Faculty of Graduate Studies, University of B.C., identified several species of molluscs found in food studies. Drs. N. J. Wilimovsky, J. E. Phillips, B. Bary, and I. E. Efford read the manuscript

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The help of all persons connected with the study is most gratefully acknowledged.

INTRODUCTION

Members of the Family Zoarcidae are found in very diverse habitats, ranging from the bathypelagic regions (*Melanostigma pammelas*) (Marshall, 1954) to the intertidal zone (*Commandorella popovi*)(Andriashev, 1937). Most zoarcids, however, are bottom dewllers of polar and temperate seas.

Lycodopsis pacifica (Collett) 1879 is a bottom dwelling zoarcid which ranges from southern California to the Alaskan coast. At several locations in the Strait of Georgia, British Columbia, the species is captured when trawling for commercial shrimp (*Pandalus* spp.). In Smith Inlet, off Queen Charlotte Sound, the species is also very abundant, and Bayliff (MS, 1954) notes the species is common in Puget Sound. *Lycodopsis pacifica* is rarely taken in trawling operations on the outer continental shelf of British Columbia but is dominant in the bottom fish fauna of some coastal inlets.

The first section of the present study deals with the general biology of *Lycodopsis pacifica*. In the second section, *L. pacifica* is used to study feeding adaptations of the bottom fish for existence on sediments. The results of trawling for the species on several bottom types are presented.

Two questions were asked: (1) Do the feeding adaptations of *Lycodopsis pacifica* restrict the species to certain sediments? (2) On what type of sediment is the species found most abundantly? Sediment characteristics may play an important role in governing the (short-term) distribution and abundance of bottom fishes particularly if their food spectra largely involves

sessile organisms. The bottom type may influence the faunistic complexes of invertebrates.

STUDY AREAS AND METHODS

Outer Burrard Inlet

Outer Burrard Inlet is the seaward (western) enlargement of a coastal fjord, Burrard Inlet, on the southern British Columbia coast (located about 49°18' N, Long. 123°12' W). The inlet is bordered on the north by Howe Sound, on the far west by the Strait of Georgia, and the southwest by the northern arm of the Fraser River (Fig. 1).

Through the cooperation of commercial shrimp fishermen, 14 samples over the period September 1965-November 1966 were obtained from outer Burrard Inlet. Samples collected using a small experimental trawl towed by the Institute launch supplemented these samples (Table I).

The sediments of southwest outer Burrard Inlet were studied in some detail in May and June 1966. This locality will be termed the experimental study area of outer Burrard Inlet. Three transects were chosen for experimental sampling. These are termed Spanish Banks, Point Grey and North Arm transects (Fig. 1).

The Cape Lazo gully was sampled through the cooperation of the Crustacea Investigation, Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C.

The gully is located on the central east coast of Vancouver Island. It is a deep trough (50 fm, 91.0m) approximately 8 miles (14.8 km) long and 2 miles (3.2 km) wide. It is bordered on the northwest by Cape Lazo (Lat. 49°37' N, Long. 124°48' W). A sill rising to within 15 fm (27.4 m) of the surface separates the

Table I. Outer Burrard Inlet Sampling Area Information

DATE	SAMPLE NO.	AREA OF FISHING OR TRANSECT	SOURCE
Dec. 3 1965	1	West Vancouver	Comm. shrimp vessel
Jan. 9 1966	2	West Vancouver	Comm. shrimp vessel
Jan. 31 1966	3	Fraser Delta	Comm. shrimp vessel
Feb. 14 1966	4	Jericho	Comm. shrimp vessel
March 6 1966	5	West Vancouver	Comm. shrimp vessel
March 21 1966	6	West Vancouver	Comm. shrimp vessel
April 10 1966	7	Gibsons	Comm. shrimp vessel
May 4 1966	8	West Vancouver	Comm. shrimp vessel
June 10 1966	9	Spanish Banks	Experimental trawling
July 4 1966	10	West Vancouver	Comm. shrimp vessel
July 21 1966	11	West Vancouver	Comm. shrimp vessel
Aug. 8 1966	12	Spanish Banks	Experimental trawling
Aug. 21 1966	13	West Vancouver	Comm. shrimp vessel
Sept. 8 1966	14	Spanish Banks	Experimental trawling
Sept. 24 1966	15	West Vancouver	Comm. shrimp vessel
Oct. 12 1966	16	West Vancouver	Comm. shrimp vessel
Nov. 13 1966	17	West Vancouver	Comm. shrimp vessel

See Figure 1 for location of fishing areas and transects.

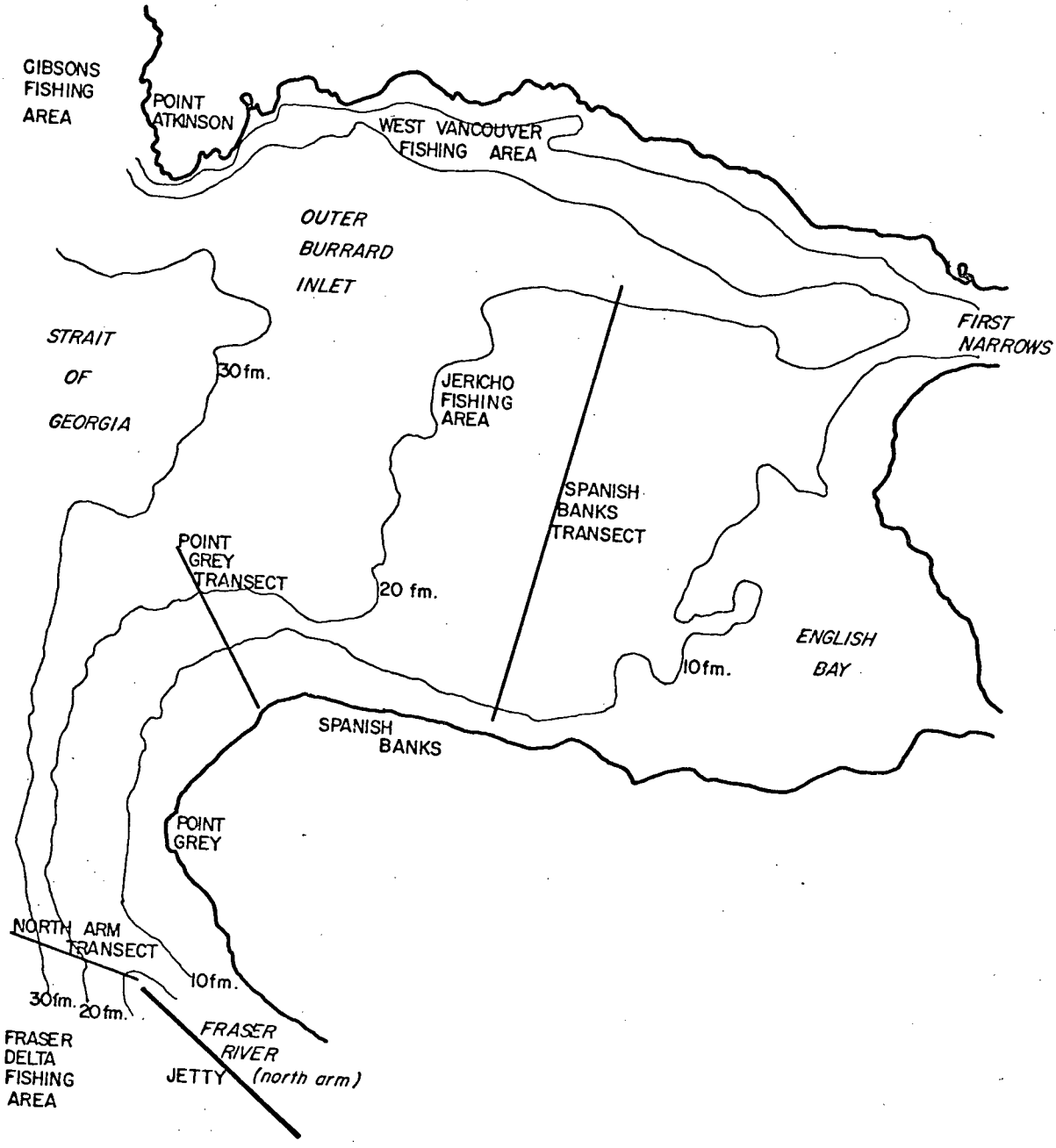


Fig. 1. Sampling locations, transects, and bathymetry at the outer Burrard Inlet study area.

trough from the depths of the Strait of Georgia (Fig. 2). On the west the gully is bordered by Denman Island and on the south by Hornby Island. The gully was divided into nine sections that crossed it in an east-west direction. As the bottom was more suitable for trawling on the west slope of the gully, most collections were made on the western ends of the sections.

The gully was sampled in November 1965, January 1966, August-September 1966 and March 1967 (Table II). Data obtained from these samples were employed primarily in investigations of the relationship of Lycodopsis pacifica to sediment type.

Description of Sampling Equipment and Limitations of Sampling

Samples obtained from commercial shrimp fishermen were from catches taken with a modified beam trawl. All other fishes examined from both study areas were captured with otter trawls. Table III shows the pertinent dimensions of sampling equipment. Of primary importance was the mesh size in the codend of the trawl. This introduced serious sampling bias in some catches.

Mesh selection is of importance when sampling fish populations; if only one fishing method (or mesh size) is employed, it will very likely provide an unrepresentative sample (Ricker, 1958). Parrish (1958) points out that in addition to mesh size, selectivity is affected by several factors, the most important of which are: (a) method of rigging the cover (chafing gear), (b) catch size, (c) towing speed, (d) towing time, (e) net material, and (f) amount of escapement through different parts of

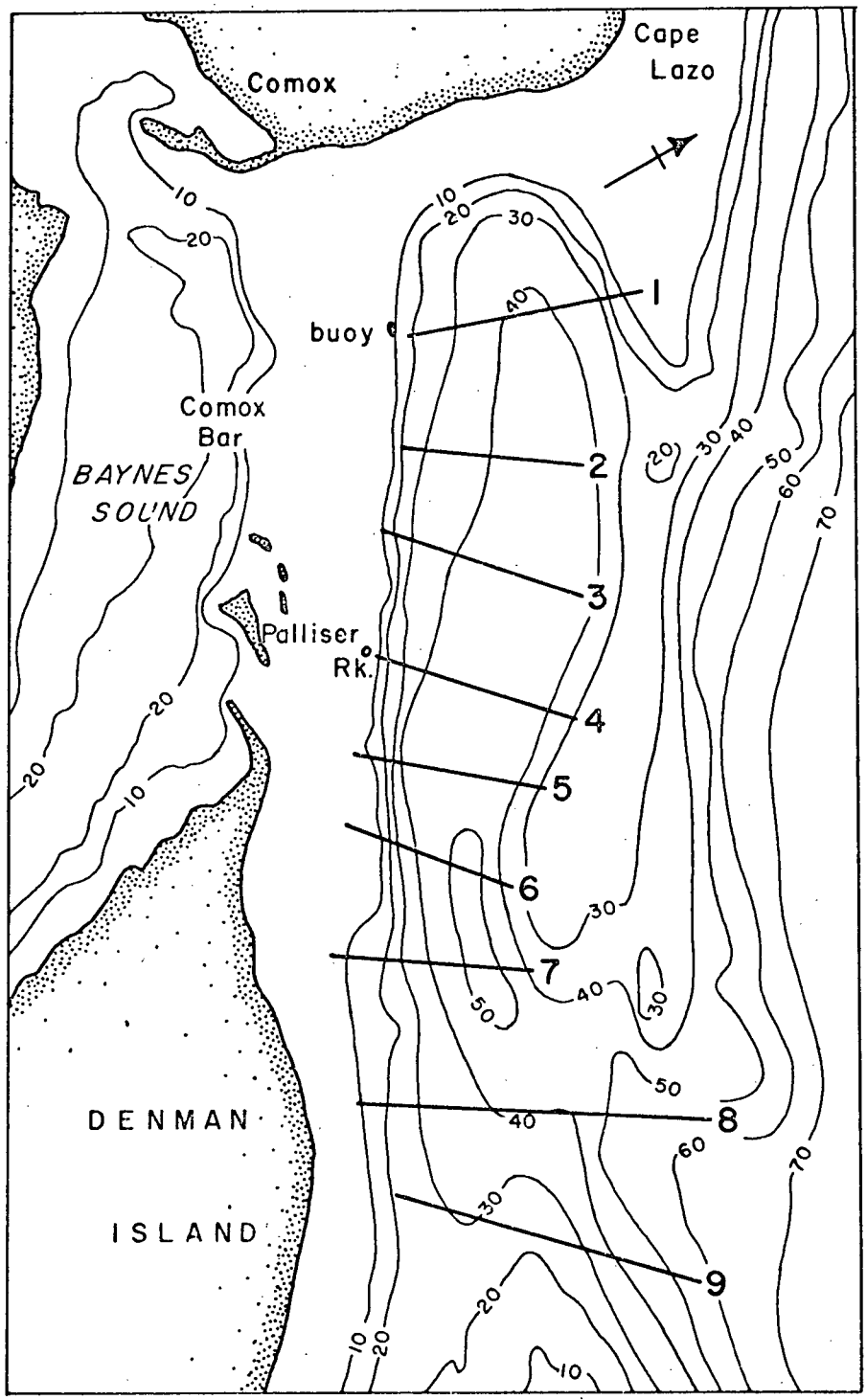


Fig. 2. Sections and bathymetry at the Cape Lazo gully.

Table II. Information on the Cape Lazo study area

DATE	SECTIONS OCCUPIED*	TOTAL NUMBER TRAWLS SAMPLED
November 2 1965	2 - 7	10
January 22-23 1966	4 - 7	14
August 24-September 1 1966	1 - 7	60
March 18 1967	1 - 3	11

*See Figure 2 for location of sections.

Table III. Pertinent dimensions of trawls employed at the two study areas.

Area and Vessels Employed	Length of Footrope	Mesh Size in Body and Wing	Mesh Size in Codend	Mesh Size of Liner
Cape Lazo Gully: "Investigator No. 1"	47.3 ft. (14.2 m)	1.5 in. (3.8 cm)	1.5 in. (3.8 cm)	0.5 in. (1.3 cm)
Outer Burrard Inlet: various commercial shrimp vessels	43.0 ft. (12.9 m)	1.3 in. (3.2 cm)	1.3 in. (3.2 cm)	None
Outer Burrard Inlet: Institute of Fisheries vessel	12.0 ft. (3.6 m)	1.0 in. (2.5 cm)	1.0 in. (2.5 cm)	0.5 in. (1.3 cm)

the net and codend. A detailed study of mesh selectivity is beyond the scope of this work.

Aquarium Methods

Lycodopsis pacifica was maintained in aquaria on two occasions.

In march 1966 seven *Lycodopsis pacifica* from outer Burrard Inlet were maintained approximately one month in a five gallon (18.9 l) aquarium. Sea water of salinity 27‰ was cooled by running tap water in glass tubing; a temperature range of 10-11°C was maintained. The seawater was circulated and aerated by an air-driven filter system. Sediment was obtained at Inner English Bay at a depth of 10 fm (18.3 m) and placed in the tank. The sediment was almost continually in suspension and could be described as "silty-mud".

On December 27 1966, 61 individuals were obtained from outer Burrard Inlet. These were maintained in a 180 gallon (683 l) wooden tank with plexiglas viewports. Material collected at extreme low tide inshore of the Spanish Banks transect served as substrate; it was relatively coarse and settled rapidly.

Preservation and Measurements

After capture, fresh specimens of *Lycodopsis pacifica* were fixed in a solution of 10% formalin for a period of approximately 24 hours. They were then immersed in running fresh water for three to five hours and finally preserved in 40% isopropyl alcohol.

Measurements throughout this study were taken from the tip of the mouth (mouth closed) to the extreme end of the caudal fin, and are to the nearest millimeter (total length - Parrish, 1958). Except where noted, all measurements were made on preserved specimens.

LIFE HISTORY SECTION

Zoarcidae are blennioid fishes characterized by elongated bodies and long anal and dorsal fins which are joined to the caudal fin to form a continuous fin edging the posterior part of the body. The pelvic fins, when present, are small and are located anterior to the pectoral fins. Many species of Family Zoarcidae are distributed in the northern part of the Pacific and Atlantic Oceans as well as in Arctic and Antarctic Seas (Nikolsky, 1961).

Bayliff (MS, 1954) records pertinent references to northeast Pacific zoarcids; most are of a taxonomic nature. There is no comprehensive account of the biology of zoarcids in the northeast Pacific. Andriashev (1937) notes observations on zoarcids from the Bering and Chukchi seas.

There is little information on the life history of *Lycodopsis pacifica* although its taxonomy and distribution have been well described. Bayliff's recent revision (MS, 1954) of the zoarcids of the northeast Pacific includes a convenient artificial key. He records the range of *L. pacifica* as being southern California to Afognak Island, Alaska. The species has been captured over a wide range of depths (5 fm, 9.2 m in Puget Sound (Bayliff, MS, 1954); 200 fm (360.0 m) in California waters (Clemens and Wilby, 1961)). Some brief observations of the biology of *L. pacifica* are found in Clemens and Wilby (1961). They report the species is caught most commonly on a mud bottom.

Reproduction

Data on the reproductive condition of specimens collected at outer Burrard Inlet were collected over the period December 1965 - November 1966. From each sample, 30 individuals, all over 100 mm in length, were studied. Information on sexual dimorphism was obtained from specimens captured at the Cape Lazo gully. Because of mesh selection, an adequate size series of small fish was not available from outer Burrard Inlet.

Sexual Dimorphism

There is strong sexual dimorphism in *Lycodopsis pacifica*. Growth studies (see p. 25) show that at a length of approximately 170 mm males begin to grow faster than females. The males continue this accelerated growth and eventually are larger than females.

Bayliff (MS, 1954) mentions that early taxonomists described the males and females of *Lycodopsis pacifica* as separate species until 1896 when Jordan and Starks pointed out that the two were merely the sexes of one species. The sexual dimorphism is exemplified in head size, particularly snout length. The larger males have large, shovel-shaped snouts; they have been described as "alligator-heads".

The appearance of sex differences in morphology may be an indication of the onset of sexual maturity. Measurements were made on specimens of *Lycodopsis pacifica* taken at the Cape Lazo gully in March 1967 to determine whether males have larger heads at all lengths (and ages). Fresh specimens of 46 females and 62

males were studied. Snout length was estimated by the length of the maxillary (Gregory, 1933). The ratio of the maxillary length to the total length was determined for each individual (Fig. 3).

The relationship of maxillary length to total length was the same for all females encountered. In males, the ratio of the maxillary length to the total length remained approximately constant until about 170 mm. After this length males have longer maxillaries in relationship to body length.

Males of 170 mm in length and greater were most frequently sexually mature in fall and winter at outer Burrard Inlet (see below).

Description of Gonads and Criteria of Sexual Maturity

Males

The bilobed testes of *Lycodopsis pacifica* lie in the postero-dorsal part of the body cavity. Each lobe of the testis is roughly rectangular in shape. The organs are connected to the genital pore by a sperm duct. The testes are whitish-grey in colour; their whiteness seems to be accentuated at sexual maturity.

The surface area of a testis lobe was determined by measuring the length and width with dividers. Individuals with lobes of 20 mm or over were considered sexually mature because they contained loose or "running" sperm.

Females

The ovary of *Lycodopsis pacifica* is a median, unpaired structure which lies in the postero-dorsal part of the body cavity. When mature eggs are present, the ovary swells and

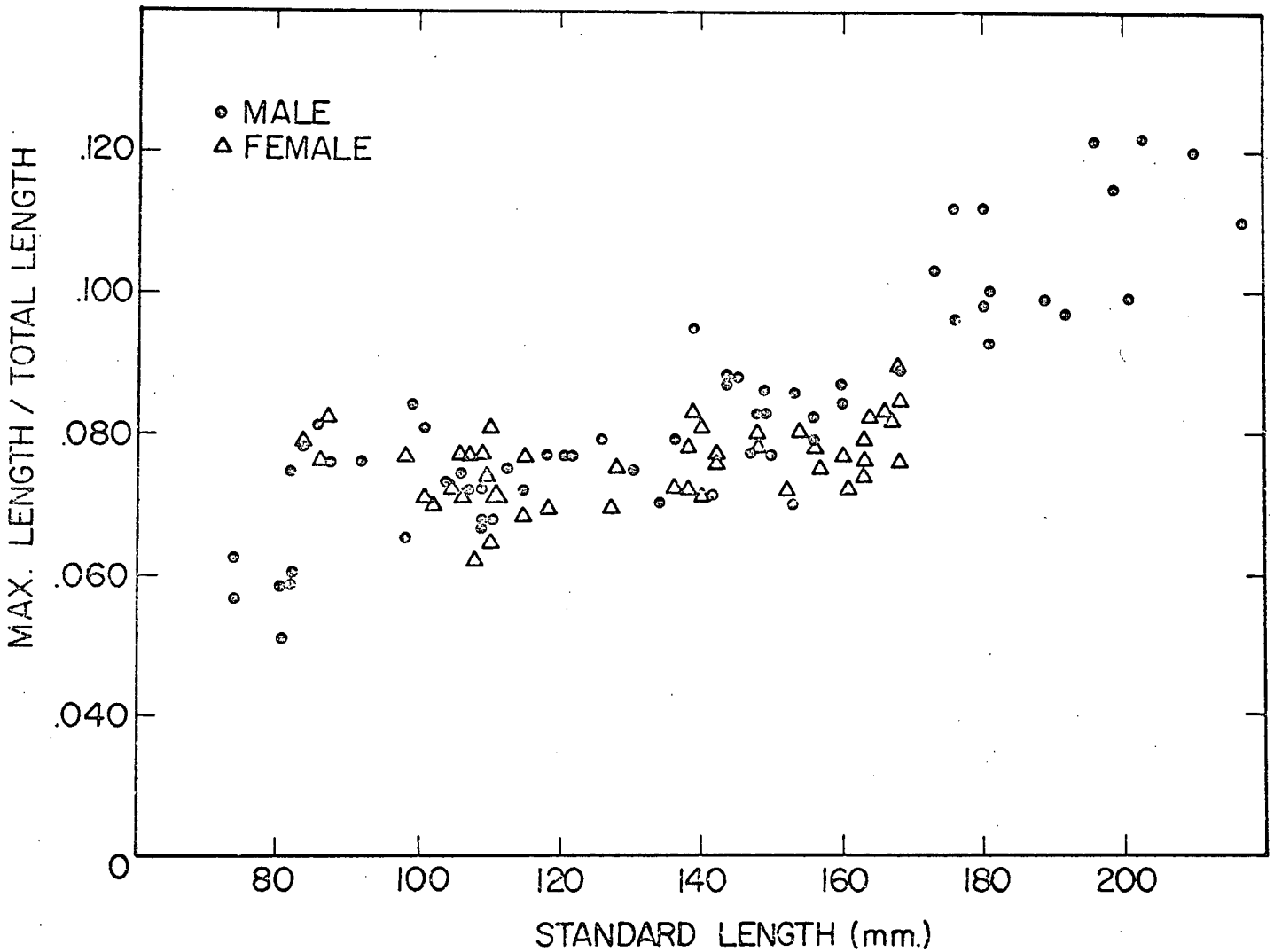


Fig. 3. Total length of L. pacifica plotted against the ratio of maxillary length to total length. Data from specimens collected at the Cape Lazo gully on March 18 1967.

mature females are noticeably bulged. The ovarian membranes are continuous with the oviduct. The larger eggs are yellow-orange whereas small eggs tend to be light yellow.

Eggs of three classes determined by size are described in this study. The average diameter was calculated from measurements on eggs made with dividers. The three classes are as follows: small - less than one millimeter diameter; medium - one to two millimeters; and large - greater than two millimeters in diameter. The large eggs were probably mature and were destined to be released in the spawning of that season. An "immature" condition was also observed. In the "immature" condition ovarian structure was recognizable microscopically, but individual eggs could not be discerned.

The numbers of eggs of each size class were counted. For the purposes of this work, the term "complement" describes the number of eggs of given size class present in a fish. As pointed out by Vladykov (1956) the term "fecundity" should be reserved for the number of mature eggs actually released at spawning.

Annual Reproductive Condition

Males

The surface area of one testis lobe was determined for each male examined; the number of males in each sample during the year ranged from 9 to 17. An average surface area value was determined for each sample (Fig. 4). Testis development was greatest during the period September to January.

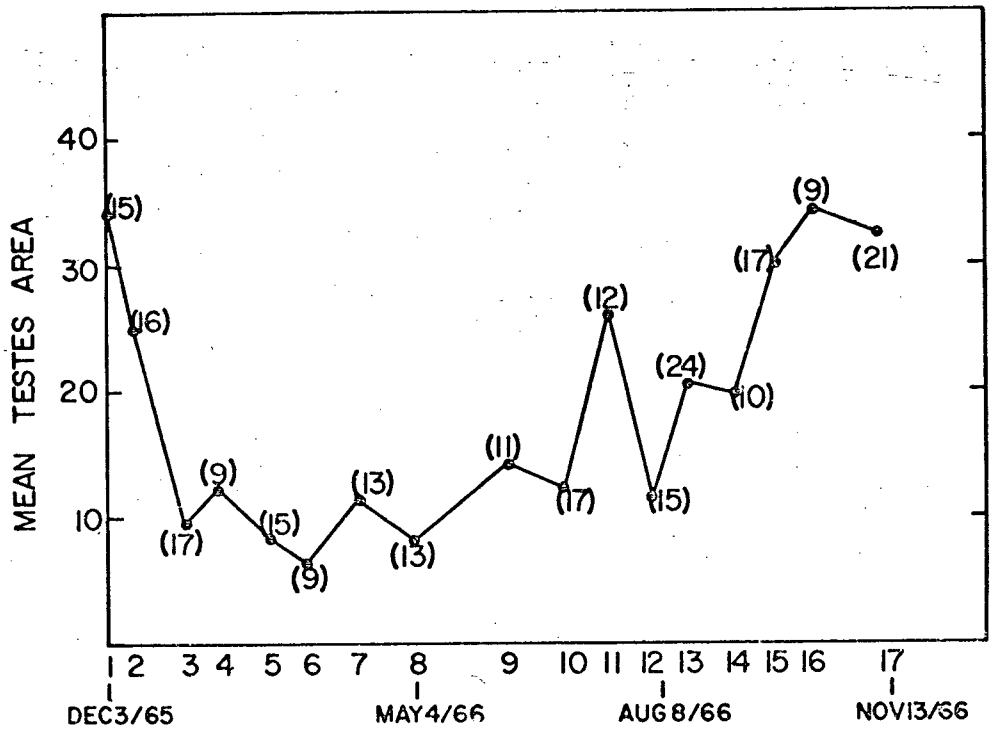


Fig. 4. Annual variation in average surface area (mm^2) of one testis lobe of L. pacifica. The figures in brackets indicate the number of males examined per sample. All fish were collected at outer Burrard Inlet.

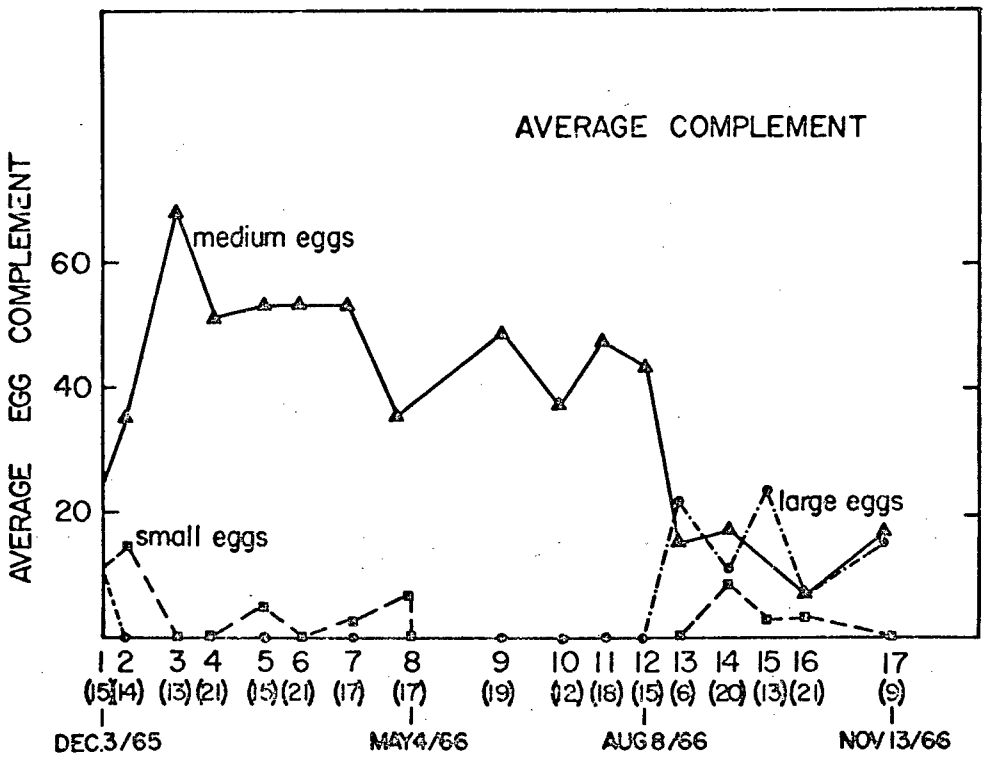


Fig. 5. Annual variation in average complement of three egg sizes in L. pacifica. The figures in brackets indicate the number of females examined per sample. All fish were collected at outer Burrard Inlet.

Females

The complement of each size class of eggs was determined during the year (Fig. 5). The average is calculated from counts made on 13 to 21 individuals per sample. It should be noted that the average complement of each size class does not adequately represent the actual number of eggs present. Some individuals would not contain any eggs of one particular size. The average complement of medium eggs increased in February, levelled off until about late August, then decreased (Fig. 5). In August mature eggs began to appear and sexually mature females were found until late November of 1966. They were also present in samples taken in December 1965.

An undetermined pattern was observed for eggs of the small category. Small fish were rarely obtained in the collections made by commercial shrimp vessels.

Age and Length at Sexual Maturity

As noted in the section dealing with growth (p. 26) there is overlap of length among the age groups of *Lycodopsis pacifica*. To determine the average age of sexual maturity in *L. pacifica* would require many more age estimations than are available. Over the period of sexual maturity (approximately September to January) the percentage frequency of sexually mature individuals in each ten millimeter length group was determined. Females ranging in length between 140 and 180 mm and males ranging in length from 170 to 230 mm were most frequently mature (Figs. 6 and 7).

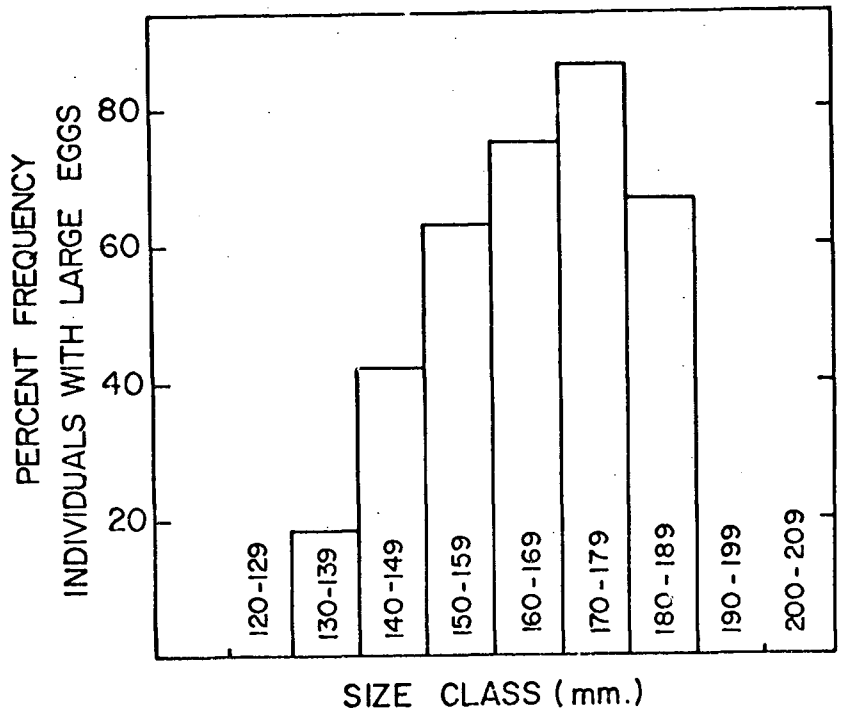


Fig. 6. Histograms showing percent frequency of mature female L. pacifica by size class. Data from collections made in December 1965, January 1966, and August-November 1966, at outer Burrard Inlet.

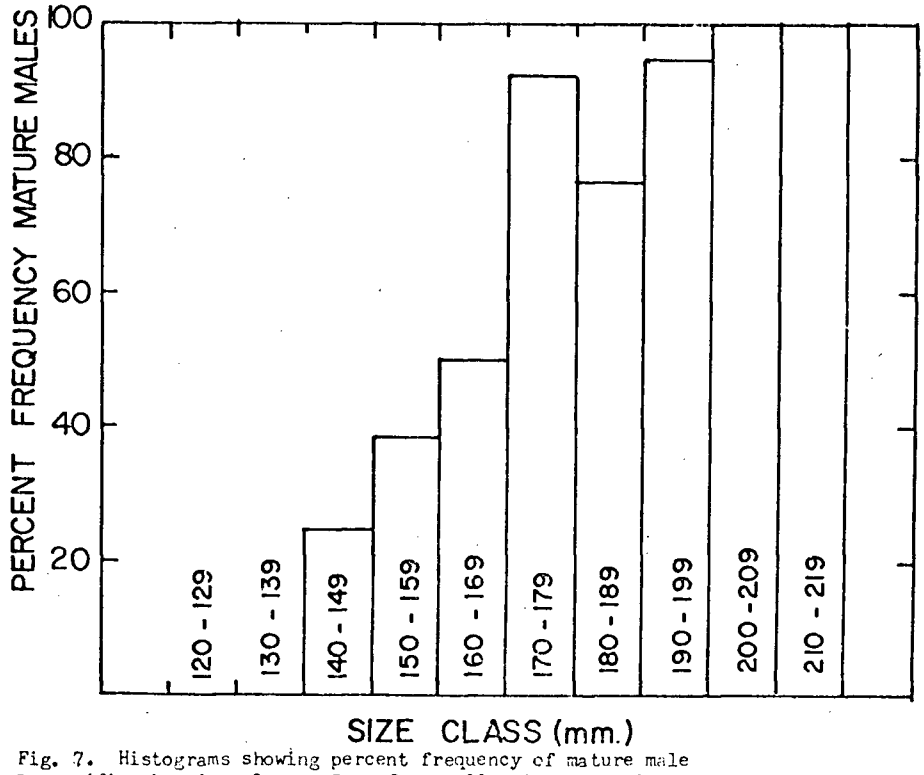


Fig. 7. Histograms showing percent frequency of mature male L. pacifica by size class. Data from collections made in December 1965, January 1966, and August-November 1966, at outer Burrard Inlet.

From the above observations it is concluded sexual maturity in Lycodopsis pacifica occurs approximately from September to January. Over this period, large sexually mature males and females appeared in the samples.

Inferences of Spawning Time

Length frequency analysis of specimens captured at the Cape Lazo area suggests breeding occurs in late fall and winter in Lycodopsis pacifica. A sharp mode of small fish is evident in November 1965 and January 1966 (Fig. 8). The mode has a peak of about 75-80 mm in these months. By August-September 1966 the mode had shifted to approximately 100 mm, presumably because sampling had "followed" the growth of individuals produced by breeding in fall and winter of 1964 and 1965.

A mode of approximately 70 mm is evident in August and September 1966 samples. This mode is probably composed of young produced during the 1965-66 spawning season.

Some individuals in outer Burrard Inlet apparently ceased feeding in the fall and winter months because individuals with empty stomachs were observed in samples at these times (Fig. 9). These individuals could have been in spawning condition. Cessation of feeding at spawning time is common in fishes (Nikolsky, 1963).

Oviparity, Ovoviviparity and Parental Care

A wide range of reproductive types is recorded among members of the Family Zoarcidae. Bretschneider and de Wit (1947) show

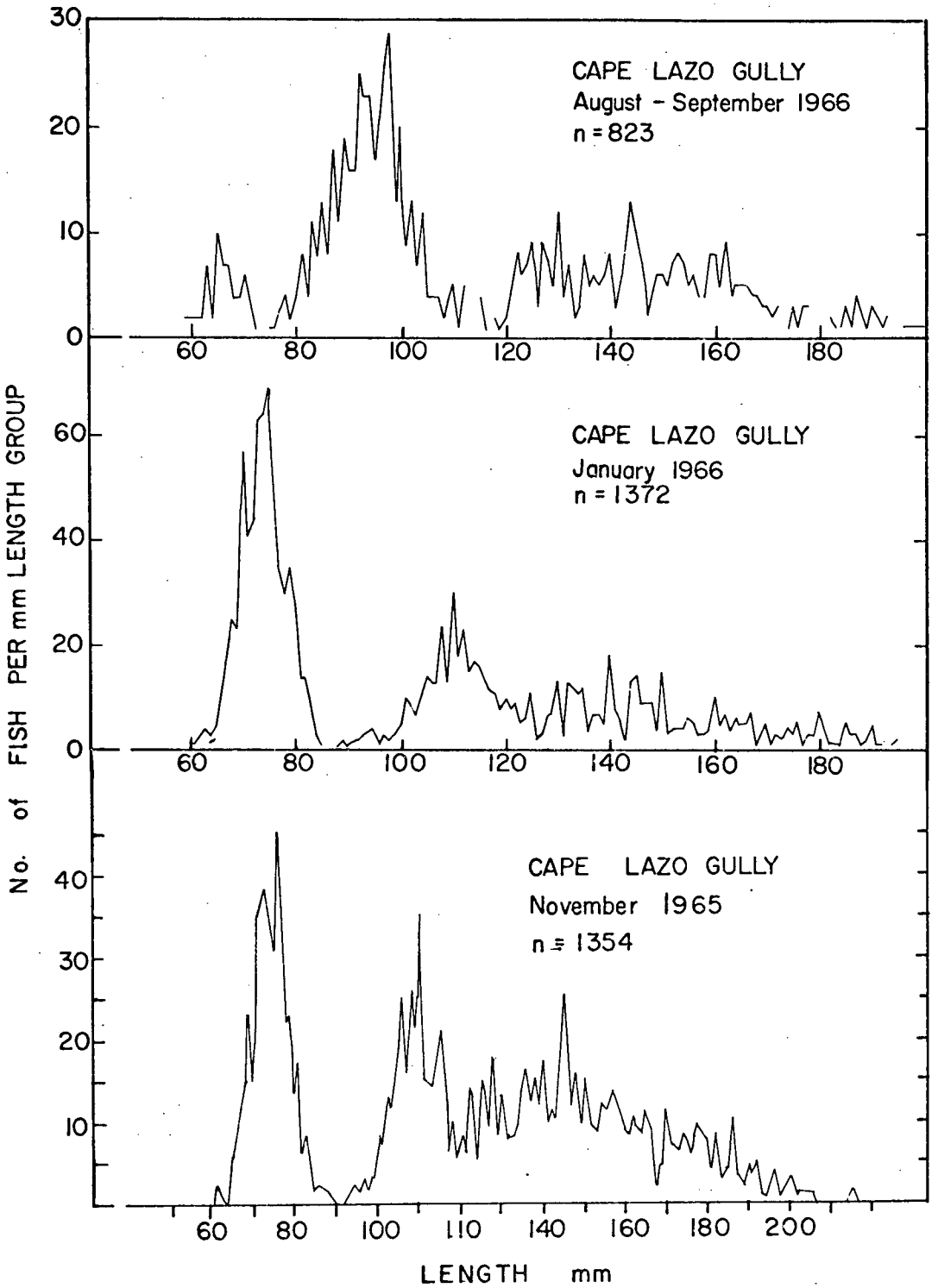


Fig. 8. Length frequency polygons of L. pacifica captured at the Cape Lazo gully at three sampling times.

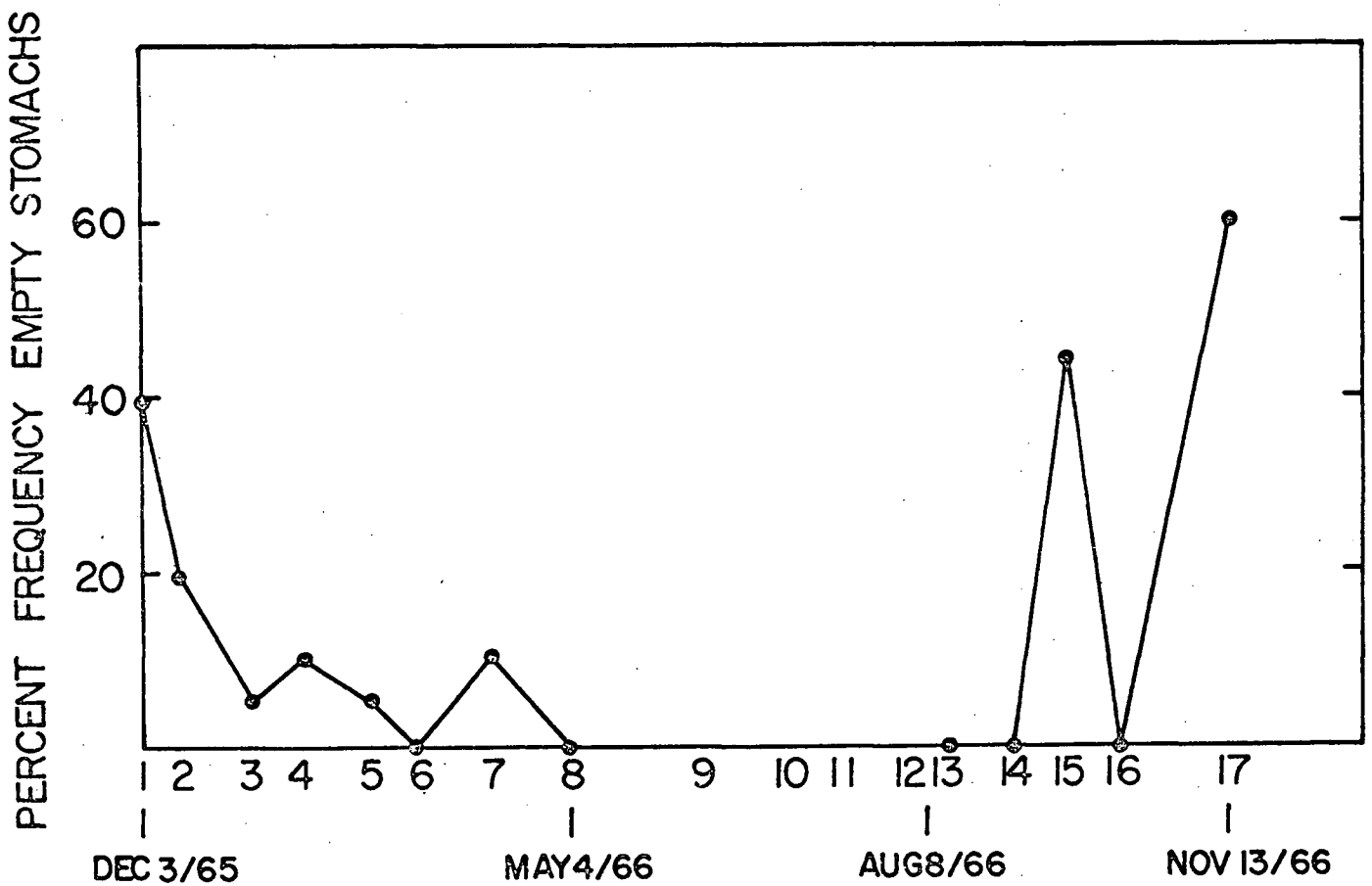


Fig. 9. Percent frequency of empty digestive tracts observed in L. pacifica during the period December 1965 - November 1966. Data from samples of 20 fish per time period collected at outer Burrard Inlet.

that the viviparus blenny, Zoarces viviparus of northeastern Atlantic waters, is an "ovary breeder". The ova are fertilized in the ovary and there develop into young. Their work and that of McIntosh (1885) show that the species is ovoviviparous. Other north Atlantic forms, for example Lycodes spp., are oviparous (Jensen, 1904). Macrozoarces americanus of the northwestern Atlantic was found to be oviparous by White (1940) who discovered an egg mass guarded by the parents. Information on the reproduction of north Pacific zoarcids is rare. Lycodes palearis spawned in an aquarium but this followed removal of the majority of the eggs by artificial means (Slipp and De Lacy, 1952). Bali and Bond (1959) record ovum size from specimens of Aprodon cortezianus from the Oregon coast. They concluded the species is oviparous and spawns in late summer or early fall. Andriashev (1937) notes the ova size of Lycodes spp. from the Bering and Chukchi Seas. Clemens and Wilby (1961) write "some of the species (of Family Zoarcidae), possibly all, give birth to young."

No evidence of ovoviviparity or viviparity was found for L. pacifica in the present study. It is possible that fertilization is internal and that development occurs for a short period inside the maternal body. There is no evidence that this is the case, however, either from direct observation or from the presence of any anatomical modifications for internal fertilization and incubation.

Most ichthyologists accept the generalization that the conditions of low fecundity and large eggs are usually accompanied

Fig. 10. Male and female Lycodopsis pacifica on the ocean floor. Photograph taken by Dr. E.W. Fager in November 1965 off La Jolla, California, at a depth of 110 m.

by some degree of parental care. The present study shows L. pacifica has a very small complement of mature eggs. The mature eggs are large, with an average diameter of 5 mm. Between September 1965 and January 1966 the average complement of large eggs was 30.4 (range 7 to 52) in 51 individuals examined. This average complement is an approximation to fecundity. Indirect evidence of parental care in L. pacifica is provided by Fager's (pers. comm. 1966) observations from submersibles off the southern California coast in 1964 and 1965. During dives in fall and winter he observed L. pacifica commonly in male and female pairs (Fig. 10). On one occasion he observed a pair clearing a patch of sediment together. It appeared as if a "burrow" were being constructed.

Age and Growth

Ages of specimens of Lycodopsis pacifica from outer Burrard Inlet were estimated using the left sacculus otolith. The annular rings were counted under direct light with a microscope of X10 magnification. Subsampling techniques for selection of otoliths and criteria for annular rings are outlined in the Appendix, p. 74. The annular rings are assumed to be formed by temperature-dependent phenomena.

The ages of 129 males and 107 females were estimated. Ages ranged up to five years for both sexes (Fig. 11 and Appendix, pp. 76 and 77). Regression lines describing growth for both sexes were obtained by least squares estimation after transforming values to logarithms. The regression equations obtained are as

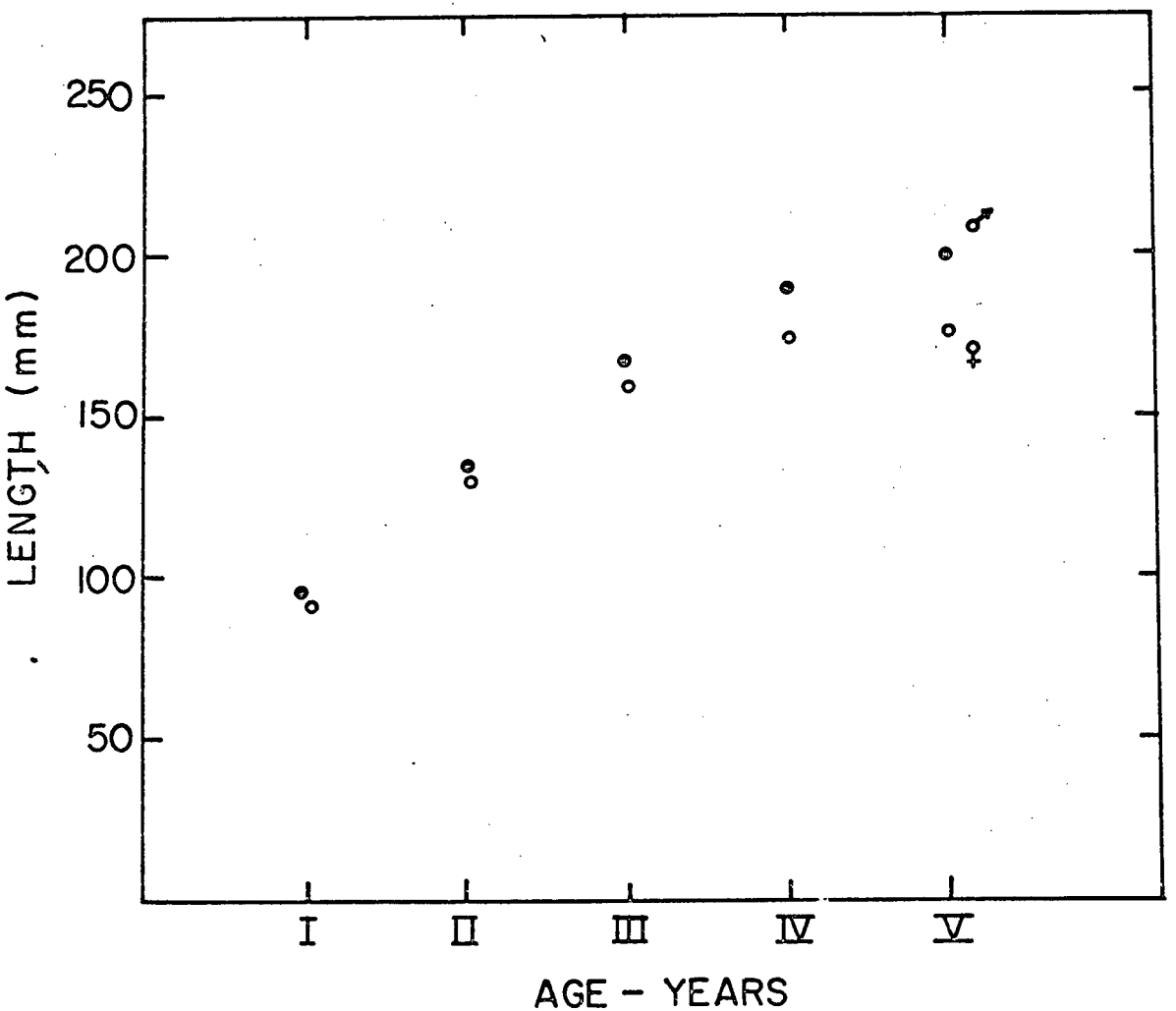


Fig. 11. Age-length relationship of L. pacifica. Ordinate - mean length in millimeters; Abscissa - age in years. Data from specimens collected at outer Burrard Inlet.

follows:

Males: $Y = 4.4982 + 0.5191X$

Females: $Y = 4.5382 + 0.4502X$

A t-test for differences between the slopes of the two equations was performed (Steel and Torrie, 1960). A t-value of 6.890 was significant at the 95% probability level. It is concluded that males grow faster than females after approximately 170 mm in length. The difference in growth rate is probably of importance in sexual dimorphism, and is discussed on p. 13.

Limited verification of the ages estimated from otoliths was obtained by analysis of length frequency data. In large samples from the Cape Lazo gully, the modes of ages I, II, and perhaps III are prominent in length frequency polygons (Fig. 8). At greater ages there is much overlapping of length groups.

Length-Weight Relationship

Specimens captured at the Cape Lazo gully on March 18 1967 were used in this investigation. After removal from the trawl the fish were wrapped individually in cheesecloth to remove excess water. Weights and lengths were obtained not more than 12 hours after capture. Weights were made to the nearest decigram and lengths to the nearest millimeter.

Weights and measurements of 62 males and 46 females were obtained (Fig. 12). A line of best fit was calculated following the least squares method outlined in Carlander (1950). The equation expressing the relationship is $W = 0.0000419L^{3.07897}$ where W (weight) is in grams and L (length) is in millimeters.

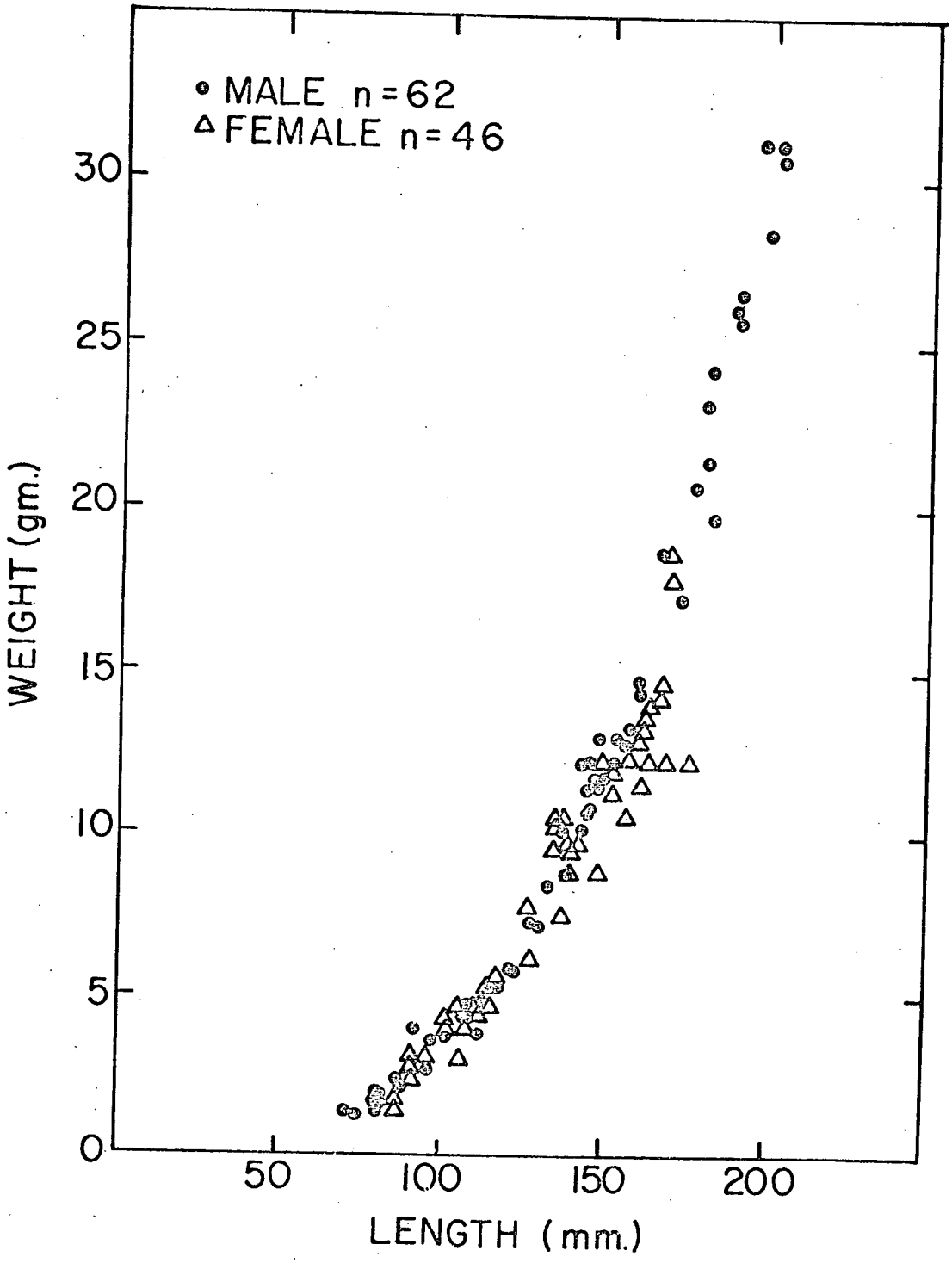


Fig. 12. Length-weight relationship of L. pacifica. Data from fresh specimens collected at the Cape Lazo gully on March 18 1967.

Food of *Lycodopsis pacifica*

From each of the 17 samples obtained during the year, the stomach and intestinal contents of 20 individuals were examined. All identifiable items were enumerated. Recognizable organisms were counted as one item. Annelid worms were often broken so a section one centimeter long was counted as an item.

Lycodopsis pacifica feeds primarily on the infauna of a soft-bottom community. Detritus and sediments were found in all individuals in trace amounts. A list of recorded food organisms follows.

Phylum Annelide
- Class Polychaeta
  - Subclass Errantia
    - F. Syllidae
    - F. Nereidae
  - Subclass Sedentaria
    - F. Chaetopteridae - *Phyllochaetopterus* spp.
    - F. Sternapsididae - *Sternapsis* spp.

Phylum Arthoropoda

Subphylum Crustacea
- Class Ostracoda
  - Order Myopoda
- Class Copepoda
- Class Malacostraca
  - Subclass Pericarida
  - Order Cumacea
  - Order Amphipoda

Suborder Gammaridea - *Amphithoe* spp.

Suborder Hyperiidea - *Hyperia* spp.

Order Decapoda

Suborder Natantia

Section Caridea - *Pandalus* spp.

Suborder Reptantia

Section Macrura - *Cancer magister* (megalopa)

- *Pinnixa* spp.

Phylum Mollusca

Class Gastropoda

F. Amphictenidae - *Pectenaria* spp.

Class Pelecyopoda

Order Protobranchia - *Yoldia ensifera*

- *Yoldia amygdalea*

Order Eulammellibranchia - *Macoma carlottensis*

- *Axinopsis sericatus*

The food items were categorized into ten major groups. These were: bivalves (Pelecypoda), amphipoda, free-living annelids (Polychaeta, F. Nereidae), "peanut worms" (Polychaeta, F. Sternapsididae), tubeworms (Polychaeta, F. Chaetopteridae), gastropods, cumaceans, ostracods, megalopa larvae (*Cancer magister*), decapod crabs, copepods, and pandalid shrimps.

The percentage abundance by number of each item in each sample (Fig. 13), and the percentage abundance by number of each item averaged over all the samples (Fig. 14) were determined. Bivalves, tube worms, amphipods, and free-living annelids dominate the food spectrum.

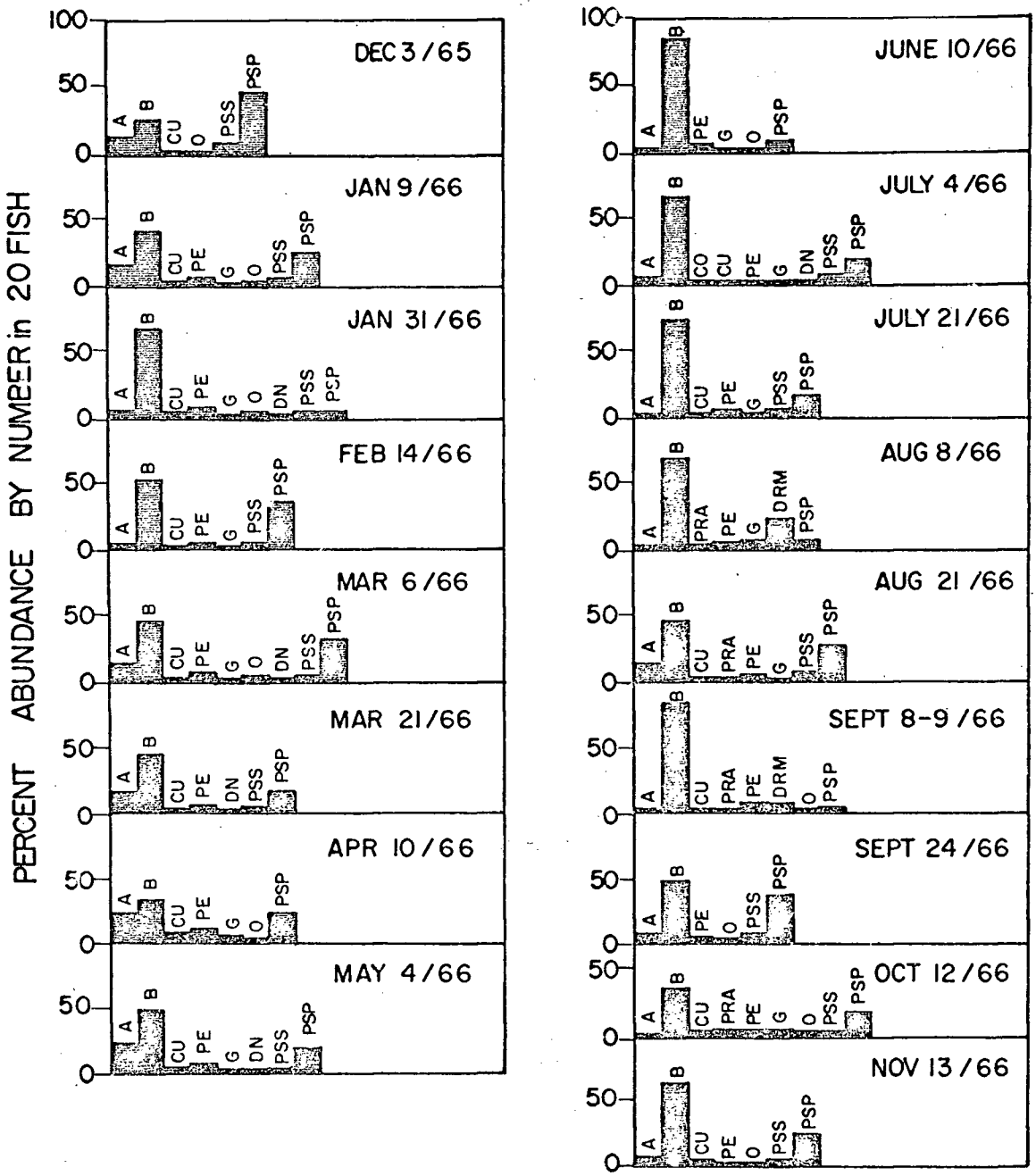


Fig. 13. Percent abundance by number of food items of L. pacifica. Data from 20 fish per time period collected at outer Burrard Inlet. A-Amphipoda; B-Bivalve molluscs; CO-Copepoda; Cu-Cumacea; DRA-Decapoda Reptantia(adults); DN-Decapoda Natantia; DRM-Decapoda Reptantia(megalopa); G-Gastropod molluscs; GP- Gastropod molluscs (Pectenaria spp.); O-Ostracoda; PE-Polychaeta Errantia; PSP-Polychaeta Sedentaria(Phyllochaetopterus spp.); PSS-Polychaeta Sedentaria(Sternapsis spp.).

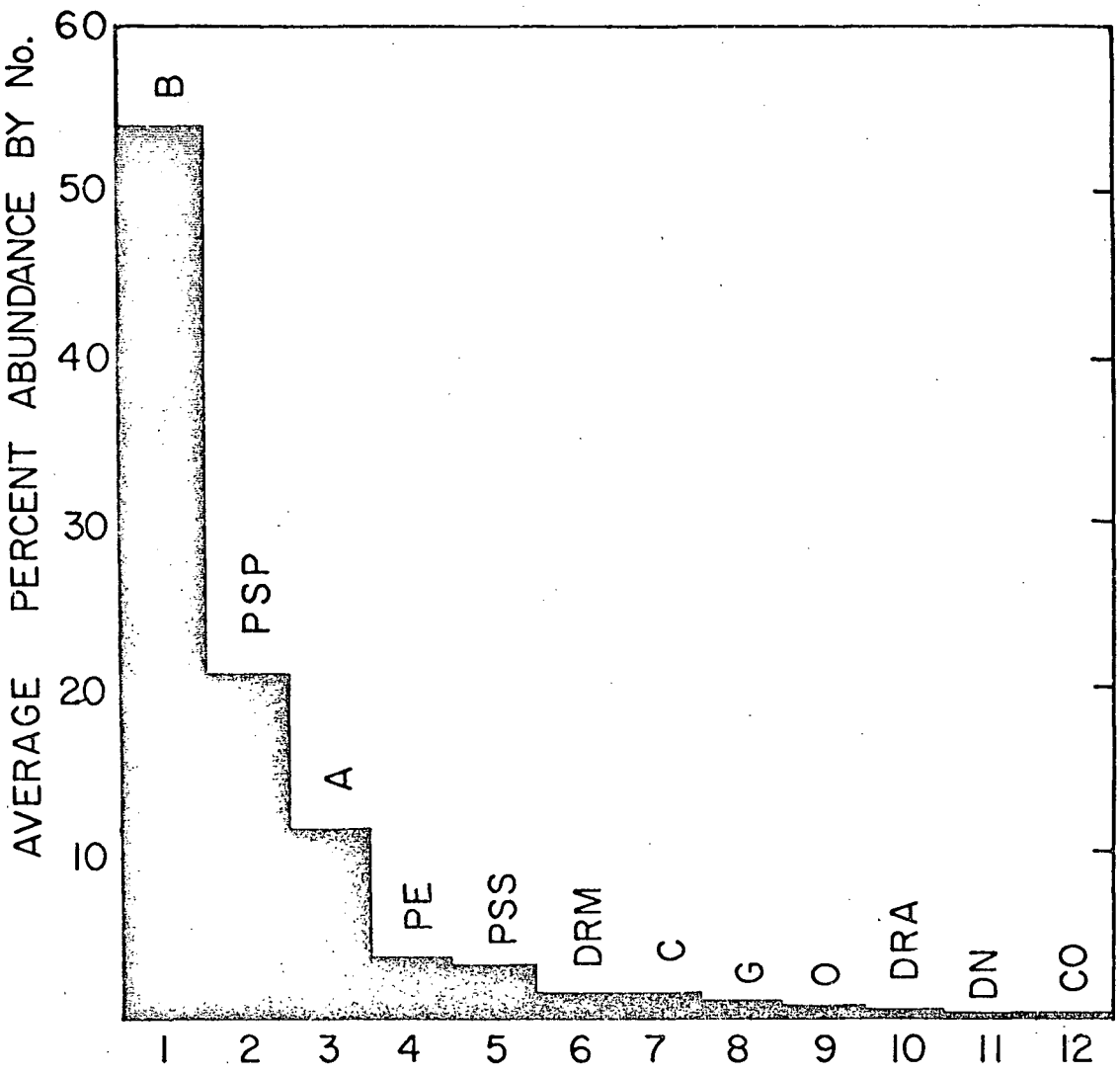


Fig. 14. Average percent abundance by number of food items found in 340 digestive tracts of L. pacifica. All fish collected at outer Burrard Inlet December 1965-November 1966. A-Amphipoda; B-Bivalve molluscs; CO-Copepoda; CU-Cumacea; DRA-Decapoda Reptantia(adults); DN-Decapoda Natantia; DRM-Decapoda Reptantia(megalopa); G-Gastropod molluscs; GP-Gastropod molluscs(Pectenaria spp.); O-Ostracoda; PE-Polychaeta Errantia; PSP-Polychaeta Sedentaria(Phyllochaetopterus spp.); PSS-Polychaeta Sedentaria (Sternapsis spp.).

Seasonal Differences in Food

Stomach content data from specimens collected at the West Vancouver fishing area were used to test the hypothesis that the food of *Lycodopsis pacifica* varied seasonally. Collections of December 3 1965 and January 9 1966 were considered winter samples. Collections of July 4 and 21 1966 were considered summer samples (Fig. 15). A nonparametric test was employed to determine if the food spectrum differed seasonally. Kendall's rank correlation coefficient, tau, was calculated as outlined in Siegel (1956). In these tests both percentage abundance by number and percent frequency of occurrence of food items were considered. For percent abundance at tau value of 0.733 is not significant at the 95% level (probability of rejecting is 0.1762). A tau value of 0.712 was computed for per cent frequency. This value is also not significant at the 95% level (probability of rejecting is 0.1814). The tests indicate that the food of *L. pacifica* can vary seasonally. Such differences as do occur may arise from seasonal variations in abundance and availability of such food items as amphipods, copepods, cumaceans, and ostracods.

Place of Collection and Food

It was hypothesized that different infaunal communities might be present at West Vancouver and Spanish Banks. The gut contents of *Lycodopsis pacifica* might indicate such a difference.

The digestive tract contents of 60 fish collected at Spanish Banks were available, and 220 were available from West Vancouver.

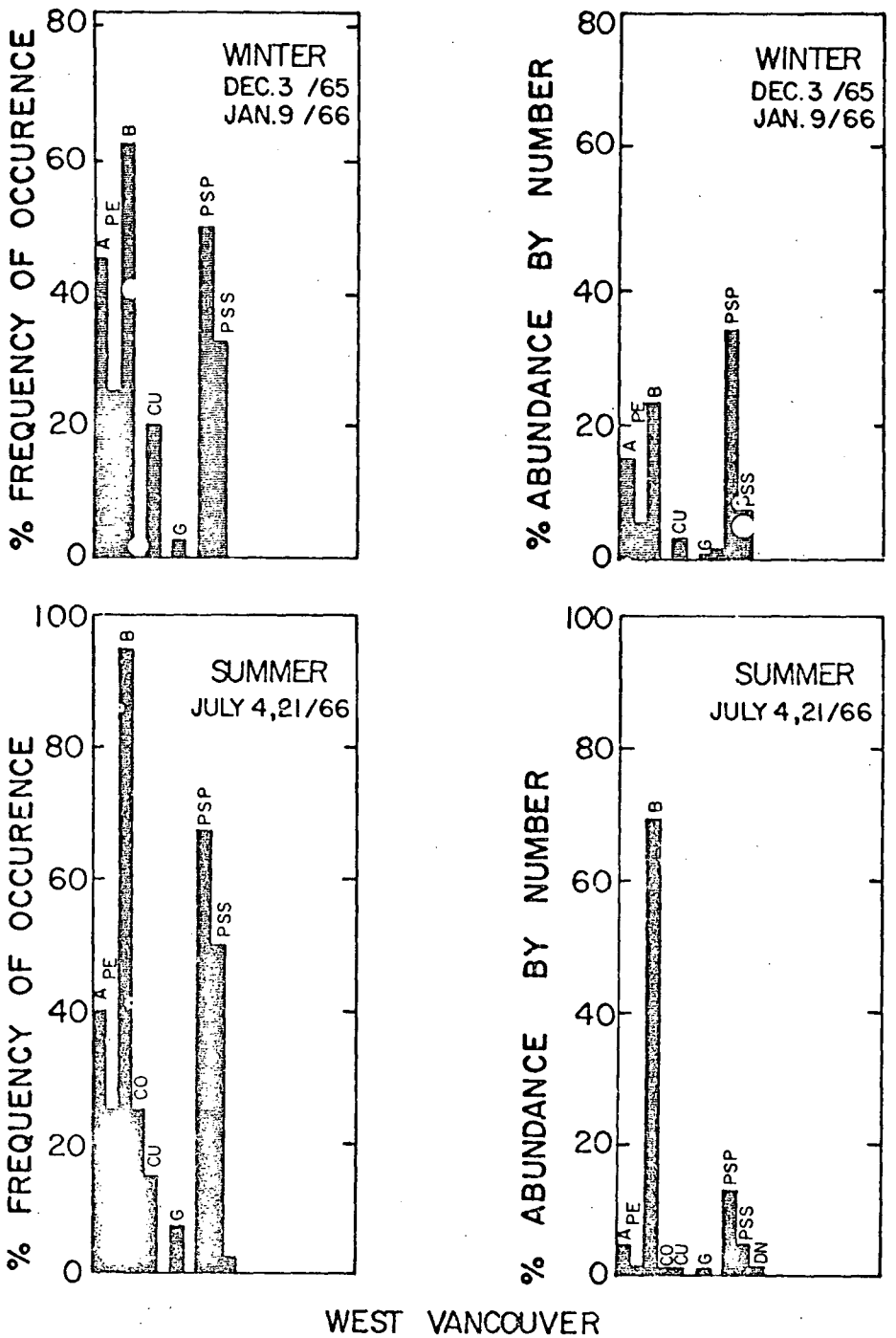


Fig. 15. Histograms displaying seasonal differences in the food spectrum of L. pacifica. All specimens collected at the West Vancouver fishing area in outer Burrard Inlet. A-Amphipoda; B-Bivalve molluscs; CO-Copepoda; CU-Cumacea; DRA-Decapoda Reptantia(adults); DN-Decapoda Natantia; DRM- Decapoda Reptantia(megalopa); G-Gastropod molluscs; GP-Gastropod molluscs (Pectenaria spp.); O-Ostracoda; PE-Polychaeta Errantia; PSP-Polychaeta Sedentaria (Phyllochaetopterus spp.); PSS-Polychaeta Sedentaria (Sternapsis spp.).

Kendall's rank correlation coefficient, tau, was calculated as outlined in Siegel (1956). Both percentage abundance by number and percent frequency of occurrence were considered (Fig. 16). Tau values of 0.192 and 0.117, respectively, were not significant at the 95% probability level. The tests indicate that the gut contents were different at Spanish Banks compared to West Vancouver. The major items which varied in importance were errant polychaetes (F. Nereidae) and sedentary polychaetes of the Families Chaetopteridae and Sternapsididae. This may indicate a difference in the soft bottom community and perhaps a difference in sediments at the two sites.

Changes in the Food Spectrum with Growth

The food spectrum of a species may change as individuals grow. Specimens collected in a single trawl at the Cape Lazo study area were used to investigate this matter. The collection was made on January 23 1966. The stomach contents of five individuals of each five millimeter length group were examined and the per cent abundance by number of each item was determined. Figure 17 indicates a greater variety of food items are found in *L. pacifica* of lengths approximately 100 mm and over.

Lycodopsis pacifica as a Member of the Bottom Community

In outer Burrard Inlet, *Lycodopsis pacifica* feeds upon a bivalve-annelid community. Many of the invertebrates recorded in the food spectrum of the species are components of the communities that Shelford (1935) suggests for Puget Sound approxi-

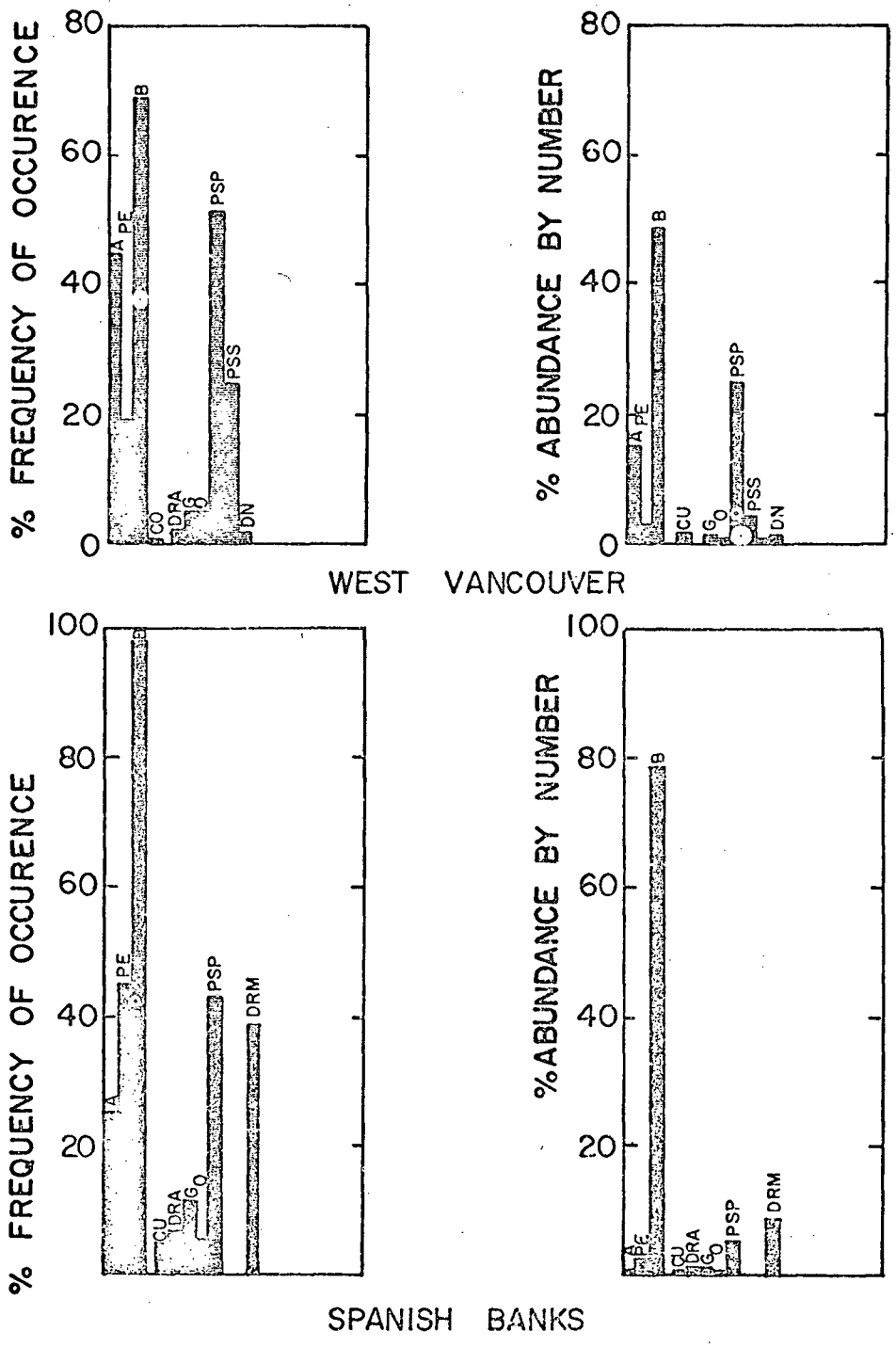


Fig. 16. Histograms displaying spatial differences in the food spectrum of L. pacifica. Spanish Banks data from 60 digestive tracts; West Vancouver data from 220 digestive tracts. Fish collected during December 1965 to November 1966. A-Amphipoda; B-Bivalve molluscs; CO-Copepoda; CU-Cumacea; DRA-Decapoda Reptantia(adults); DN-Decapoda Natantia; DRM-Decapoda Reptantia(megalopa); G-Gastropod molluscs; GP-Gastropod molluscs (Pectenaria spp.); O-Ostracoda; PE-Polychaeta Errantia; PSP-Polychaeta Sedentaria(Phyllochaetopterus spp.); PSS-Polychaeta Sedentaria (Sternapsis spp.).

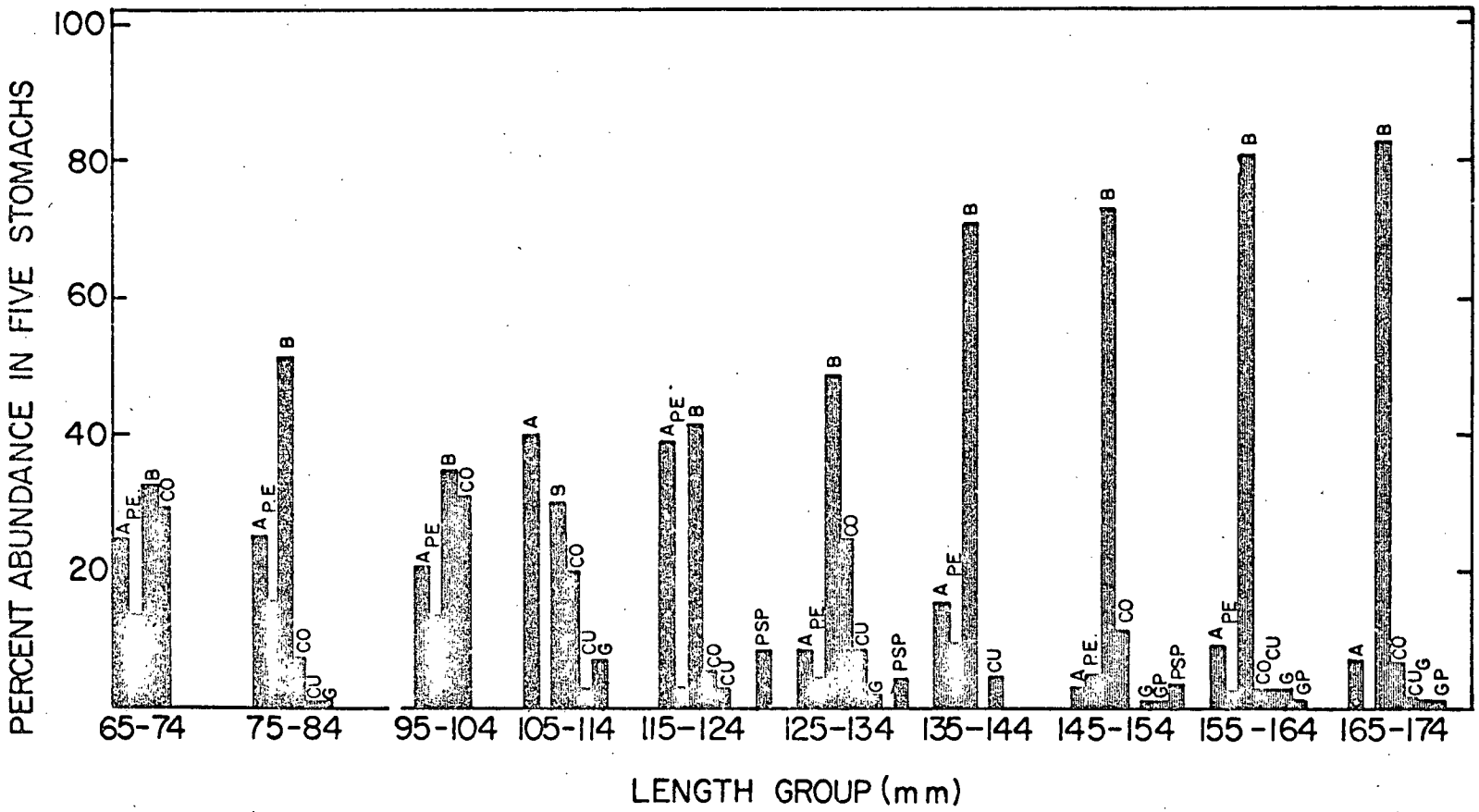


Fig. 17. Histograms of percent abundance by number of various food items of L. pacifica over the indicated length range. Samples taken at the Cape Lazo study area in January 1966. A-Amphipoda; B-Bivalve molluscs; CO-Copepoda; CU-Cumacea; DRA-Decapoda Reptantia(adults); DN-Decapoda Natantia; DRM-Decapoda Reptantia(megalopa); G-Gastropod molluscs; GP-Gastropod molluscs(Pectenaria spp.); O-Ostracoda; PE-Polychaeta Errantia; PSP-Polychaeta Sedentaria(Phyllochaetopterus spp.), PSS-Polychaeta Sedentaria (Sternapsis spp.).

mately 100 miles south of Burrard Inlet. Shelford (1935) terms L. pacifica an influent species of an "association", a "biome", and an "ecotone community". He does not define the term "influent species" but probably means an organism which occurs often in association with a discrete assemblage of animals. Mobile epifaunal animals such as L. pacifica are difficult to categorize into discrete assemblages.

Ting (MS 1965) developed a new type of sampler for demersal animals and he tested the device in Puget Sound for use in community analysis on muddy bottoms. He determined a close association among Lycodopsis pacifica, Lyopsetta exilis, Porichthys notatus, Compsomya subdiaphana, Macoma inflatula, Nucula castrensis and Phacoides centilosa in the mud community. These data indicate that L. pacifica is a component of a mud community.

All animals collected in the experimental trawling at outer Burrard Inlet were enumerated. The census included 75 ten-minute trawls made in May and June 1966. Pertinent dimensions of the trawl are found in Table III, p. 8. Fishes collected were mainly demersal or bottom forms although some pelagic species were recorded. The invertebrates captured were a mixture of infaunal and epifaunal species (definition according to Petersen, 1913 in Thorson, 1957).

Lycodopsis pacifica occurred in trawls with members of 15 families of fishes (classification of Berg, 1941). Pleuronectids were represented by 11 species. Gadidae and Cottidae were represented by three species each. One or two species of the remaining families were captured. A faunal list of the fish

species collected is found in the Appendix, page 78.

Lycodopsis pacifica dominated the catches. The species occurred in 90.6% of the trawls. The pleuronectid species Glyptocephalus zachirus, Microstomus pacificus and Lyopsetta exilis ranked after L. pacifica in per cent frequency of occurrence. Glyptocephalus zachirus occurred in 77.4% of the trawls, Microstomus pacificus in 77.0%, and Lyopsetta exilis in 55.4%.

There is no evidence that any of the species captured in the trawls prey on L. pacifica. The piscivorous species recorded, for example Atheresthes stomias, were immature and were incapable of ingesting L. pacifica of the size range encountered.

The invertebrates captured in the trawls were members of the Phyla Echinodermata, Coelenterata, Mollusca, Platyhelminthes and Subphylum Crustacea (classification following Barnes, 1963 and Borraidile and Potts, 1963). Members of the Order Decapoda (Subphylum Crustacea), in particular Tribe Natantia, were most abundant and occurred most frequently. Cragnon communis, for example, occurred in 93.2% of the trawls. Spirontocaris holmesi and Pandalus spp. were also frequently captured. A member of the Tribe Reptantia of this order, Cancer magister, occurred in 87.9% of the trawls. For faunal list of the invertebrates captured see the Appendix, pp. 80 and 81.

MORPHOLOGY, FEEDING AND SEDIMENTS

The objective of the following section is to describe and interrelate the anatomy of the feeding structures and feeding habits of Lycodopsis pacifica. The original working hypothesis for this investigation was based on statements from Jones (1950): "There is ..... no complete specialization (of feeding) on any one type of deposit, and the evidence does not indicate that feeding habit, in the broad sense, is of paramount importance in restricting species to a particular type of bottom. Nevertheless, it is possible that closer examination of individual animals will show it to be important in many cases".

In the above statements, Jones is referring to the morphological, physiological and behavioural adaptations of infaunal invertebrates. It was hypothesized that the concept of "specialization of feeding habit on one particular deposit" might be applicable to Lycodopsis pacifica. Studies of the food show L. pacifica is capable of feeding on several components of a soft-bottom community. The species is probably an "opportunist" and is able to ingest a variety of infaunal (and epifaunal) organisms, within the capabilities of structures associated with food getting.

The feeding adaptations of marine bottom fishes have not been studied. Nikolsky (1963) points out that the feeding habits of fishes are determined primarily by the abundance of food organisms present in the environment to which the fishes are adapted. Thorson (1957) has pointed out the stability in abundance of most infaunal organisms of the soft-bottom communi-

ties. Keast and Webb (1966) show how differences in mouth and body form in relation to feeding ecology may separate co-habiting species of freshwater fish.

Moiseev (1952), in a paper dealing with fishes of the northwest Pacific, states "... a fairly well-guaranteed food supply, the variety and relative stability of the biocoenotic grouping has led to a clear differentiation of the most numerous species (small-mouthed flounders, large-mouthed flounders, cod and Alaska pollack)." Here is mention of feeding morphology in relation to food supply. The comment may have its parallel in some fjords of the British Columbia coast. In at least some inlets, L. pacifica is a dominant member of the bottom fish fauna.

A. Mouth Form

The mouth of L. pacifica may be described as "shovel shaped." Large mature males have been termed "alligator heads." The snout terminates in a blunt point and the mouth is nearly horizontal with the body axis. The lower jaw is included in the gape. The lips are well-defined and fairly large. In this description of the species, Bayliff (MS, 1954) gives pertinent measurements. In the present study the mouth form of L. pacifica in several aspects is shown in Figs. 18 and 19.

B. Buccal, Pharyngeal and Esophageal Regions

The buccal apparatus of L. pacifica is well-equipped with structures for holding food in the oral cavity. The 15 premaxillary teeth are arranged in a single series. The dentaries are each covered with 20 teeth which form a patch anteriorly and which are reduced posteriorly to a single series. All teeth are approximately equal in size (Bayliff, MS, 1954). Further

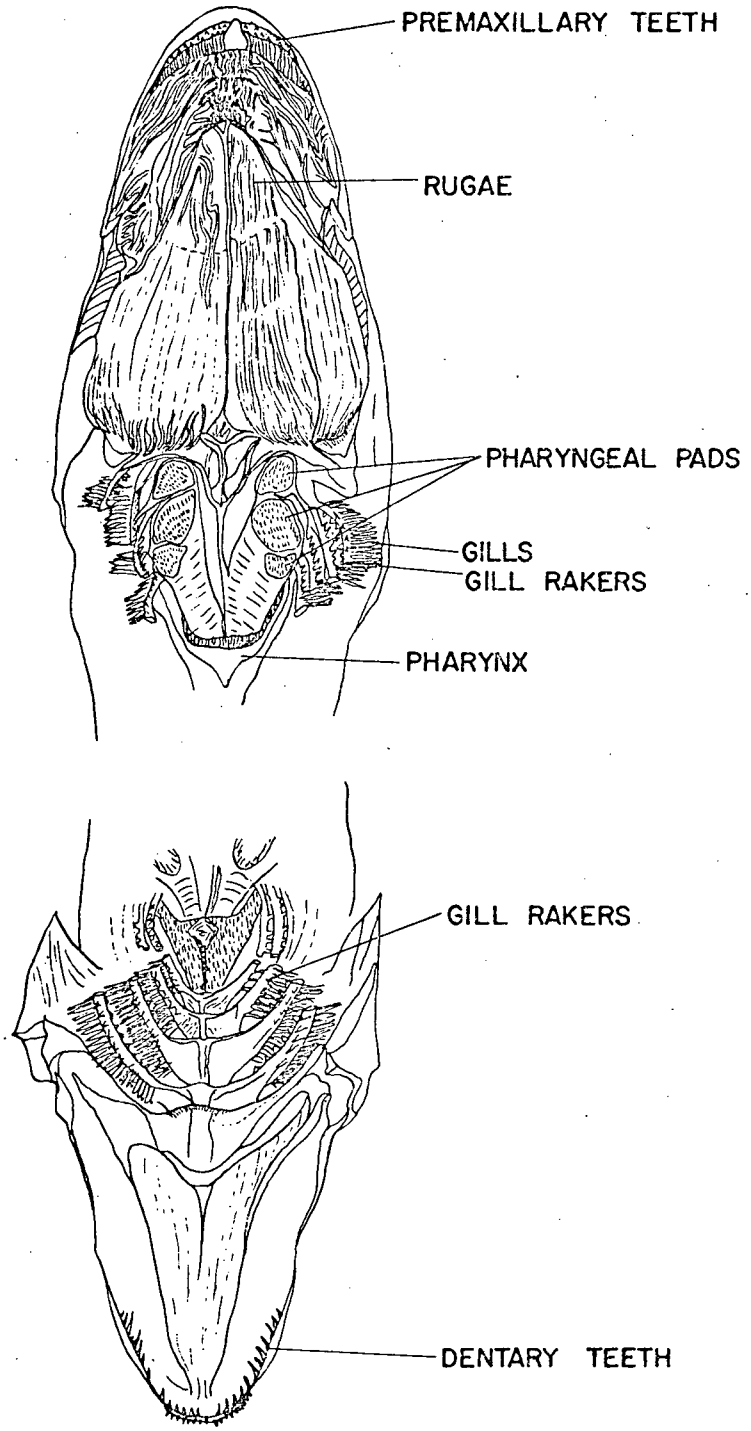
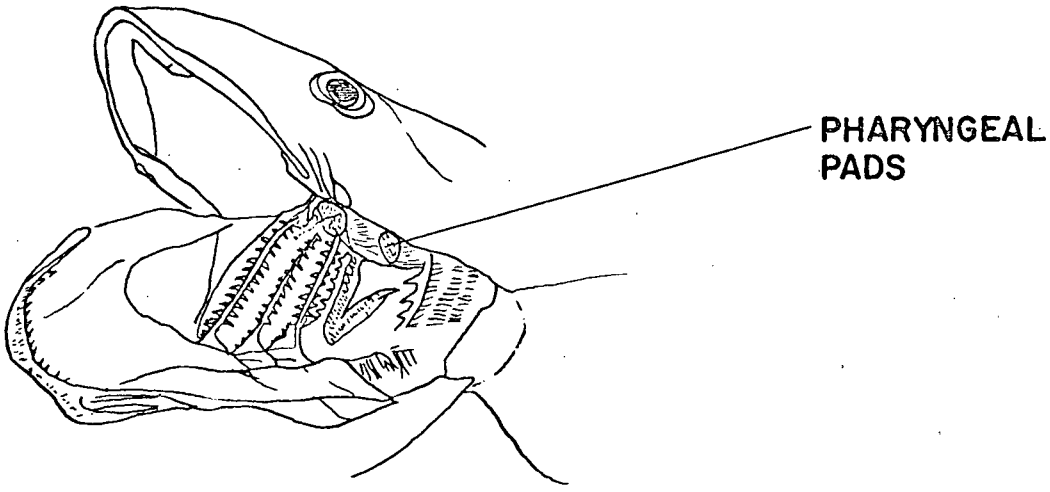
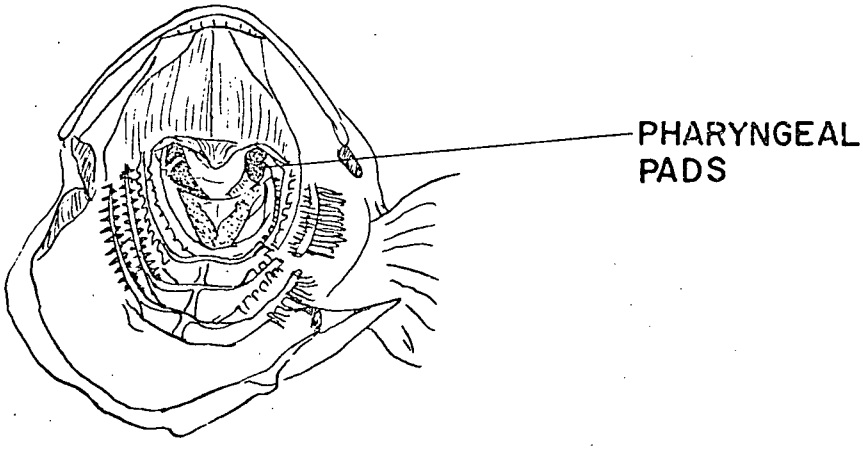


Fig. 18. Anterior views of the buccal region of L. pacifica(X1½)



SIDE VIEW - CUT THROUGH LEFT ANGLE OF JAW



FRONT VIEW SLIGHTLY FROM THE LEFT

Fig. 19. Lateral and anterior views of the buccal region of L. pacifica (X1½)

posterior on the floor and roof of the buccal cavity two ellipitical developments of "flesh folds" or rugae occur. Posterior to these are a series of folds which extend to the region of the pharyngeal pads (Fig. 18).

The pharyngeal pads are large fleshy mats (length ratio 0.46 of premaxillary length in ten mature male specimens) located in the posterior part of the buccal cavity. They are separated medially by continuations of the rugae, and each pad is divided into three parts by muscular septa continuous with the branchial apparatus. The pads are set loosely in depressions, and are covered with several hundred horny "teeth" which are opposed by the flattened gill rakers. The isthmus of the branchial apparatus is triangular-shaped, covered with "teeth", and partly opposes the pharyngeal pads. The pharynx opens at the posterior end of these pads.

C. Stomach and Intestine

The elongated intestine ranged in length from 0.36 to 0.59 of the total length of the fish (mean of 0.48 based on 20 individuals). Bivalve molluscs are digested in the intestine when not crushed by the pharyngeal pads. A variable number of small caeca (6 to 7 in ten specimens) are located near the duodenum. Location of other digestive organs is approximately as described by MacKay (1926) for *Macrozoarces americanus*.

The feeding morphology of *Lycodopsis pacifica* enables the species to obtain the most abundant food in its habitat. *L. pacifica* is restricted to close association with the bottom. No swim bladder is present, and the species probably rarely swims

off the bottom. It is speculated L. pacifica removes infaunal organisms from the sediments by a "sifting" process. The pharyngeal pads and associated structures are adaptations which aid in crushing and grinding of infaunal invertebrates. The elongated intestine may be an adaptation to digestion of pelecypods.

Sense Organs and Food Detection

Anatomical observations of the brain of Lycodopsis pacifica were made. The olfactory nerve (I) is reduced, and the olfactory lobes of the brain are poorly developed. The nerve leads anteriorly and innervates a rosette located under the nasal flap. The facial nerve (VII) was found to be very well developed, and equalled the optic (II) in diameter. A branch of the facial nerve innervates the masseter muscle, and a major component continues anteriorly to the rosette mentioned above. Other branches innervate the fleshy folds of the maxillary and premaxillary regions (Fig. 20). The facial nerve is composed of mixed sensory and motor fibers (Erickson, 1963).

Erickson (1963) emphasizes that "oro-pharynageal sensations" are essential when an animal must find food and eat it. For fishes living on a soft bottom, gustation would be of advantage in locating infaunal food items. Gustatory sense fibers in the facial and other nerves may be of considerable importance in the feeding behaviour of L. pacifica.

Animals maintained in the aquarium were observed to rest on their expanded pectoral fins. The reduced pelvic fins contact

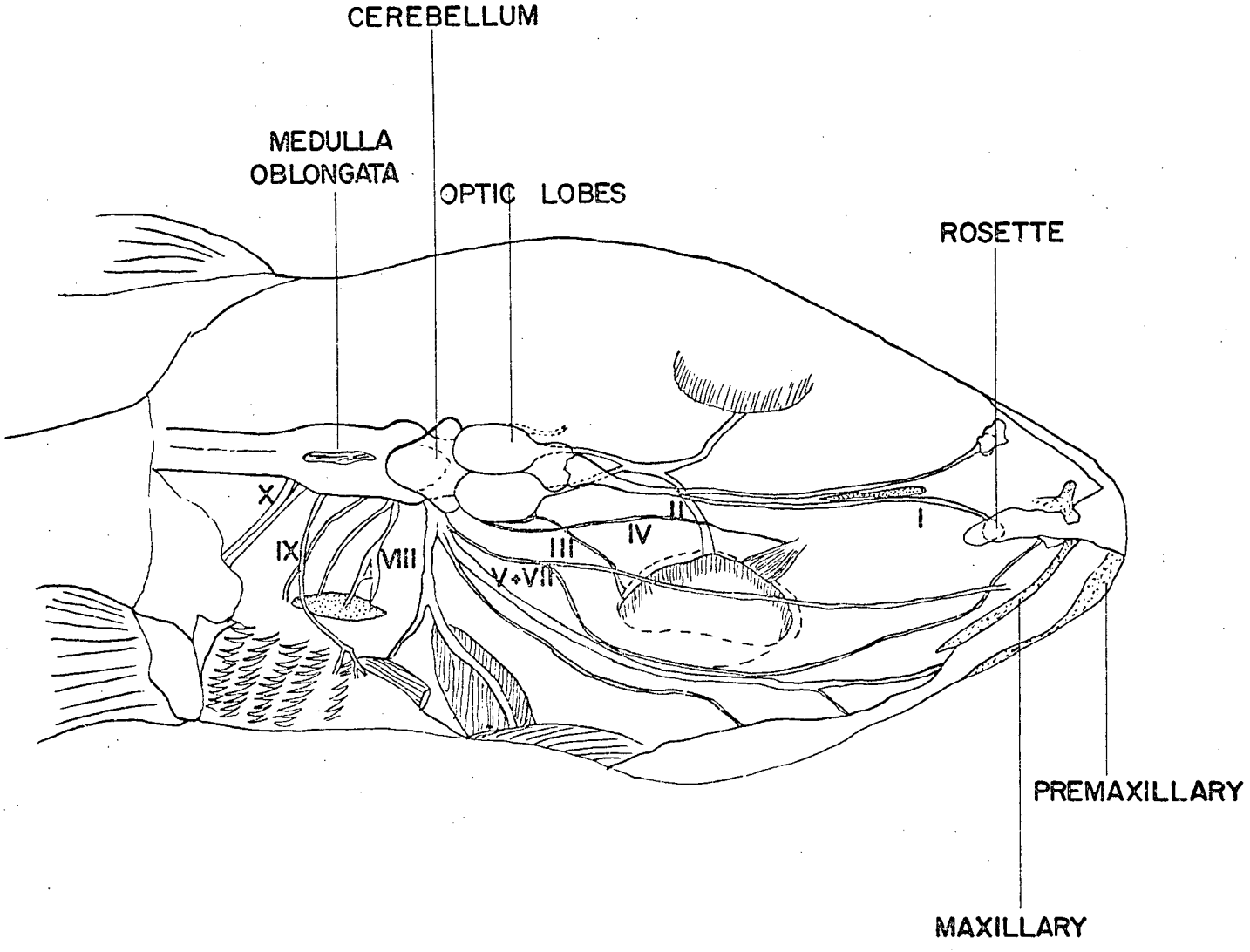


Fig. 20. Dorsal view of the brain and cranial nerves of L. pacifica (X3)

the substrate. Friehofer (1963) describes the pattern of innervation via the facial nerve (VII) in this region for Lycodopsis pacifica. It was hypothesized that cutaneous sense organs might be found in the reduced pelvics of L. pacifica.

The pelvic fins of five specimens were stained with haemotoxylin and eosin, sectioned, and examined under the microscope. "Sense organs" were not observed. However, in the epidermis of the ventral body surface were found cells located in pits. The structures resembled "sense organs" or "sense cells" described by other workers in different species of fish. Jakubowski (1960) reported similar structures in the viviparus blenny (Zoarces viviparus) and the eel (Anguilla anguilla). Epidermal sense organs were recorded by Moore (1950) for minnows living in the muddy fresh waters of central North America.

Observations of feeding behaviour in the aquarium are of interest in this discussion. The individuals maintained on fine sediments in March 1966 were observed to cough frequently. "Coughing" released infaunal invertebrates from the mud. The food items might be ingested during the inhalent respiratory movement.

Individuals maintained in the aquarium on "coarse" sediments in December 1966 did not show the "coughing" behaviour mentioned above. They were not observed to feed on the infaunal Phyllochaetopterus spp. that were abundant in the substrate. The fish fed readily on chopped raw oysters and fish. They appeared to be able to detect food items dropping from the

surface before the items reached the bottom. Samples from outer Burrard Inlet indicate that Lycodopsis pacifica occasionally ingested pelagic organisms that ventured close to the bottom. Examples of such organisms found in the digestive tracts are megalopa larvae of Cancer magister and Hyperid amphipods (Hyperia spp.). These organisms might be detected visually by L. pacifica. The eyes of the species are directed dorsally (Fig. 10), enabling detection of material floating near the bottom.

However, the vast majority of the food items recorded from the digestive tracts of the species are relatively sessile infaunal invertebrates (for example, sedentary polychaetes, cumaceans, gastropods, and pelecypods) (Fig. 14). Some of these organisms are probably found below the mud surface, and might not be detected visually.

The food spectrum of the species indicates Lycodopsis pacifica is an "opportunist". Anatomical evidence suggests the species is adapted to eat benthic infaunal invertebrates, but is not specialized to one particular type of food organism. If bottom type restricts the components of the bottom community in outer Burrard Inlet, the evidence indicates L. pacifica is not specialized to one particular type of deposit. Within the scope of its morphology a variety of organisms are removed from sediments and eaten by the species. For a given area, there are probably certain locations where maximum concentrations of suitable infaunal food organisms are found. These locations may by correlated with sediment type.

SEDIMENTS AND ABUNDANCE OF *Lycodopsis pacifica*

Elton (1949) pointed out that no habitat is homogeneous and that clumping of animal populations is common. The pattern of "clumping" is probably determined by two sets of factors, the behaviour of the species and the physical heterogeneity of the habitat. It is particularly difficult to study these two factors simultaneously in the sub-littoral marine environment.

Verwey (1949) mentions that "non-burrowing, bottom-dwelling, mobile" forms do not show distinct habitat selection for a particular substratum. For a particular area, however, the feeding aggregations of the species may be largest where suitable food organisms are concentrated and where feeding morphology can operate most efficiently. The concentrations of infauna may be related to the physical nature of the substrate.

A field experiment was performed in outer Burrard Inlet to try and determine if *Lycodopsis pacifica* aggregated on certain sediment types. Additional information was collected at the Cape Lazo area.

Description of Sediments

Sediments are described by marine geologists according to systems based on median or modal diameter of the particles composing the sediment (Shepard, 1963). Generally, particles of diameters greater than 62 microns are called sand. Silts and clays are particles of diameters less than 62 microns diameter. Folk (1965) outlines techniques for determining median or modal grain size. The method involves screening and fractional

weighing of sands. Silts and clays are analyzed by pipette or hydrometer, utilizing differential settling rates in water.

Beanland (1940), Holme (1949), Chapman (1949), Okuda and Sato (1955), and Webb (1958) have stressed the importance of the interstitial spaces between sediment particles. These workers feel some measure of the interstitial space may be a critical factor for bottom-dwelling animals. The interstitial space may be measured by a variety of methods including median or modal grain size, permeability or porosity as measured by water content, per cent fine and per cent coarse sediments (silt and sands), and various packing models.

At the outer Burrard Inlet experimental area, the per cent silt and per cent sand in each sediment sample was used as a description of the substrate. The value was computed from the dry weight ratio of particles less than 62 microns in diameter to particles greater than 62 microns in diameter.

Bottom samples from the Cape Lazo gully were analysed for modal grain size in August 1966 by Dr. R. Sheldon. The data were kindly made available to the writer. The techniques employed for analysis involved use of the Coulter counter. Technical details are found in Sheldon and Parsons (1967).

Sampling Patterns

At outer Burrard Inlet, three sampling transects were designated (Fig. 1); trawl and grab stations were at 5 fm (9.2 m) intervals. The depth range was 5 fm (9.2 m) to 25 fm (45.4 m). Each station was sampled with the experimental trawl

five times in May and June 1966. The following abbreviations are used when referring to the transects: SB represents Spanish Bank transect, P represents Point Grey transect, and N represents North Arm transect. The number following the abbreviation indicates the depth of sampling in fathoms.

The Cape Lazo gully was sampled along nine sections (Fig. 2). The sampling depths across the sections were at approximately 5 fm (9.2 m) intervals. Each depth was sampled a variable number of times.

To obtain sediments, a Dietz-Lafond bottom sampler (see Shepard, 1963) was used at both study sites.

Results and Analysis

Catches of *Lycodopsis pacifica* at outer Burrard Inlet ranged from 0 to 143 individuals per trawl (Table IV). At the Cape Lazo gully, the catches ranged from 0 to 474 individuals per trawl.

Sediment at outer Burrard Inlet ranged from 2.4% silt to 99.7% silt (Table IV). Modal grain size in the Cape Lazo gully ranged from 58 to 250 microns. Approximate contours of modal grain size in the gully are shown in Fig. 23.

The sampling pattern at outer Burrard Inlet was designed to test station differences in abundance by analysis of variance. Normalization of data was achieved by a log (X + 1) transformation (Steel and Torrie, 1960). The procedure was necessary because of zero catch values in several hauls.

All analyses of variance applied to the catch data were

Table IV. Catches of *L. pacifica* per ten minute trawl at the outer Burrard Inlet experimental area. Dates of sampling May and June 1966. The sediments at each station are also described.

	DEPTH				
	5 fm (9.2 m)	10 fm (18.3 m)	15 fm (27.4 m)	20 fm (36.7 m)	25 fm (45.6 m)
Spanish Banks Transect	1	7	9	7	0
	23	43	20	1	2
	37	27	5	7	4
	143	36	27	1	1
	8	53	15	0	1
	43.5% Silt	97.5% Silt	89.6% Silt	91.7% Silt	86.2% Silt
Point Grey Transect	0	9	96	7	13
	0	73	14	57	33
	6	10	13	16	10
	3	32	19	37	23
	2	27	13	7	36
	2.4% Silt	93.9% Silt	99.7% Silt	95.7% Silt	94.7% Silt
North Arm Transect	0	15	32	1	7
	0	5	42	4	3
	6	42	42	0	68
	2	8	5	63	105
	4	2	15	2	7
	67.6% Silt	72.8% Silt	81.1% Silt	79.4% Silt	88.4% Silt

Table V. Catches of *Lycodopsis pacifica* per ten minute trawl at the Cape Lazo gully. Data averaged over sampling in November 1965, January 1966, and August-September 1966.

SECTION	DEPTH (fm)	NUMBER	SECTION	DEPTH	NUMBER
1	30	56	5	30	1
	35	59		35	118
	40	93		40	143
	42	113		45	235
	44	232		50	1250
2	30	0	6	30	1
	35	208		35	10
	40	201		40	75
	45	127		50	197
3	30	135	7	30	7
	35	72		35	113
	40	178		40	178
	45	474		45	293
	50	334			
4	35	264	8	40	221
	40	257		45	389
	45	146			
	50	319			

significant at the 95% level (Table VI). The results verified the hypothesis that Lycodopsis pacifica was not uniformly abundant over the transects sampled. Bartlett's test for homogeneity of variance (Steel and Torrie, 1960) was applied to the variance data from the three transects. A chi-square value of 1.200 (2 d.f.) was not significant at the 95% level. The test verified the additivity of the variance information. Subsequently analysis of variance over the three transects combined was performed. Once again the above-mentioned hypothesis was accepted.

A multiple comparison technique developed by Scheffé (1953) was utilized to test the significance of differences in catches at the various stations. This is a system for constructing confidence limits for all imaginable contrasts of an experiment employing analysis of variance. Its advantage lies in the fact the comparisons are independent of each other. Significance of a contrast is judged by noting whether the confidence interval brackets a value of zero. If, for each experiment we perform, we construct confidence limits, in (1 - alpha) of these experiments all the confidence statements will be correct, and in α of the experiments one or more confidence statements will be incorrect. Alpha (α) is the complement of the probability level being used - here 0.95 (see Appendix, p. 81).

Differences in catches of Lycodopsis pacifica at the various depths and sediment types were compared for statistical significance using the technique (Table VII). Catches at five

Table VI. Analysis of variance of catch data for *L. pacifica* at the outer Burrard Inlet experimental area (* indicates significance at the 95% probability level; ** indicates significance at the 99% probability level).

ANALYSIS OF VARIANCE DATA FOR THE THREE TRANSECTS

Spanish Banks

Source	d.f.	Sum. Squares	Mean Squares	F-ratio
Treatment (Stations)	4	5.0371	1.1259	
Error	20	3.5188	0.1759	
Total	24	7.9259		6.4007*

Point Grey

Source	d.f.	Sum. Squares	Mean Squares	F-ratio
Treatment (Stations)	4	3.6218	0.9054	
Error	20	2.4233	0.1211	
Total	24	6.0451		7.4764**

North Arm

Source	d.f.	Sum. Squares	Mean Squares	F-ratio
Treatment (Stations)	4	3.1991	0.7997	
Error	20	5.4129	0.2706	
Total	24	8.6120		2.9552*

stations, namely P5, N5, N20, SB20 and SB25 were found to be significantly different (lower) than catches at the other ten stations (Table 7). The per cent silt ranged from 2.4% to 94.7% at the five stations. The depth range was 5 to 20 fm (9.2m-45.6m).

These conclusions are based on all transect data. The variances in catches differed from one transect to another. The F-ratio of the analysis of variance carried out on catches from North Arm transect is quite low (Table VI). Even though the additivity of the transect variance is proved by Bartlett's test (see above) divergent results are obtained depending on which variance data are used. For example, using data from the Spanish Banks and Point Grey transects only, the contrast is significant. A number of combinations were tested (Table VII). In general, statistical tests suggest rejection of the original hypothesis. At outer Burrard Inlet, aggregations of Lycodopsis pacifica were not found to occur on sediments of a certain physical nature as measured by per cent silt and per cent sand. In addition, diagrams relating catches of L. pacifica to sediment type (% silt) and depth (fm) were constructed (Figs. 21 and 22). There is no suggestion from these plots that aggregations of L. pacifica are affected by these two factors.

A statistical approach was not adopted at the Cape Lazo study site. Following discussion will be limited to sampling on the west side of the gully. On the east slope, the hard bottom required sampling with a trawl equipped with "rollers" on the groundline. This type of trawl is probably far less efficient at capturing Lycodopsis pacifica than the standard trawls utilized on the west slope. The catch data were averaged over the

Table VII. Tests of significant differences between catches of *L. pacifica* at outer Burrard Inlet transect stations. Contrasts according to the method of Scheffé (1953).

CONTRAST	VARIANCE DATA USED	SIGNIFICANCE (95% prob. level)
SB5 vs SB25	All inter-transect data	Not significant
N25 vs SB25	North Arm, Spanish Banks data	Not significant
N15 vs N20	North Arm data	Not significant
SB5 vs P5	Point Grey, Spanish Banks data	Significant
SB5 vs SB25	Spanish Banks	Significant
all SB, P vs N	All inter-transect data	Not significant
P15 vs SB15	Point Grey, Spanish Banks data	Not significant
SB20, SB25, P5, N5, vs remaining stations	All inter-transect data	Significant
SB20, SB25, P5, N5, vs remaining stations	All inter-transect data	Significant
N20 vs SB20, SB25, P5, N5	All inter-transect data	Not significant

Key to abbreviations:

SB = Spanish Banks Transect
P = Point Grey Transect
N = North Arm Transect

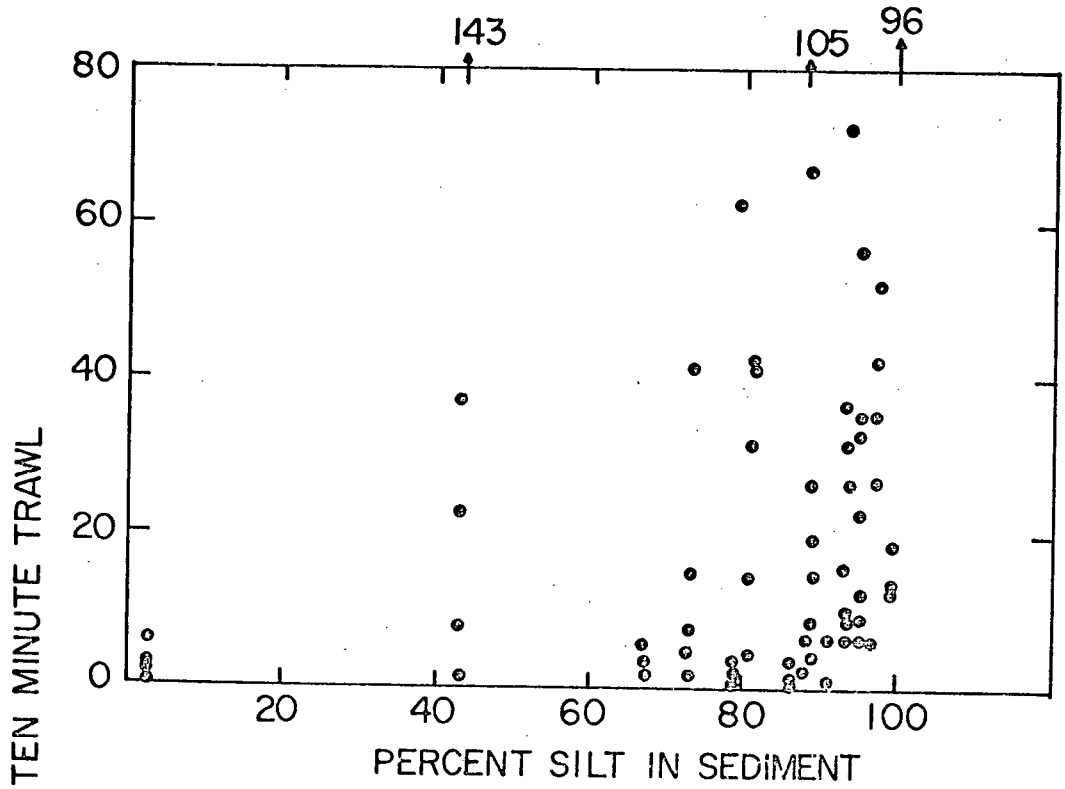


Fig. 21. Catches of L. pacifica at outer Burrard Inlet related to sediment type.

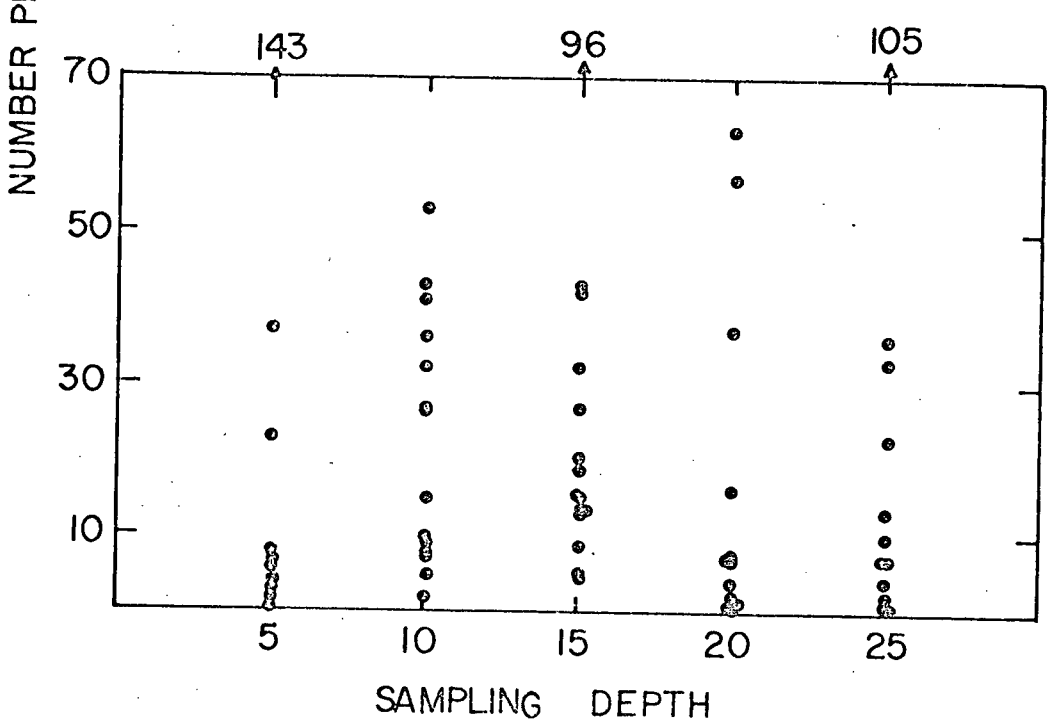


Fig. 22. Catches of L. pacifica at outer Burrard Inlet related to sampling depth.

three sampling times (Table V), indicating the species was more abundant in the bottom of the trough (Fig. 23). Diagrams relating L. pacifica to sediment type and depth (fm) were constructed (Fig. 24 and 25). The plots suggest that L. pacifica was more abundant at depths greater than 40 fm (73.2 m) where modal diameter of the sediment was less than 80 microns and may be considered "silt".

Discussion of Results

Results at the two study areas indicate two different environments are present. At outer Burrard Inlet, Lycodopsis pacifica was captured in high abundance on several sediment types, ranging from a silt-sand mixture to soft silt. At the Cape Lazo gully the species was captured in high abundance on silt. The premise of the preceding studies is that L. pacifica will aggregate where suitable infaunal food organisms are concentrated, and where feeding morphology can operate most efficiently. Discussion of results, then, should involve three topics: Firstly, factors influencing the "habitat preference" of L. pacifica; secondly, the possibility of direct nutritive value of the sediments; and finally, factors influencing the infauna, in particular, sediment properties.

Factors Influencing Lycodopsis pacifica

Temperature and salinity are two major physical factors that can affect the habitat preference of fishes. In the present study, L. pacifica was found in abundance over consider-

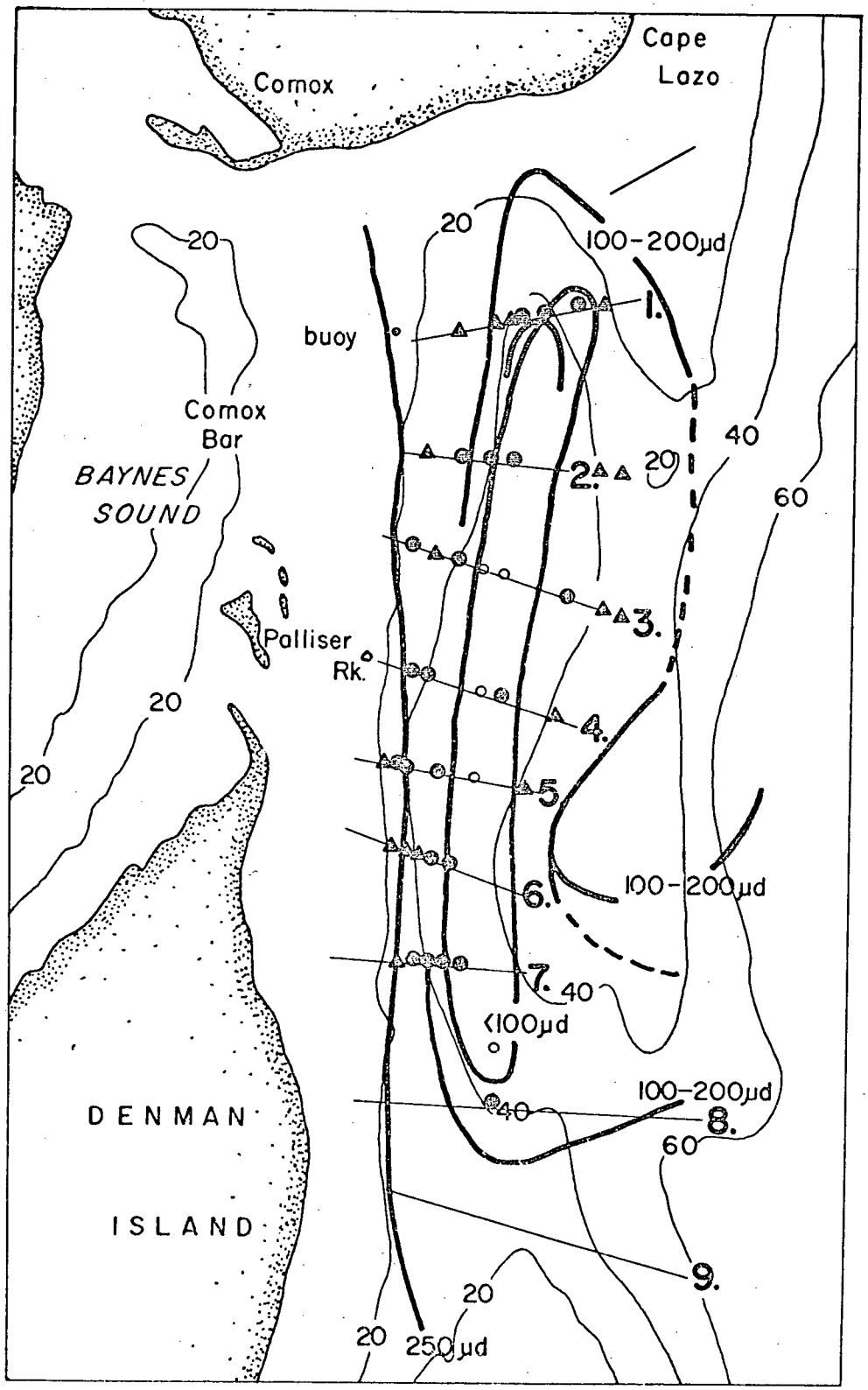


Fig. 23. Average catches of L. pacifica in relation to modal grain diameter of sediments (in microns) at the Cape Lazo gully. Data from collections in November 1965, January 1966, and August-September 1966. △ - 0 to 100 individuals per 10 minute trawl; ◉ - 101 to 299 individuals per ten minute trawl; ○ - 300 individuals per ten minute trawl.

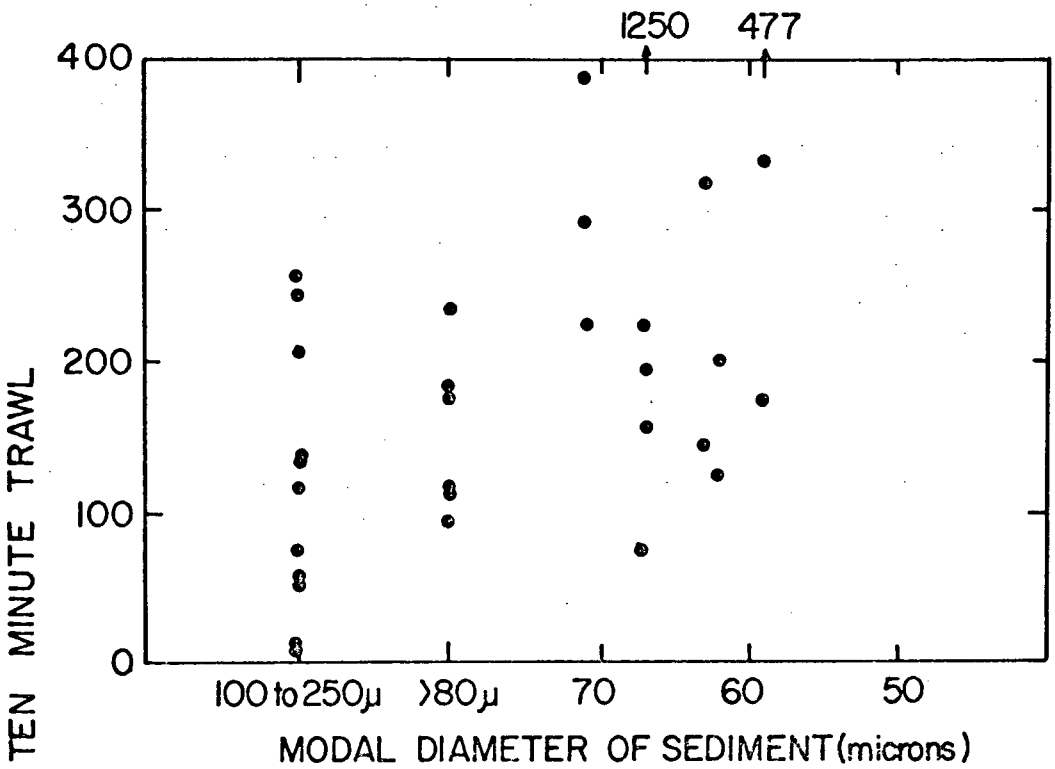


Fig. 24. Catches of L. pacifica at the Cape Lazo gully related to sediment type.

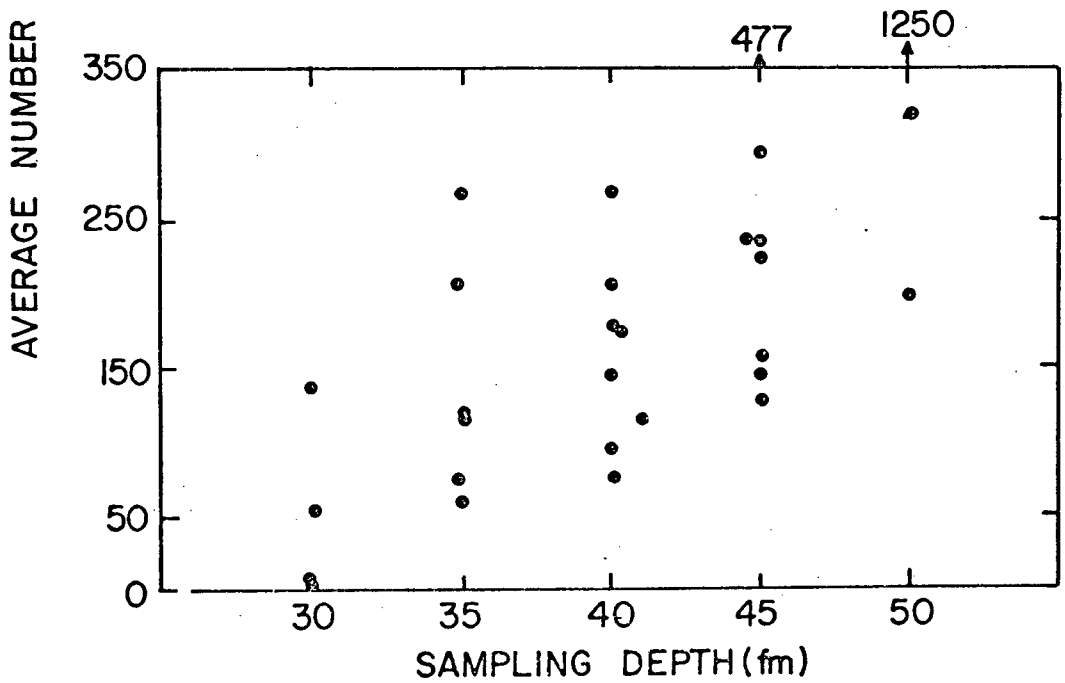


Fig. 25. Catches of L. pacifica at the Cape Lazo gully related to sampling depth.

able ranges of temperature and salinity. At the Cape Lazo gully, for example, bottom temperatures ranged from 7.02°C to 10.60°C. Salinities ranged from 28.79 ‰ to 30.42 ‰. As outer Burrard Inlet is an estuarine environment, these parameters may vary widely. The stage of the tide, for example, may affect the temperature and salinity regimes at the shallow locations. Fjarlie (1950) encountered temperatures ranging from 8.90°C to 15.50°C, and salinities ranging from 15‰ to 30‰. In general, Fjarlie found shallow stations have higher temperatures and lower salinities than deeper stations at outer Burrard Inlet. L. pacifica was found in high abundance at both shallow and deep locations. More hydrographic information would be needed to determine the importance of temperature and salinity at both study areas.

The recorded depth range of the species is from just below the intertidal zone (Bayliff, MS, 1954) to over 200 fm (365.5 m) (Clemens and Wilby, 1961). Depth may not be important factor affecting the habitat preference of the species. The situation is very complicated. At least three variables may be correlated with depth - sediment type, temperature, and salinity. The relative importance of the factors may vary from one location to another.

Habitat preference can vary with the life history of the species. There is some evidence from the present study which indicates age groups of Lycodopsis pacifica differ in their habitat preference. For example, Stations SB5 and N25 differ in sediments. The sediments at SB5 contained much more sand

than did N25. The two stations cover a depth range of 20 fm (36.5 m). Lycodopsis pacifica was captured in high abundance at both stations. Length frequency polygons of individuals captured at the two stations show younger fish were caught more frequently at Station N25 than SB5 (Fig. 26). However, more sampling would be necessary to show and age-specific difference in habitat-preference.

Possibilities of Direct Nutritive Value of Sediments

Lycodopsis pacifica ingests sediments in trace amounts. The species may prefer habitats rich in some organic or inorganic constituents. Some marine sediments may be of significant nutritive value of a particular chemical is associated with them. There is little information on the matter. Sheldon and Warren (1966) note that several species of crustaceans and fishes ingest sediments. The fiddler crab (Uca spp.) has been shown to obtain nutritive material from fine sediments (Miller, 1961).

Sediment Properties Influencing Concentrations of Infauna

The factors influencing concentrations of the infaunal food organisms of Lycodopsis pacifica will now be considered. Sediment characteristics in particular will be discussed.

In the past it has been assumed that standard geological methods describing sediments are useful in studies concerning marine bottom fauna. As pointed out by Thorson (1957) this is probably true over wide ranges of particle size, e.g., sand

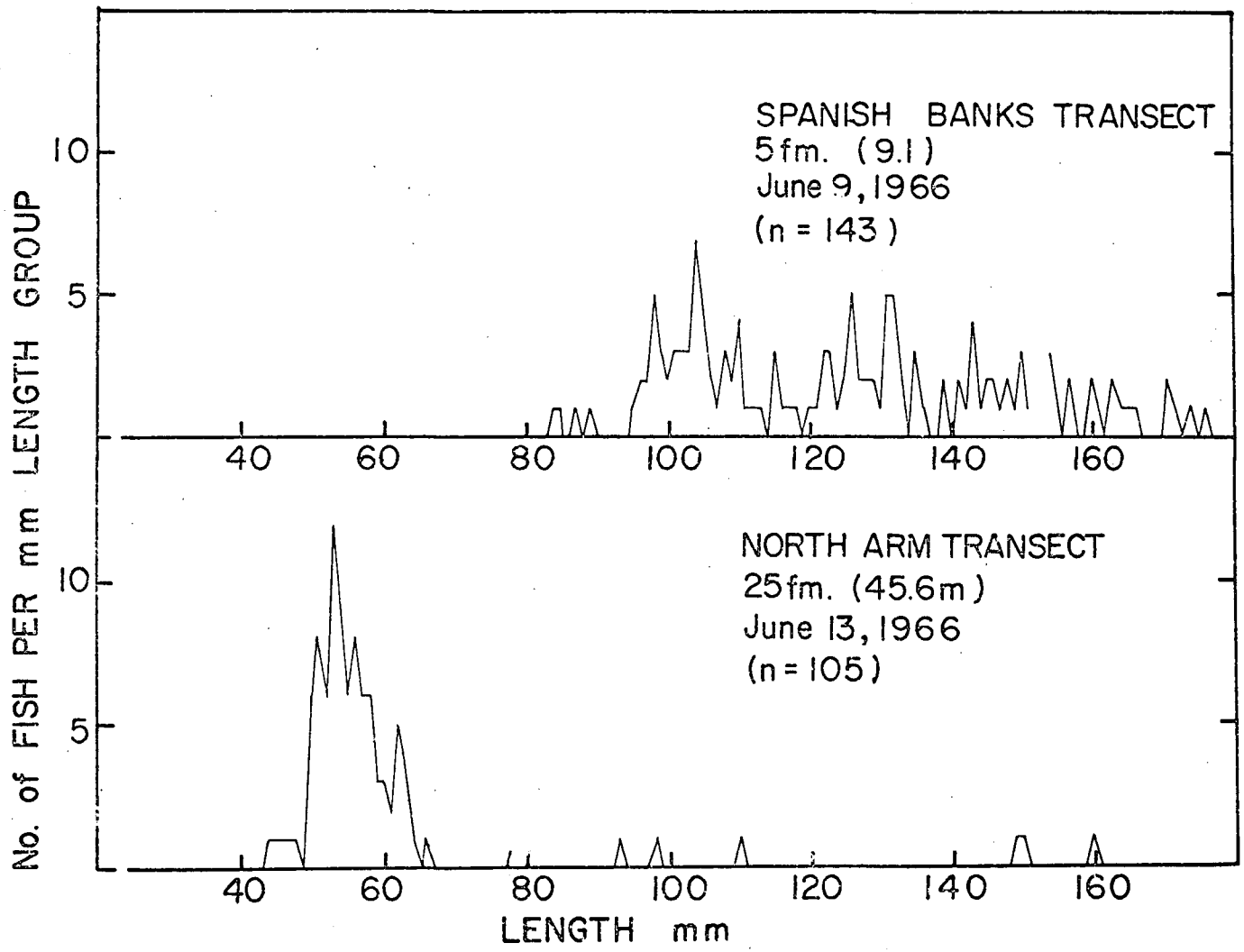


Fig. 26. Length frequencies of L. pacifica captured at two stations at the outer Burrard Inlet experimental study area.

versus silt. Recently, the usefulness of simple mechanical analysis in studies of causal factors affecting the benthos has been questioned by Buchanan (1963) working in the North Sea and Longhurst (1959) working off West Africa. Beanland (1940), Holme (1949), and Chapman (1949) suggest the fauna of the North Sea mud and sand communities, both tidal and subtidal, are limited by sediment texture and/or permeability. Webb (1958) showed the distribution of lancelets (Branchiostoma nigerience) was limited by the permeability of sand deposits, which reflects interstitial space. Permeability and porosity may be estimates of particle surface area. The binding of nutritive material may be dependent on the availability of a large surface area. The availability of nutrient material in sediments is of importance for the feeding of infaunal organisms.

Interstitial space may also be an important factor governing settlement of invertebrate larvae. Cancer magister megalopa larvae were abundant in food samples from Lycodopsis pacifica captured at Spanish Banks (10 fm, 18.3 m) in August 1966. No megalopa were found in specimens captured at West Vancouver in the same month. There is probably a difference in sediment types between the two sites. The sediments at Spanish Banks (10 fm, 18.3 m) are probably of the correct physical nature for the settling of C. magister larvae. Wilson (1958) reviews the problems of determing settling sites of invertebrate larvae.

Cockbain (1963) worked in the Strait of Georgia and Juan de Fuca Strait. He mentions that depth, median diameter of

sediment, and the number of benthic foraminifera are apparently related, but the relationship between the sediments and the foraminifera may be fortuitious. At outer Burrard Inlet, a complicated estuarine system governs the deposition of sediments in the area. Waldichuk (1953) and Fjarlie (1950) show the "sediment cloud" discharging from the North Arm of the Fraser River can extend far into Burrard Inlet. The pattern of deposition of silt from the sediment cloud may be of importance to the infaunal invertebrates in the food spectrum of *Lycodopsis pacifica*. Spanish Banks sand is of different (terrestrial) origin than that carried onto the foreset beds of the North Arm (Mathews, 1967, pers. comm.). All silt in outer Burrard Inlet, however, is probably of Fraser River origin. The silt may contain concentrations of elements of importance to infaunal organisms. There is the possibility that precipitation of suspended sediment of a critical size or mineral composition may occur in an optimum area of the "sediment cloud" (Shepard, 1963). Stations P5, N5, SB20, and SB25 may be outside the periphery of the optimum area. *L. pacifica* occurred in low abundance at these stations.

The Food Spectrum, Feeding Adaptations, and Aggregations of *Lycodopsis pacifica* in Relation to Sediment Type

An examination of the food spectrum of the species shows *Lycodopsis pacifica* is catholic in its feeding habits (p. 29). A study of the feeding anatomy of *L. pacifica* indicates the species is adapted to detect, remove, ingest, and digest in-

faunal invertebrates from sediments (p. 47). It was assumed that L. pacifica would aggregate where concentrations of suitable infaunal food organisms would be found. The parameters per cent silt and modal grain size (in microns) were used to describe sediments in this study. The results of experimental trawling at two study areas in the Strait of Georgia indicate that L. pacifica is found in abundance on a range of sediment types (p. 58). Feeding aggregations of the species are apparently not limited by grain size (sediment type) over the range encountered in this study. The species is adapted to feed on a benthic infaunal community, the components of which may be limited by sediment type.

SUMMARY

Lycodopsis pacifica (Collett) 1879 (Zoarcidae) was studied at two locations in the Strait of Georgia, British Columbia. The study period was from September 1966 to March 1967. Trawls were used as sampling devices.

Sexual dimorphism is present. The older males are larger than females. Males start to grow larger than females at approximately 170 mm in length. The information supports the hypothesis that breeding occurs only in larger individuals. Sexual maturity occurred in older (larger) individuals between September and January. *Lycodopsis pacifica* has a remarkably small complement of mature eggs which develope from a larger complement of smaller ova. Although one zoarcid has been shown to be ovoviviparous, there is no evidence for this condition in *L. pacifica*. Observations of the species from submersibles off California indicate *L. pacifica* has a reproductive behaviour pattern involving parental care.

Age was estimated by otoliths. Both males and females ranged up to five years of age. Regression equations describing growth for both sexes are presented. The length-weight relationship for the species was found to $W = 0.0000419L^{3.07897}$, where W (weight) is expressed in grams, and L (length) is expressed in millimeters.

At outer Burrard Inlet, *Lycodopsis pacifica* feeds primarily on infaunal invertebrates of the Phyla Mollusca and Annelida and Subphylum Crustacea. The samples indicate the food spectrum may vary seasonally, from place to place, and with the age

of the fish.

At outer Burrard Inlet, the species was found to occur in trawls with members of 15 families of fishes. Invertebrates captured in the trawls were a mixture of epifaunal and infaunal organisms.

The anatomy of structures associated with feeding is described. *Lycodopsis pacifica* is probably not specialized to feed on a particular sediment type. Visual and "chemical" senses are probably important in food-getting behaviour.

It was assumed that *Lycodopsis pacifica* would aggregate where high concentrations of infauna suitable as food would be found. At outer Burrard Inlet, the species occurred in high numbers on several sediment types, ranging from silt-sand to silt. At the Cape Lazo gully, *L. pacifica* was captured most commonly on a silt sediment. *L. pacifica* is probably not restricted to certain sediments by its feeding adaptations and likely is capable of foraging over a range of sediment types. Some sedimentary factors affecting the infauna are discussed, and the usefullness of simple mechanical analysis of sediments in benthic ecology is questioned.

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APPENDIX

Age and Growth Studies

Subsampling Techniques

From each of the 17 samples obtained over the study period in outer Burrard Inlet, 20 fish were taken for age estimation by means of otoliths. Age determinations were made until two consecutive readings agreed.

Following the stratified subsampling technique outlined by Ketchen (1950), the fish were categorized by sex and by five millimeter length group. Because of mesh selection all length (and therefore age) groups were not represented in samples from the commercial shrimp vessel catches. Supplemental data were obtained from collections made with the experimental trawls.

Results

A total of 236 (129 males and 107 females) age estimations were utilized under the stratified subsampling scheme. Ages ranged up to five years for both sexes. Mean length at age values are plotted in Text Fig. 12 and are shown in tabular form in Appendix tables I and II.

"Translucent" vs "Opaque" Zones and Temperature

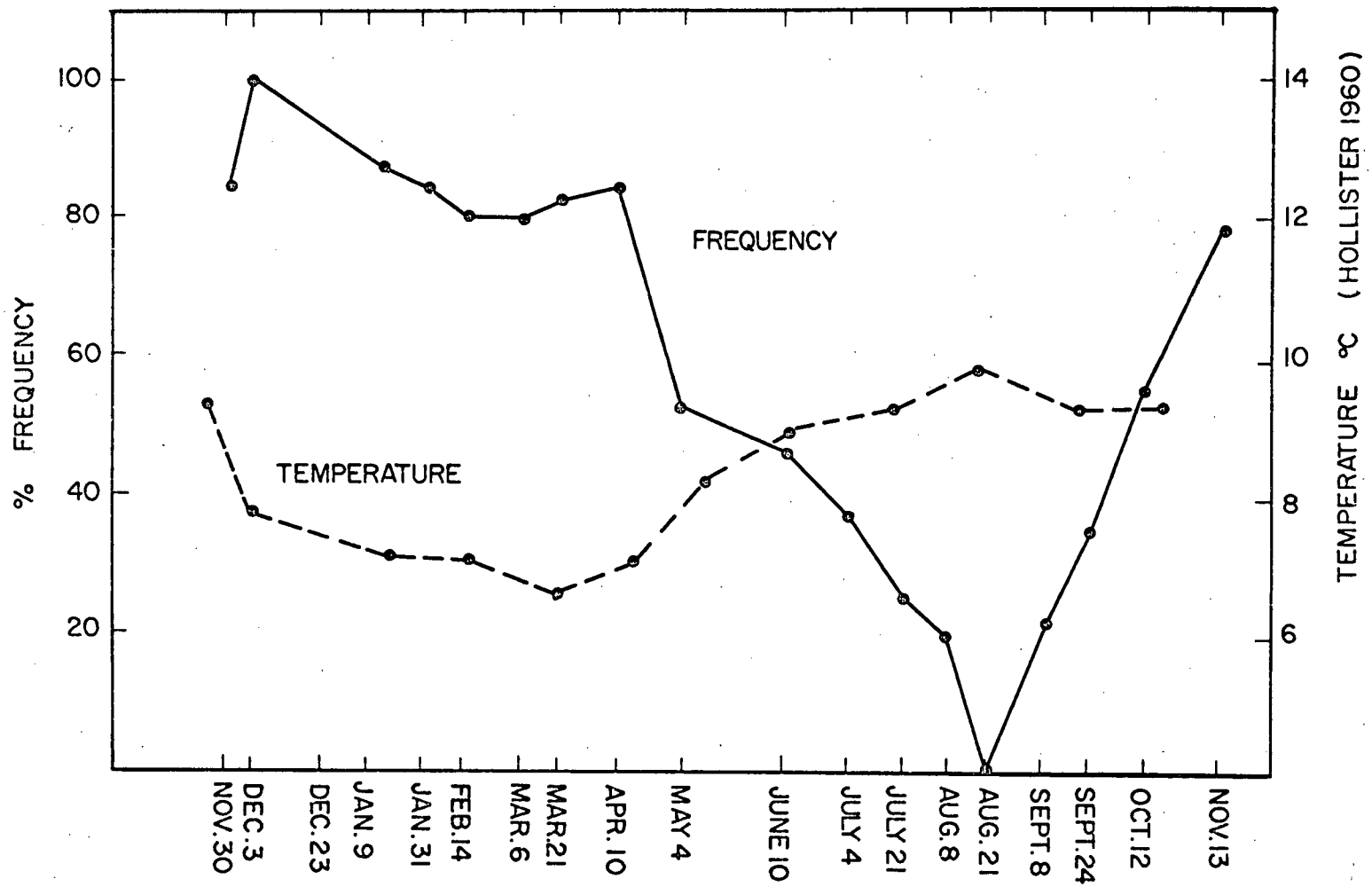
The use of otoliths in age and growth studies involves the important assumption that the annular rings are deposited seasonally. That is, it is assumed there have been no environmental or physiological conditions throughout the fishes' life that would cause a recognizable ring to be formed other than seasonal variations in temperature, etc. "Translucent zone" refers to

Table II. Age (years) - Length (centimeters) table for female *L. pacifica* collected at the outer Burrard Inlet study area. Data obtained by stratified subsampling according to the method of Ketchen (1950).

	I	II	III	IV	V
6					
7	3				
8	11				
9	5				
10	2				
11	3	3			
12	7	7			
13	2	7	1		
14		7	4		
15		1	9		
16			4	4	1
17			6	5	2
18			1	6	
19			2	3	
20					
21					
22					
23					
24					
Total	33	25	27	18	3
Mean Length (cms)	9.6	12.3	15.8	17.4	17.6
Std. Dev.	1.90	2.78	1.54	1.05	0

Table I. Age (years) - Length (centimeters) table for male *L. pacifica* collected at the outer Burrard Inlet study area. Data obtained by stratified sub-sampling according to the method of Ketchen (1950).

	I	II	III	IV	V
6					
7	4				
8	13				
9	4				
10	1	1			
11	5	4			
12	3	6	1		
13	1	4	2		
14		9	0		
15		2	8		1
16		2	7	3	0
17			3	6	0
18			3	5	2
19			1	6	1
20			2	4	3
21				4	2
22				0	4
23				0	
24				2	
25					
Total	31	28	27	30	13
Mean Length (cms)	9.1	13.1	16.1	18.8	20.0
Std. Dev.	1.78	1.55	1.94	2.09	2.08



App. Fig. 1. Percent frequency of L. pacifica otoliths with an opaque edge during the period November 1965-November 1966. Data from samples of 20 per time period collected at outer Burrard Inlet. Temperature data from Hollister, 1960.

concentric areas on the otolith where the protein:calcium ratio is low and therefore appears white under direct light. Such an area would be representative of rapid growth. An "opaque zone" refers to an area of high protein:calcium ratio; it appears dark, and represents a period of reduced growth. This follows the terminology of Irie (1960) whose experimental work verified the supposition that the rings of otoliths may be caused by temperature-dependent phenomena.

The percentage of otoliths in each sample of 20 whose outer perimeter consisted of an opaque zone was noted. These data are shown graphically in Appendix Fig. 1. Also shown in the figure is the annual temperature fluctuation typical of B.C. coastal waters (data from Hollister, 1960). It would appear we are justified in counting the opaque zones as annual phenomena. They are laid down in winter months when the environmental temperature of L. pacifica is lowest.

Species Composition of Fishes Caught in Trawl Hauls (after Berg, 1941; Families in Alphabetical Order)

F. Agonidae

Agonus acipenserinus

F. Bathymasteridae

Bathymaster signatus
Ronquilus jordani

F. Batrachoididae

Porichthys notatus

F. Bothidae

Citharichthys sordidus
Citharichthys stigmaeus

F. *Chimaeridae*

Hydrolagus collei

F. Clupeidae

Clupea pallasii

F. Cottidae

Leptocottus armatus
Radulinus asperellus
Dasycottus setiger

F. Embiotocidae

Cymatogaster aggregata
Damalichthys vacca

F. Gadidae

Theragra chalcogrammus
Gadus macrocephalus
Microgadus proximus

F. Gobiidae

Lepidogobius lepidus
Clevelandia ios

F. Hexagrammidae

Ophiodon elongatus
Hexagrammos stelleri

F. Icelidae

Icelinus tenius

F. Osmeridae

Spirinchus dilatus

F. Pleuronectidae

Atheresthes stomias
Eopsetta jordani
Glyptocephalus zachirus
Hippoglossoides elassodon
Iopsetta isolepis
Lepidopsetta bilineata
Lyopsetta exilis
Microstomus pacificus
Parophrys vetulus
Platichthys stellatus
Psettichthys melanostictus

F. Psychrolutidae

Psychrolutes paradoxus

F. Rajidae

Raja rhina

F. Scorpaenidae

Sebastodes maliger

F. Squalidae

Squalus acanthia

F. Stichaeidae

Lumpenus sagitta
Poroclinus rothrocki

Invertebrates Taken in Trawl Hauls (after Barnes, 1963; and Borradaile and Potts, 1963).

Phylum Coelenterata

Class Anthozoa

Subclass Zoantharia

Order Ceriantharia

Metridium spp.

Phylum Platyhelminthes

Class Turbellaria

Order Polycladida

Phylum Arthropoda

Subphylum Crustacea

Class Malacostraca

Order Isopoda

Order Decapoda

Suborder Natantia

Section Caridea

Gragon communis

Pandalopis dispar

Pandalus borealis

Pandalus platyceros

Pandalus hypsinotus

Pandalus danae

Paracrangon echinata

Spirontocaris holmesi

Suborder Reptantia

Section Macrura

Cancer magister

Cancer oregonensis

Chronoecetes bairdi

Section Anomura

Dagurus spp.

Munida quadrispina

Phylum Mollusca

Class Gastropoda

Subclass Opistobranchia

Order Tectibranchia

Order Nudibranchia

Phylum Echinodermata

Class Asteroidea

Luidia foliolata

Pisaster brevispinis

Class Holothuroidea

F. Synaptidae

Outline of Scheffés (1953) Technique of Multiple Comparisons in Analysis of Variance

Treatment means are assigned "contrast coefficients" (c_i values). Each contrast is defined as $\theta = \sum_1^k c_i \cdot \mu_i$ where $\sum_1^k c_i = 0$ and μ is a mean. An estimate of θ ($\hat{\theta}$) is H which equals $\sum_1^k c_i \bar{x}_i$; here x_i estimates μ_i with $\frac{S^2}{n_i}$ estimating $\frac{\sigma^2}{1} c_i \bar{x}$; here x_i estimates N with $\frac{S^2}{n_i}$ estimating, i.e., variance on a "per replicate" scale. S^2 is error mean square from the analysis of variance. H has variance of $\sum_1^k c_i^2 \frac{\sigma^2}{n_i}$; this may be estimated from $S^2 \sum_1^k \frac{c_i^2}{n_i}$. The value "$S^2$" is now obtained from tables of the F-ratio used in analysis of variance. $S^2 = (t-1) F_{\alpha}(t-1, tr-1)$, where t is the number of treatments, and r is the number of replicates. In this experiment, treatments are sampling stations. Confidence limits are constructed; the confidence statement is as below:

$$P_r\left\{H - S\sqrt{\hat{V}[H]} < \theta < H + S\sqrt{\hat{V}[H]}\right\} = 1 - \alpha$$

α is the complement of the probability level being used - here 0.95.