POPULATION ECOLOGY OF THE NUDIBRANCH

Archidoris montereyensis (COOPER, 1862)

by

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ABSTRACT

Population fluctuations of the nudibranch *Archidoris montereyensis* were studied at field sites at Lantzville on Vancouver Island, B. C. from May, 1969 to October, 1970. For comparison another site was maintained at Bamfield for a short time. Data were obtained on population fluctuations, intertidal positions and length of nudibranchs, spawn and copulations. Measurements were taken on the sponge cover upon which *A. montereyensis* feeds. Laboratory experiments tested the effects of desiccation at various temperatures on mortality. Two field experiments at Bamfield tested the effects of nudibranch grazing on the standing crop of sponge, and of sponge removal on nudibranch movements.

The results indicated that *Archidoris montereyensis* is a fast growing annual which settles and spawns year round in the intertidal, shows no evidence of vertical migration, and dies from innate post-reproductive mortality. Observed fluctuations in numbers are probably the result of sporadic settlement and the chance timing of adverse physical factors such as hot weather coinciding with low tides resulting in mortality through desiccation, and storms.

Scarcity of food may be a limiting factor at times, since there is a rough correlation between the availability of sponge and the number of nudibranchs at Lantzville, and because nudibranchs were larger and more abundant at Bamfield where the sponge cover was heavier than at Lantzville. Feeding experiments revealed *Archidoris montereyensis* to be a voracious predator of *Halichondria panicea*, eating an average of 2.23 cm^3/nudibranch/day. A removal of sponge resulted in a downward movement in the intertidal zone. This may account for subtidal sitings of *A. montereyensis*. Alternate sponge species in the subtidal may constitute a refuge when food disappears in the intertidal.

Life history data were obtained on *Onchidoris bilamellata*, *Diaulula sandiegensis* and *Aeolidia papillosa* which were found on the Lantzville grid sites.

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INTRODUCTION

Nudibranchs, a suborder of opisthobranchiate gastropods, have long attracted the attention of marine biologists because of their striking coloration and diversity of form. Perhaps the sheer abundance of species (over 5,000 are known) accounts for the fact that to date most work on them has been taxonomic. A major problem confronting workers on nudibranchs is their relative scarcity. About eighty species of nudibranchs live along the Pacific coast of North America and not one is very common as compared with many other predatory gastropods (Thais, for example). Many species are known from only a few individuals, and even the most common are difficult to find in any abundance. Most early reports along the Pacific coast of North America were written by F. M. MacFarland (1905, 1906, 1912, 1925, 1926, 1966) and by C. O'Donoghue (1921a,b; 1922a,b,c; 1924; 1926; 1927a,b), but they concentrated upon systematics. Recent systematists (Marcus, 1961; Steinberg, 1959, 1961, 1963a, 1963b; Roller, 1969, 1970; Robilliard, 1970) are attempting to straighten out the systematic confusion in North American nudibranchs. In the last ten years, this group has been studied intensively, especially by physiologists and embryologists, but the basic ecology of nudibranchs remains largely unknown. Most of the ecological information on North American nudibranchs comes from comments in natural history books (for example, MacGinitie and MacGinitie, 1949; Ricketts and Calvin, 1952) as additions to taxonomic descriptions (MacFarland, 1966; O'Donoghue, 1921a,b; 1922a,b,c; 1924; 1926; 1927a,b), or short notes on field observations like those of Agersborg (1919) and Costello (1937, 1938).

From scattered published information on the ecology of various species, some basic questions have arisen. One such question concerns the sporadic abundance of many species of nudibranchs both in time and space. Nudibranchs relatively common one year have been found to be rare the next, although they sometimes could be found in other areas. To account for the sporadic appearance of nudibranchs in the intertidal zone, several theories have been proposed. The major controversy is whether or not nudibranchs migrate. Proponents of the migration theory believe that migration takes place either (a) when juveniles which had settled in the subtidal move into the intertidal (Garstang, 1890; Eliot, 1910; Costello, 1938), (b) when post-reproductive adults migrate to the subtidal after spawning (Alder and Hancock, 1845-1855; Aboul-Ela, 1959), (c) in both cases, the intertidal only being occupied in the breeding season (Hecht, 1896; Balch, 1908; McMillan, 1944), or (d) for reasons unrelated to breeding (Crozier, 1917; Chambers, 1934; Miller, 1962). Those who do not believe migration occurs uphold one or more of the following theories: (a) sporadic settlement of veligers in the intertidal (Alder and Hancock, 1845-1855; Miller, 1962; Potts, 1970), (b) sporadic effects of intertidal limiting factors such as temperature and salinity, food supply, or predation (Crozier, 1917; Chambers, 1934; Swennen, 1961), or (c) the nudibranchs die from an inherent post-reproductive mortality (Garstang, 1890; Hecht, 1896; Behrentz, 1931; Thompson, 1961a,b, 1964; Potts, 1970). This abundance of theories points out the lack of information on life cycles and general ecology of nudibranchs. However, three areas which have been studied are feeding, defence and reproduction.

Feeding has been studied intensively in Europe and Great Britain (Forrest, 1953; Graham, 1955; Aboul-Ela, 1959; Miller, 1961; Swennen, 1961; Thompson, 1964), but many North Pacific coast species do not occur there and the prey for most of these remains unknown. Nudibranchs, in general, feed upon coelenterates, tunicates and sponges. They tend to be specific in their food habits and further study of this should lead to greater success in finding specimens.

Nudibranchs have developed several systems to inhibit predation. Many are highly acidic or have copious mucous secretions which make them distasteful (Thompson, 1960a,b,; Johannes, 1963; Edmunds, 1968). There is an accumulation of nematocysts in those species feeding upon anemones (Herdman, 1890; Cuénot, 1907; Crossland in Eliot, 1910; Crossland, 1911; Graham, 1938, 1955). Some nudibranchs appear to have warning colours, others to have protective coloration. Archidoris montereyensis is yellow, and feeds upon a yellow sponge, Halichondria panicea (Cook, 1962). Other yellow Archidorids such as Archidoris tuberculata also feed on yellow Halichondria (Garstang, 1890), but the red Archidoris flammea feeds on red sponge (Garstang, 1890; Fisher, 1937). However, the effectiveness of this coloration is in some doubt as the nudibranchs are not always on their prey (Fisher, 1937). Mimicry appears in some nudibranchs, for example, Corambella steinbergae which resembles its prey, the bryozoan Membranipora (Lance, 1962; McBeth, 1968). Many of the aeolids are capable of autotomizing their cerata (Flatterly and Walton, 1922). Such protective devices indicate that these nudibranchs are subject to predation pressure. However, with the exception of a few opisthobranch predators and cases of cannibalism (Robilliard, 1971), no predators have been demonstrated.

The reproductive patterns of nudibranchs remain largely unknown. Egg masses and spawning have been studied in detail; the works of O'Donoghue and O'Donoghue (1922) and Hurst (1967) are important references for this coast. References are available to the months in which egg masses are found, but as these are from different collecting areas, and often from seasonal collections, it is impossible to get a clear picture of the year-round reproductive pattern from these data. Workers rarely concentrated on one particular species, and as a result, little detail was included (Garstang, 1890; Renouf, 1916; Swennen, 1961; Miller, 1961; Thompson, 1964). The lack of specific data added to the natural scarcity of nudibranchs led to many conflicting speculations on their life histories. Recently, workers have begun to concentrate on one particular species in one locality (Thompson, 1958a, 1961a, 1966; Roginskaya, 1963;

Potts, 1970) to obtain a more detailed idea of life cycles. The studies of Thompson stressed the development of eggs, larvae and adults. Adults were collected from the same area all year round and the reproductive maturity determined by morphological criteria. The emphasis was placed on anatomy; field samples were small and not quantitatively measured. Roginskaya's study consisted of non-quantitative field observations over a period of two years. The study by Potts (1970), on the other hand, was a quantitative study of a fixed area in which the numbers and length of individuals in the total population of Onchidoris fusca in a specific area were measured.

These studies pointed out the necessity of a detailed survey to obtain information on the ecology of a single species of nudibranch. For this reason, I decided to study the population ecology and life history of one species of nudibranch. The species I chose was Archidoris montereyensis (Cooper, 1862) (Fig. 1) which ranges along the Pacific coast from Alaska to San Diego (Steinberg, 1963b). The population fluctuations or life cycle of A. montereyensis have not been studied, but because it is relatively common, many details of its ecology are known. Adult

Figure 1. <u>Archidoris montereyensis</u>.

Approximately 1½ x.

(Photograph by Ron Long,

Bio Sciences Photographer).

A. montereyensis are considered to be largely intertidal but have been sighted subtidally to a depth of 34 meters (Lance, 1961). A. montereyensis typically occurs in association with its prey, the sponge Halichondria panicea (Long, 1968), but it has also been observed eating other sponge species (G. A. Robilliard, pers. comm.). A food choice experiment (Cook, 1962) offering several sponge species to A. montereyensis resulted in only Halichondria panicea being eaten, but the four other sponges offered did not include the same sponges that A. montereyensis was observed eating (G. A. Robilliard, per. comm.). Except for the work of Cook (1962) and Long (1968), no work has been done on the relationship of A. montereyensis with Halichondria panicea.

The only other Archidorids which occur along the Pacific coast of North America are A. odhneri, which I found to be common at Bamfield, Vancouver Island; and perhaps A. tuberculata, although there have been only two conflicting reports of the latter so its presence is dubious (Burn, 1968). Archidoris odhneri feeds upon the sponges Craniella, Stylissa and Mycale (G. A. Robilliard, pers. comm.) and although it is often found in the same general locality as _A. montereyensis_, it is strictly subtidal and the two species do not appear to interact. Other species of _Archidoris_ have also been found to eat sponge, but the prey varies according to the species (Garstang, 1890; Fisher, 1937; Forrest, 1953; Miller, 1961; Thompson, 1964, 1966; Merilees and Burn, 1969).

Archidoris montereyensis lays egg masses all year round and these masses have been described in detail (O'Donoghue and O'Donoghue, 1922; McGowan and Pratt, 1954; Hurst, 1967). Eggs hatch into pelagic veliger larvae (Hurst, 1967) but the fate of the larvae is not known. Settling has not been observed or induced in the field or in the laboratory. The length of adult life, growth rates, or number of spawning periods have not been studied for _A. montereyensis_. McGinitie and McGinitie (1949) observed _A. montereyensis_ to die after spawning. The life cycle of another species of _Archidoris_ have been studied with conflicting results. Renouf (1916) found that _A. pseudoargus_ (= _A. tuberculata_) produced two generations in a year. Miller (1962) found this species to live about two years, but only observed one breeding season per year. Thompson (1966) found only one generation per year. He concluded that _A. pseudoargus_ was an annual, growing in the autumn and winter, spawning in the spring, and then dying. Juveniles appeared in the late summer. Although Thompson's study appears to be comprehensive, further research will be needed to establish which, if any, of these patterns holds true for A. montereyensis.

By concentrating on one species I hoped to obtain details of the life cycle to add to the relatively few studies which have been done. The main purpose of this study was to examine under field population conditions, the life cycle and certain population characteristics of Archidoris montereyensis, such as age structure, density, mortality, growth, and position in the intertidal zone. I wanted to know when the nudibranchs were reproducing, how fast they grew, how long they lived and what caused them to fluctuate in numbers. Possible answers to the question of why do nudibranchs fluctuate in numbers, were that they were hiding, migrating, or dying (due to lack of food, physical factors, predation, postreproductive mortality, or a combination of several factors). What the relationship was between A. montereyensis and its food supply particularly interested me. Because of their specificity to their prey, food supply may influence life cycle characteristics and population dynamics. To obtain data on these questions, I monitored the population in one particular area regularly for a year and a half, and a population in a contrasting area for a short time. The nudibranchs were counted, measured and the spawn noted. To test the theory of migration, the positions of the animals in the intertidal were recorded and scuba dives made below the study areas. To test for the effects of food as a possible limiting factor in distribution and abundance, a record was kept of sponge fluctuations and the two experiments were performed in the field. To study the effects of temperature and desiccation on mortality, an experiment was performed in the laboratory. Some incidental information on the life cycles of a few other species was obtained during the course of this study.

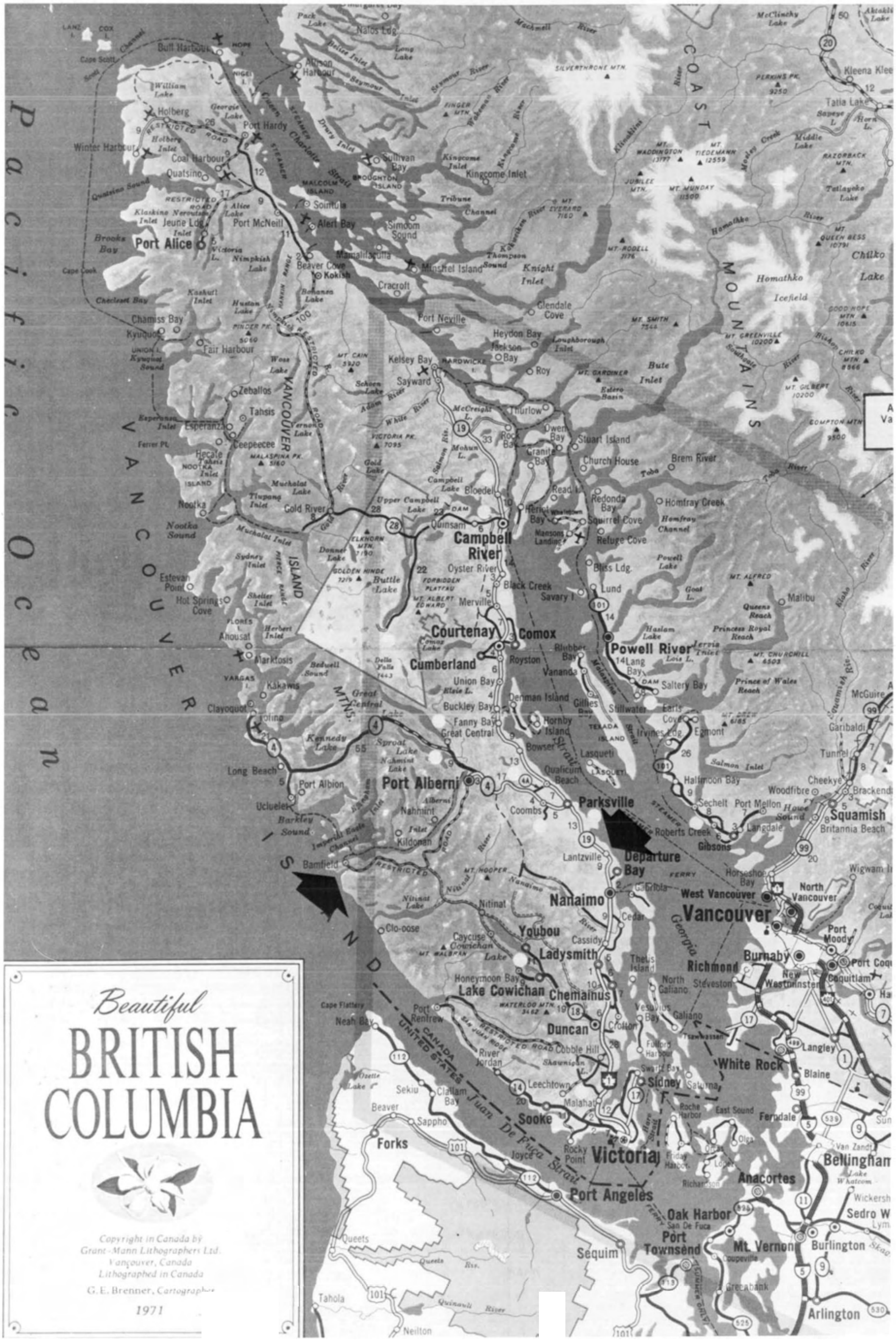
MATERIALS AND METHODS

Population Studies

Population characteristics and behaviour of Archidoris montereyensis were followed at two fixed field sites in the rocky intertidal zone on Vancouver Island, British Columbia. The principal site was at Lantzville, which is on the sheltered shore of the Strait of Georgia; the other was near Bamfield on the wave-exposed outer coast (Fig. 2). The Lantzville site was selected after searching the coastline on the mainland and Vancouver Island for an accessible area which supported a large enough number of nudibranchs for a population study. The Bamfield site was chosen to allow comparisons between two areas having different environmental and population characteristics.

Permanent grids - four at Lantzville, one at Bamfield - were made by marking square meter areas with nails fired into the rock with a cement gun. This low velocity cement gun (Omark #724) fired nails by exploding 22 calibre blanks. The depth that the nail entered the rock could be adjusted so that where the rock was nearly vertical, the nails stuck out, giving a place to hang a plexi-

Figure 2. Location of the two study areas, Lantzville and Bamfield on Vancouver Island (from Grant-Mann Lithographers Ltd.).


Pacific Ocean
VANCOUVER ISLAND
COAST MOUNTAINS
Port Hardy
Port McNeill
Alert Bay
Port Alice
Sointula
Kelsey Bay
Sayward
Campbell River
Courtenay
Comox
Cumberland
Powell River
Port Alberni
Parksville
Departure Bay
Nanaimo
Vancouver
West Vancouver
North Vancouver
Burnaby
Richmond
Ladysmith
Lake Cowichan
Chemainus
Duncan
Sidney
Victoria
Sooke
Port Angeles
Forks
Sequim
Port Townsend
Oak Harbor
Anacortes
Bellingham
Mt. Vernon
Burlington
Arlington
White Rock
Squamish
Gold River
Tofino
Ucluelet
Bamfield
Strait of Georgia
Juan De Fuca Strait
CANADA
UNITED STATES
Beautiful
BRITISH COLUMBIA
Copyright in Canada by
Grant-Mann Lithographers Ltd.
Vancouver, Canada
Lithographed in Canada
G.E. Brenner, Cartographer
1971

glass grid. This portable grid (Fig. 4a) had an inside diameter of one square meter and was subdivided into 100 1-dm squares, each identified by a number and a letter for co-ordinates.

Twice a month, at the lowest tides, the number and positions of all nudibranchs within the grids were recorded. The length of each animal was measured to the nearest mm _in situ_ with a pair of dividers. Size was the only available means of estimating the age of the nudibranchs. For convenience, the animals were classified as young (under 1 cm), juvenile (1-3 cm), or adult (over 3 cm). Although these classes are arbitrary, they were chosen because 1 cm was the size at which _Archidoris montereyensis_ became readily conspicuous in their natural habitat, and 3 cm is approximately the size at which the animals became sexually mature. These divisions may not apply to the size range of _A. montereyensis_ on sites other than at Lantzville. Copulation and spawning were noted, and the position and size of spawn, if present, were recorded. Data were obtained at Lantzville from May, 1969 to October, 1970 and at Bamfield from May, 1970 to September, 1970.

Sponge cover (Halichondria panicea and Haliclona permollis) was completely estimated four times at Lantzville (February 5; April 24 and May 25; June 21 and July 17; September 12) and once (July 19 and 21) at Bamfield. Each square of the grid was classified according to visual estimates of the area covered by sponge. The classes used were absent, sparse (less than 1/3 cover), moderate (1/3 to 2/3 cover), and heavy (2/3 to complete cover).

Scuba diving was used occasionally to study the grid sites when submerged and to check for the presence of Archidoris montereyensis below the grid areas.

Description of Study Sites

The four grid sites at Lantzville (Figs. 3, 4) varied in area to include the majority of nudibranchs present when the survey began (Table 1). Each grid site was on a vertical cliff of hard sandstone which is only exposed at spring tides. Above the cliffs is a gravel sand beach, and below them a long, sandy beach. Sites I and II were on the east side of Blunden Bay, sites III and IV were on the west side of Blunden Point. The top of each site was covered by Fucus sp., but the vertical surface had an algal cover which consisted of Ulva sp., Iridaea sp., and

Figure 3. Map of Lantzville (A) and aerial photograph (B) showing the location of the four study sites (map from Canadian Hydrographic Service #3577; photo #7075-228 from British Columbia Lands Service).

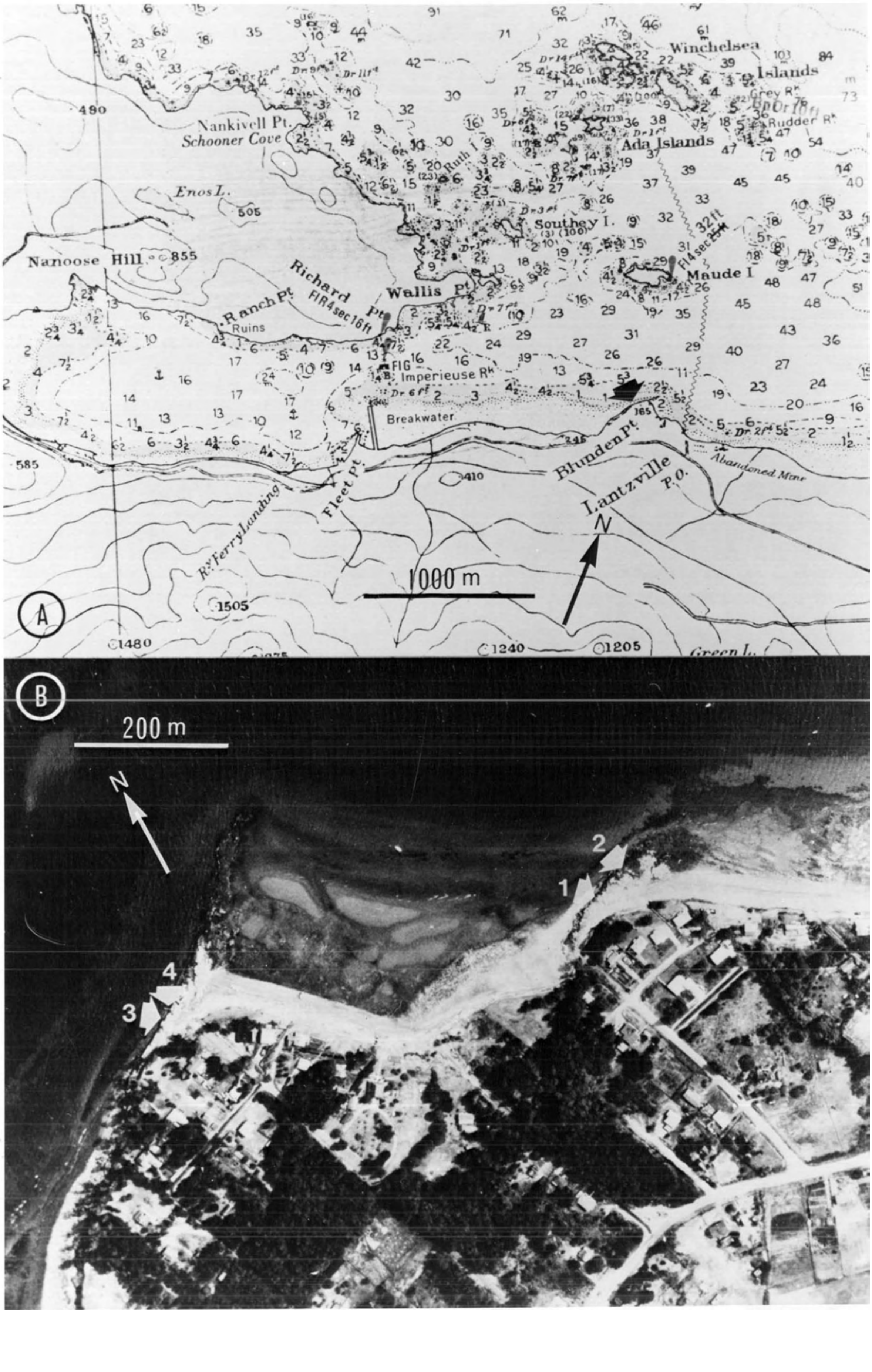

Winchelsea Islands
Grey Rk
Rudder Rk
Ada Islands
Nankivell Pt.
Schooner Cove
Enos L.
Ruth I.
Southey I.
Maude I.
Nanoose Hill
855
Richard Pt.
Fl R 4 sec 16 ft
Wallis Pt.
Fl 4 sec 32 ft
Ranch Pt.
Ruins
FIG
Imperieuse Rk
Breakwater
Blunden Pt.
Abandoned Mine
Lantzville
P.O.
Fleet Pt.
Ry Ferry Landing
N
1000 m
A
B
200 m
N
1
2
3
4

Figure 4. Grid sites at Lantzville.

A. Portion of site 1 with grid in position.

B. Portion of site 2.

C. Site 3. The bare area at the bottom is the result of sand blasting by storms.

D. Site 4.

Photos by Ron Long, June, 1970.

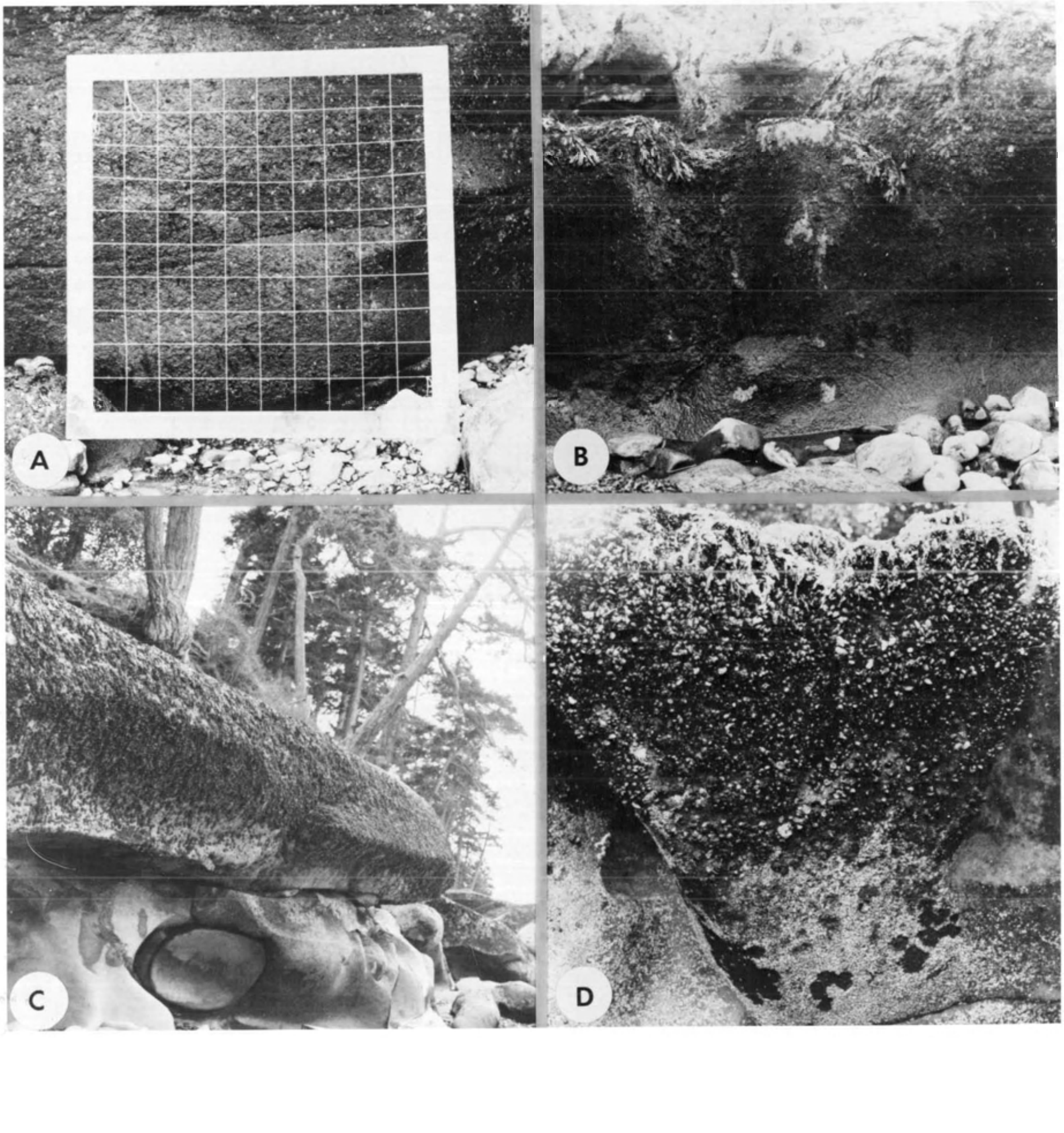


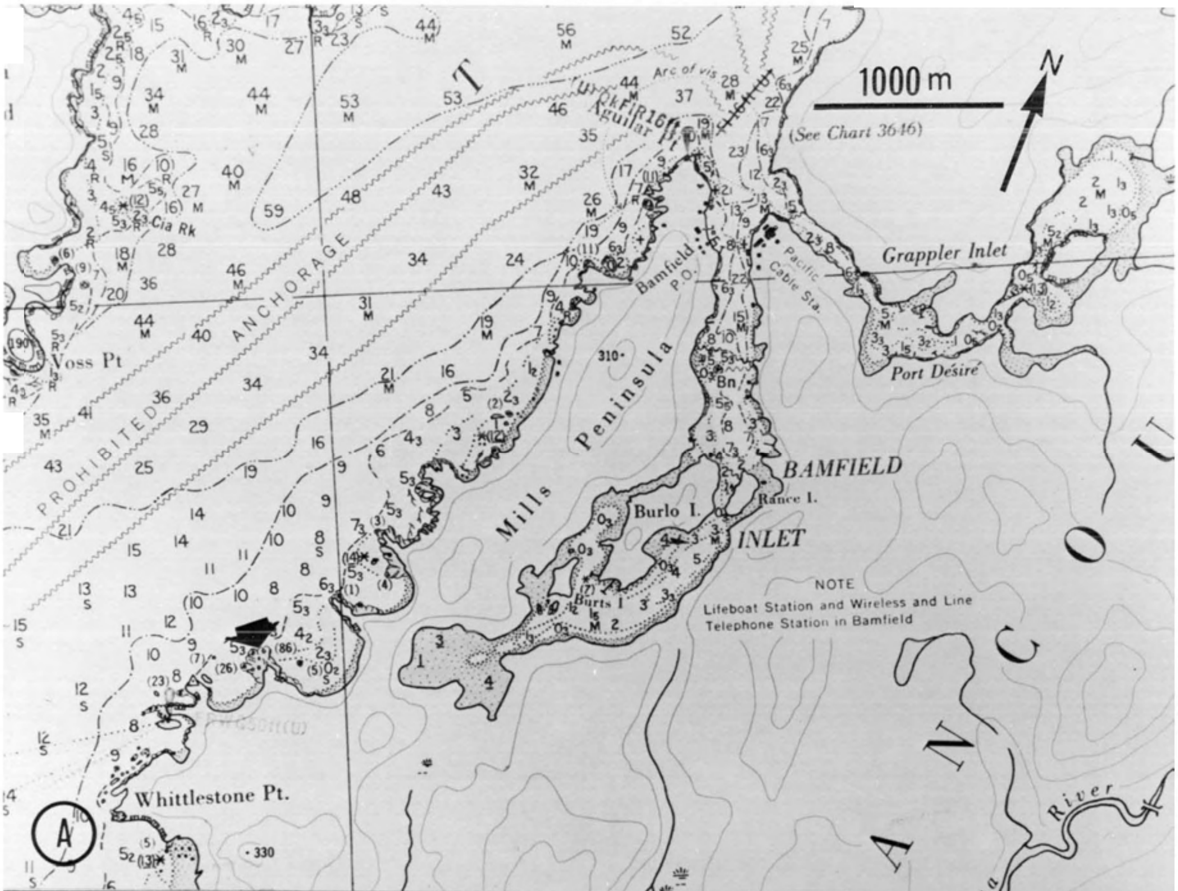
Table 1. Physical characteristics of the grid sites at Lantzville and Bamfield.

	Site	Width (m)	Length (m)	Direction	Tidal ht. top (m)	Tidal ht. bottom (m)
Lantzville	1	5	1.9	NW	3.09	1.15
	2	3	1.1	N	2.69	1.55
	3	3	1.5	N	2.72	1.25
	4	2	2.3	N	4.66	2.40
Bamfield	1	2	9.0	W	2.60	1.00

many small red and green algae, among which Cladophora, Cryptosiphonia, Gelidium, Plocamium, and Rhodomela were identified. The upper portion of all sites had a patchy distribution of Balanus glandula, and sites III and IV had in addition, Mytilus edulis. The middle and lower sections had little conspicuous animal life. There were a few anemones (Metridium senile), tunicates, and starfish (Pisaster ochraceus). Closer inspection revealed a covering of hydroids, and a thin layer of the sponges, Halichondria panicea and Haliclona permollis.

At Bamfield, one grid site was chosen on exposed coast at "Nudibranch Point" (Figs. 5, 6). The area selected was of gently sloping basaltic rock which descended unevenly from the intertidal zone to a depth of 16 m below 0 datum. The sample grid site area began just below the Fucus zone. The top four meters (measured along the slope) were covered with Corallina sp.; the lower five meters had Laminaria setchellii as the dominant plant. In the upper and mid-regions, starfish (Pisaster ochraceus), gooseneck barnacles (Pollicipes polymerus), mussels (Mytilus californianus), and the hydrocoral (Allopora) were predominant. The sponge Halichondria panicea was present throughout the study site, but was most abundant in the middle region where it covered

Figure 5. Map of Bamfield (A) showing the location of the study area, "Nudibranch Point". Aerial photograph (B) showing the location of the grid site (G), fence experiment (F) and cage experiment (C) (map #3637 from Canadian Hydrographic Service; photo #7238-180 from British Columbia Lands Service).


A
1000 m
N
(See Chart 3646)
Aguilar
Arc of vis
Grappler Inlet
Port Desire
Bamfield P.O.
Pacific Cable Sta.
Mills Peninsula
BAMFIELD
INLET
Burlo I.
Rance I.
Burts I
NOTE
Lifeboat Station and Wireless and Line Telephone Station in Bamfield
PROHIBITED ANCHORAGE
Cia Rk
Voss Pt
Whittlestone Pt.
River

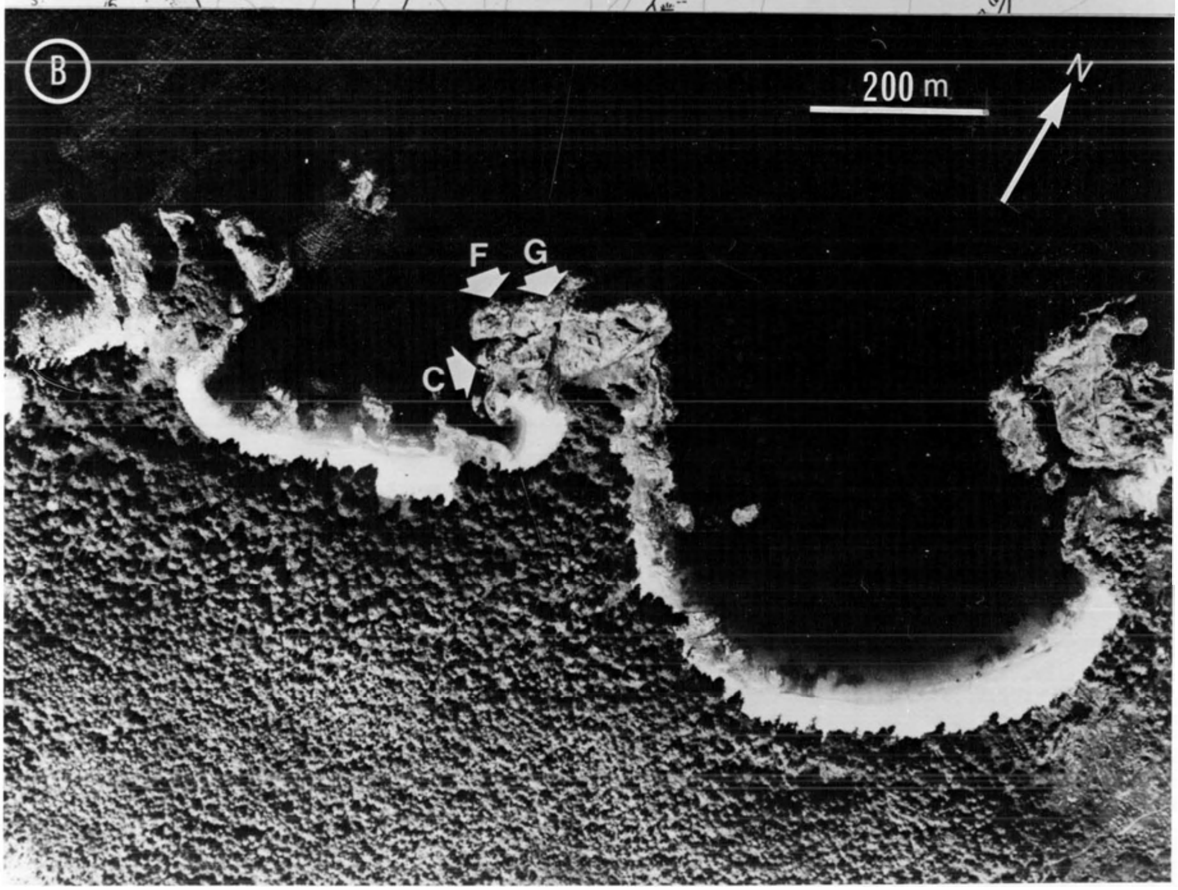
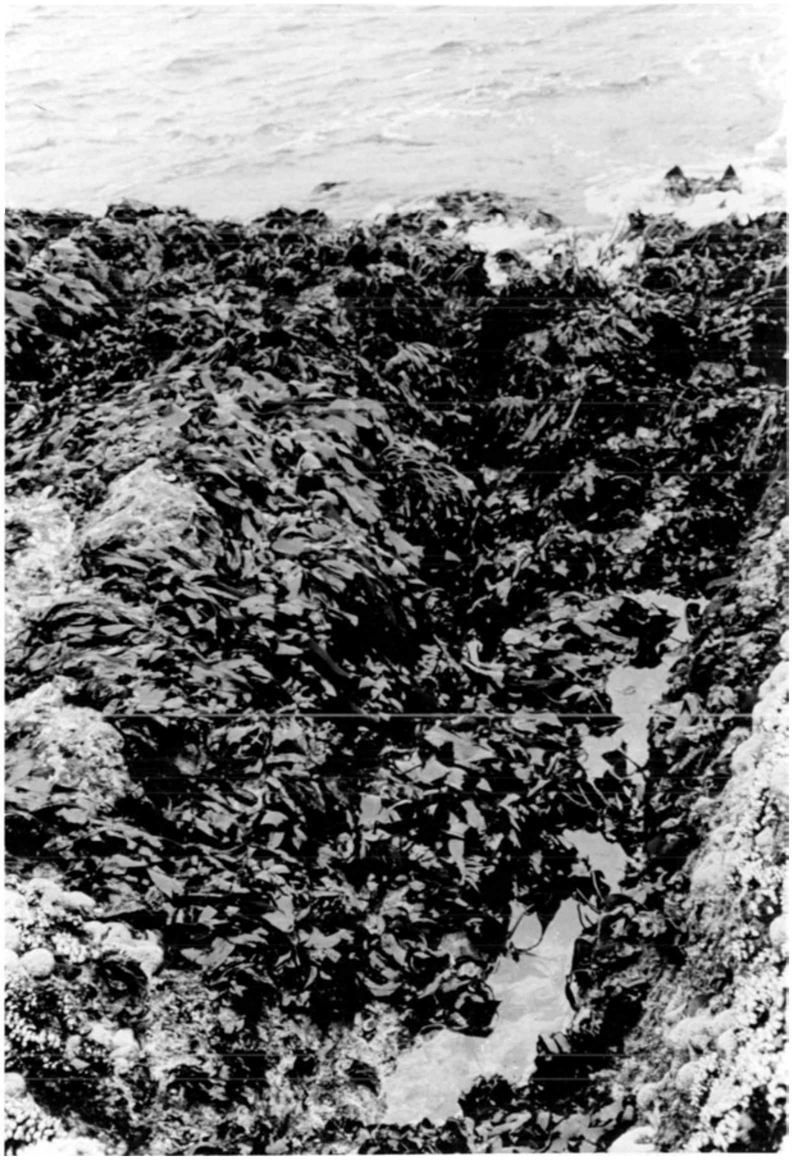

B
200 m
N
F
G
C

Figure 6.   Grid site at Bamfield.

Photo by Stoner B. Haven, August, 1971.



the rock between the Laminaria to a depth of several centimeters. The lowest two meters, which were submerged except by the lowest spring tides, had large colonies of tunicates.

Marking Animals

Animals were marked in field experiments and on a few of the permanent grids. Since nudibranchs have a delicate mantle and no shell, it was impossible to mark the animals by attaching labels to them. Instead, a number of vital stains were tested: Nile Blue Sulphate, Methylene Blue, Trypan Blue, Janus Green and Neutral Red. Only Neutral Red was successful. This dye, when applied to an *Archidoris montereyensis in situ* with a "Q-tip" (cotton-tipped swab), penetrated the mucous covering, leaving a red patch on the skin. Marks could be placed on different parts of the nudibranch in order to distinguish one individual from another. Animals in the laboratory retained their markings for as long as four months with no apparent side effects. The markings were still distinguishable when the animals died (from causes unrelated to staining) and it is possible the stain would be effective for longer periods. In the field, none of the marked animals remained over two and a half months, but since they disappeared at the same time as unmarked nudibranchs of the same size, it does not appear that the markings caused their disappearance.

Field Experiments

Two field experiments were performed at Bamfield using fenced areas and marked nudibranchs. The experimental sites were near the permanent grid site at "Nudibranch Point" (Fig. 5).

The first experiment, designed to test the relationship between nudibranch movements and the amount of food present, utilized a heavy sponge patch divided in two by a long wire mesh fence oriented perpendicularly to the sea which prevented nudibranchs from crossing from one side to the other. This was at an intertidal height of 1.2 meters above 0 datum on basaltic rock sloping slightly to the sea in a direct line with the heavy surf. The fence was made from stainless steel mesh, ten strands to the inch and was 40 cm long and 8 cm high, with a 3 cm base. To attach the fence, the rock was scraped clean with a spatula and a thick coating of "Sea-Go-In" epoxy putty #1324 (Permalite Plastics Co., Costa Mesa, Calif.), which can be used on wet rock surfaces, was applied to the rock and to the base of the fence. The fence was then pressed to the rock and moulded to its contours. Nails were fired from a concrete gun through the base of the fence into the rock to attach the fence securely. Any remaining gaps were filled with putty.

All sponge and other organisms were removed from one side of the fence with a spatula. Nudibranchs and large organisms were removed from the other side. Twenty Archidoris montereyensis were collected nearby and marked with Neutral Red, half on the left side of the body, and half on the right. Those marked on the right were placed in the cleared area, 12 to 25 cm from the fence and 4 to 14 cm up from a reference point marked on the fence. The other nudibranchs were placed the same distance away from the fence on the side with sponge. The animals recoiled upon contact with the substrate and were washed away by the surf unless a thin stream of water was poured on them from a bucket, and the flow gradually increased to a bucketful dropped from several feet. Once attached, the twenty nudibranchs were examined twice a day at low tide for the three remaining days that tides were low enough to expose them, and the distance and direction moved was recorded by measuring from the reference point with a ruler.

The second experiment, which tested the effect of nudibranch feeding on the sponge cover, used a sponge patch on the vertical wall of a surge channel, subjected to heavy surf at an intertidal height of 1.1 meters above 0 datum. A rectangular cage 8 cm high, 34.5 cm long and 32 cm wide, inside dimensions, was made by lashing four strips of wire mesh together with nylon fishing line, and bending the bottom to the outside to form a base. Another strip was lashed so it divided the cage in two lengthwise, forming upper and lower compartments containing sponge. The cage was attached in the same manner as described for the fence.

Sponge volume in the upper and lower rectangles was estimated by measuring the depth at 20 random points, determined by choosing co-ordinates from a table of random numbers. Five _Archidoris montereyensis_ were measured with dividers, marked with Neutral Red so they could be individually distinguished, and attached to the sponge in the upper section. The lower section was the control. The top of the cage was covered with nylon screening sewn to the wire mesh with nylon fishing line to exclude predators and contain the nudibranchs. The top could be removed to examine the cage contents. The cage was examined twice a day for a period of three days and the area cleared of sponge by the nudibranchs was measured by drawing the shape of the area and taking measurements of the area with dividers.

Desiccation Experiments

Two laboratory experiments tested the effects of desiccation on *Archidoris montereyensis*. Animals were collected in the field and kept at 8°C in an aquarium for two days. The animals were individually blotted with cheesecloth, placed in plastic petri dishes, and weighed to the nearest mg. Experimental animals were then placed in Sherer controlled environment chambers under three temperature regimes and kept at a constant relative humidity of 75%, control animals were kept in the aquarium at 8° C. In the first experiment ten groups of ten animals each were used; a control group, and three experimental groups at each of three temperature regimes, 16°, 21°, and 27°C. One group was removed from each of the chambers after four hours, a second after six hours and the last after eight hours. Upon removal, the ten animals in each group and the petri dish were blotted with cheesecloth and weighed. The groups were staggered 1/2 hour apart to allow enough time for the weighings. The animals were then returned to the 8°C aquarium and checked for recovery eighteen hours later. The second experiment followed the same procedure as the first, but only thirty animals were used, ten as a control, ten at 16°C and ten at 21°C. All animals were exposed for six hours.

The times and temperatures used in the first experiment were chosen to bracket the natural conditions found during the lowest summer tides in June, 1969 where nudibranchs were exposed for at least six hours three days in succession to air temperatures from 18 to 23°C at a humidity of 75%. During this period the population declined greatly. The second experiment was designed to approximate the natural exposure time of six hours with temperatures of 16 and 21°C.

RESULTS

Field Population Studies

Fluctuations in Population Size and Age Composition

Fluctuations in population size of Archidoris montereyensis at Lantzville from May, 1969 to October, 1970 are shown in Fig. 7. Both short-term and large year-to-year variations were evident. Numbers were highest in the spring of 1969, but underwent a drastic decline in June. The population never reached the numbers found in May-June, 1969 during the rest of the eighteen month study, although by late fall, 1969, numbers had increased considerably. The population size fluctuated little throughout the winter and spring of 1970 until June, when numbers began to steadily decline to a low of three nudibranchs in August. In the autumn the population increased slightly. The maximum numbers in June, 1969 represented a population density of 10.9 per m^2 over the 21.9 m^2 grid area; the minimum density in August, 1970 was 0.1 per m^2.

Examination of the 1969 spring population peak (Fig. 8) reveals that the majority of the nudibranchs were under one centimeter in length. Many animals were under 5 mm and were difficult to spot in the algal growth on the

Figure 7. The total number of *Archidoris montereyensis* found on the grid sites at Lantzville, 1969-70.

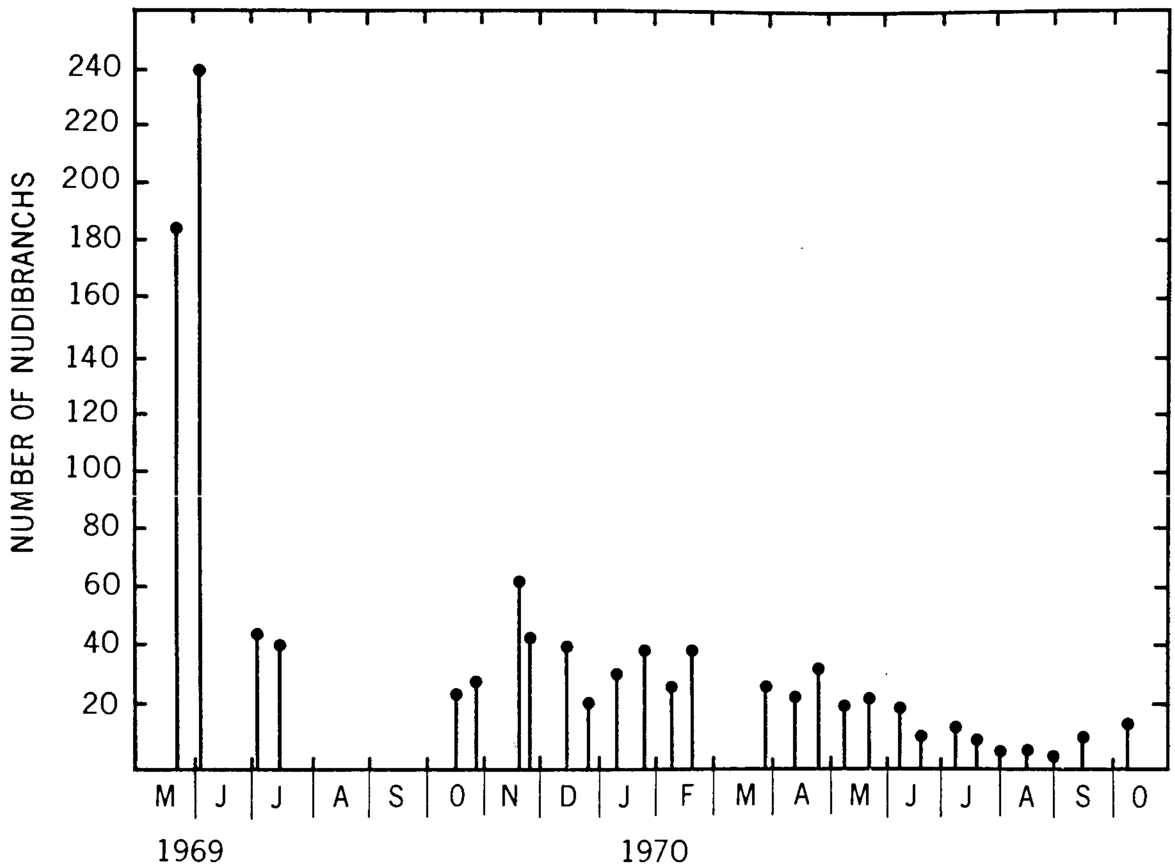
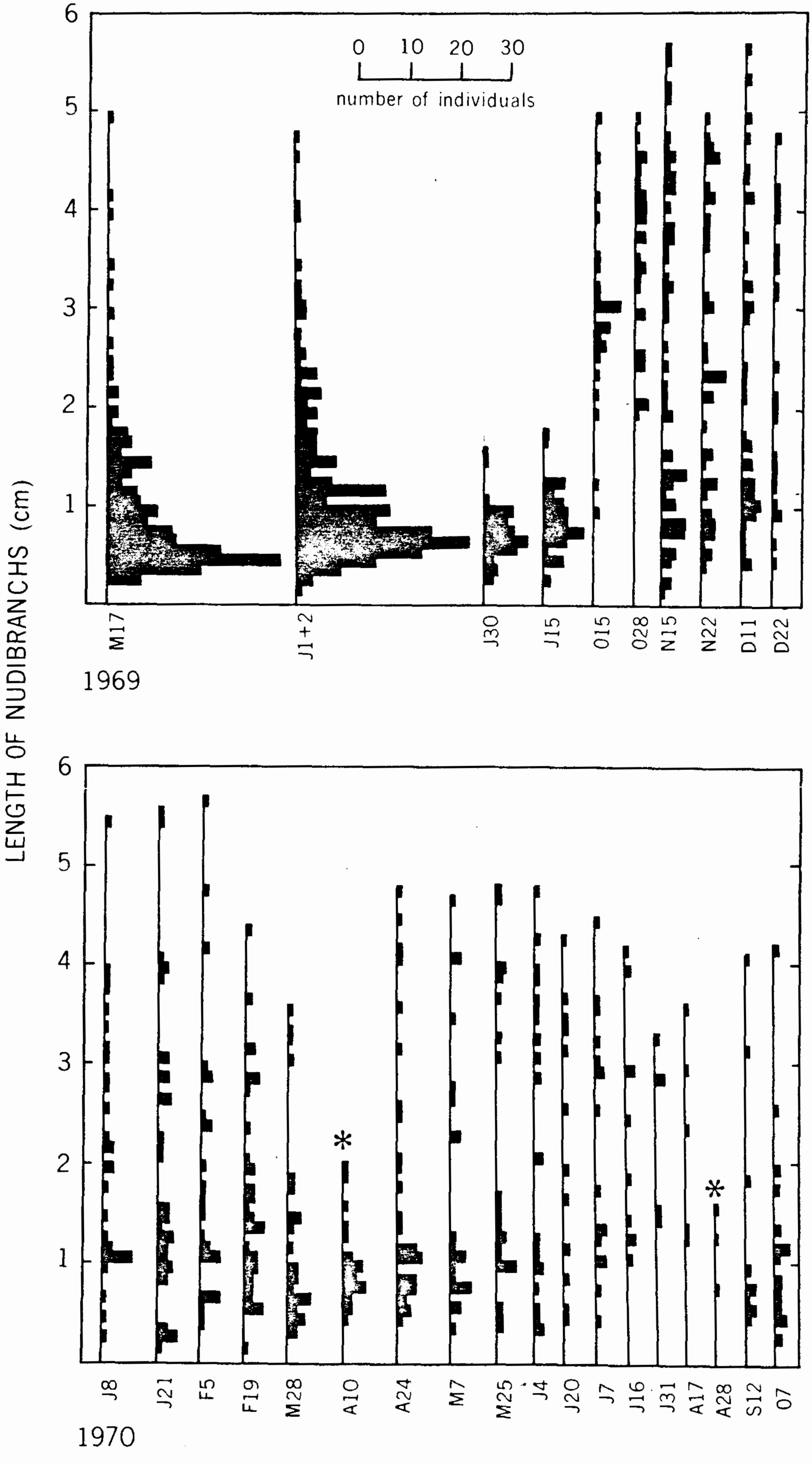

NUMBER OF NUDIBRANCHS
240
220
200
180
160
140
120
100
80
60
40
20
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
1969
1970

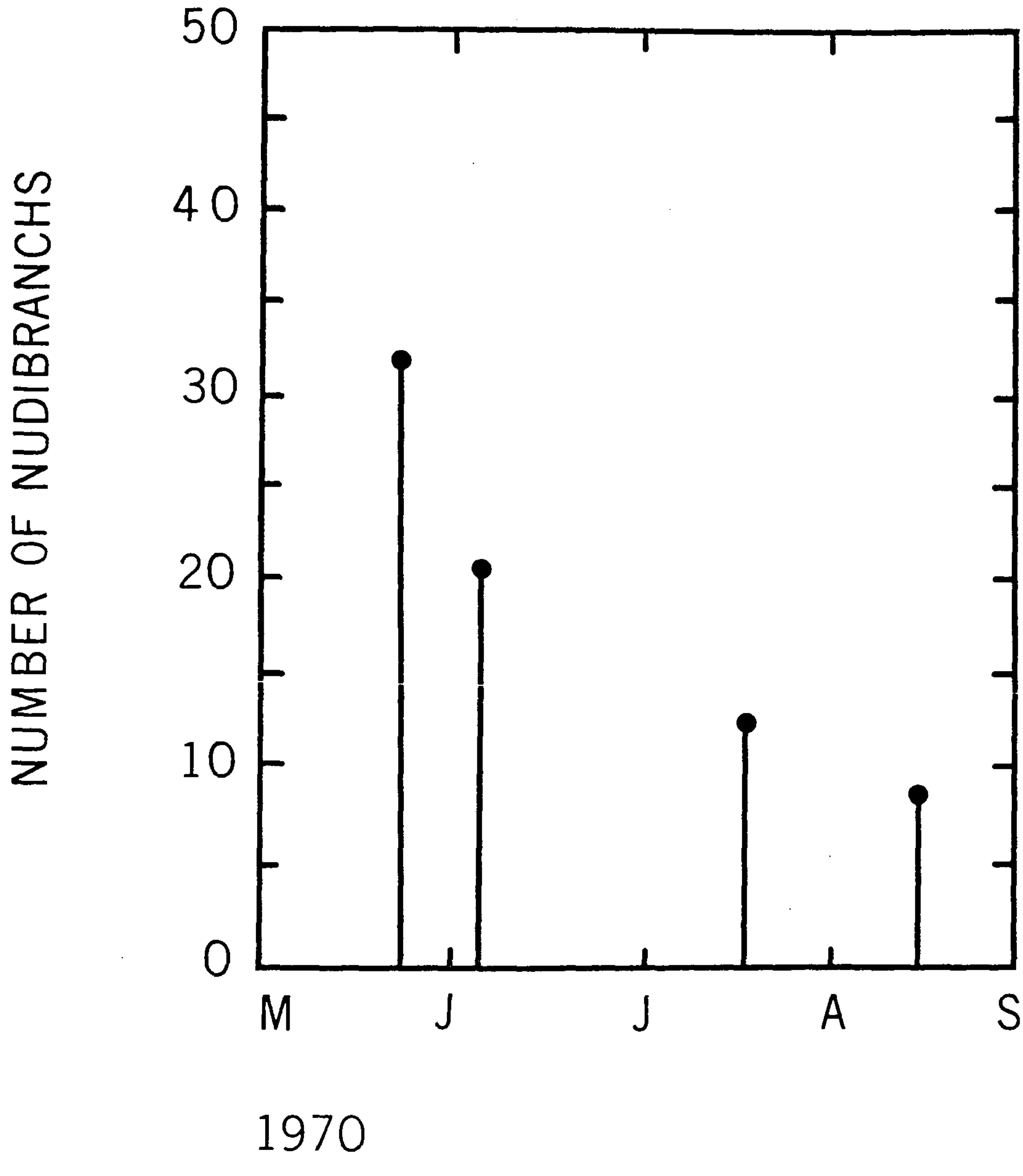
Figure 8. Size-frequency distributions of _Archidoris montereyensis_ at Lantzville, 1969-70. Occasionally, adults recognizable from previous counts were spotted just off the grid sites. Asterisks denote dates when this resulted in a lack of adults on the grid sites.


LENGTH OF NUDIBRANCHS (cm)
0 10 20 30
number of individuals
6
5
4
3
2
1
M17
J1+2
J30
J15
O15
O28
N15
N22
D11
D22
1969
6
5
4
3
2
1
*
*
J8
J21
F5
F19
M28
A10
A24
M7
M25
J4
J20
J7
J16
J31
A17
A28
S12
O7
1970

rocks. Undoubtedly there were more in this area than were found. Although the crash in June, 1969 affected all sizes of nudibranchs, some individuals under two cm remained. The few individuals found in October consisted of juveniles and adults, probably representing growth of the animals present in July, but young were absent. Young appeared in November, increasing the total numbers of nudibranchs, but the larger specimens began to disappear throughout the winter. Enough mature individuals remained to account for some spawn appearing all winter. There was a large settlement visible from late February to May which was balanced by the disappearance of more juveniles and adults. The decline in numbers from June to September was not differential as it was in 1969. Although all size classes were affected, by July no young under 1 cm were found on the grid sites and very few juveniles and adults. In September the slight increase can be ascribed to new settlement.

The Bamfield population at "Nudibranch Point" during May to August, 1970 showed a decline in numbers similar to that found during this period at Lantzville (Fig. 9). With a grid area of 9.0 m^2, population density declined from $3.\dot{5}$ per m^2 to $0.\dot{7}$ per m^2. The decline covered all size

Figure 9. Total numbers of <u>Archidoris montereyensis</u> on the grid site at Bamfield, 1970.


NUMBER OF NUDIBRANCHS
50
40
30
20
10
0
M
J
J
A
S
1970

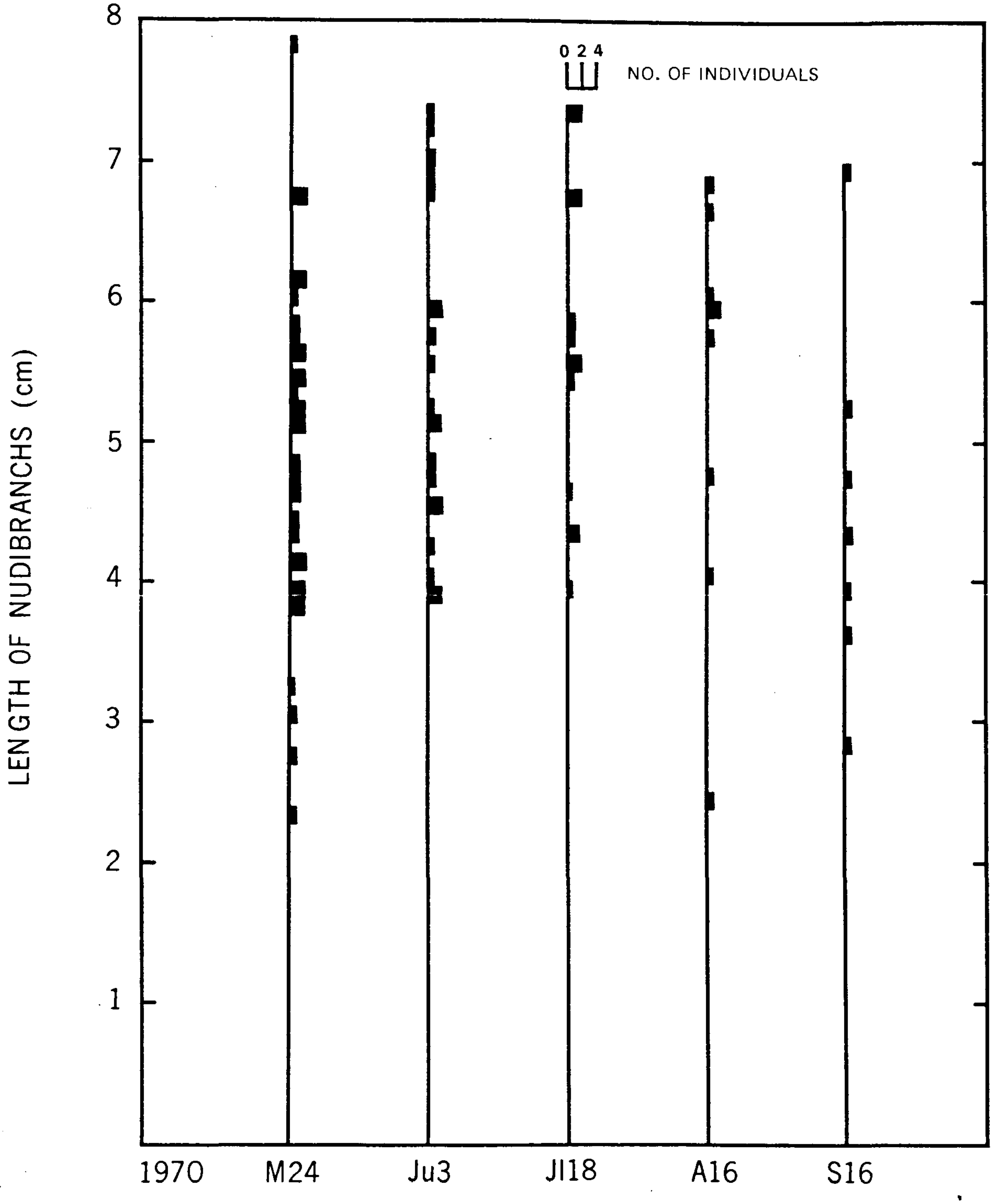
classes present in May (Fig. 10). No nudibranchs were found on the Bamfield study site under 2 cm.

The most striking difference between the two areas in the summer, 1970 was that at Bamfield, Archidoris montereyensis was larger and more abundant. There was an average density of 1.1 per m^2 at Bamfield compared to 0.6 per m^2 at Lantzville, and a maximum length of 8 cm at Bamfield compared to 5 cm at Lantzville (Fig. 11).

Vertical Intertidal Distribution: Numbers, Age, Season

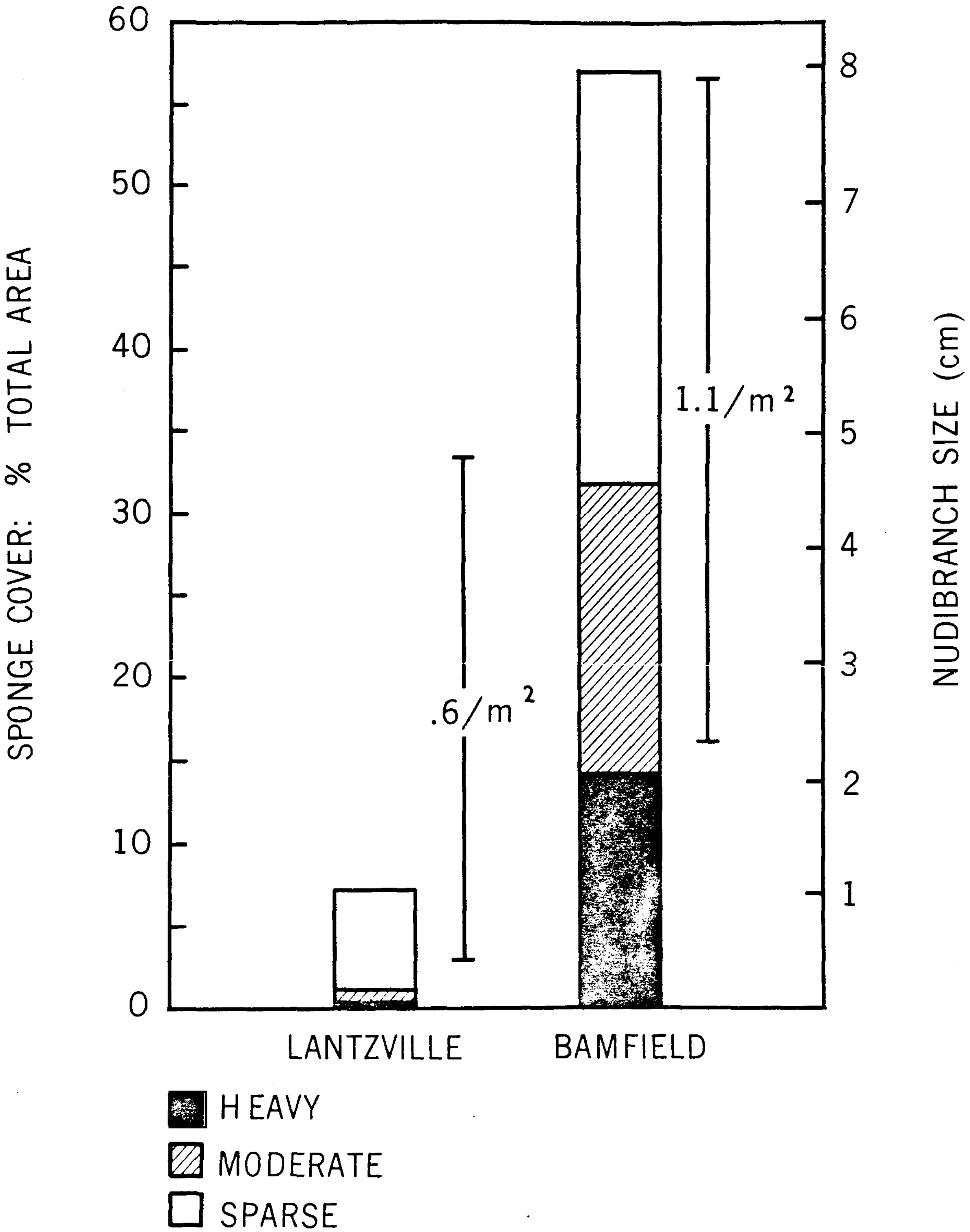
The intertidal height of each nudibranch was recorded and the frequency at each height was plotted for different seasons to find out if there was any seasonal variation in the vertical position of the population at Lantzville (Fig. 12). An analysis of variance was carried out (Table 2). This revealed that the distribution of Archidoris montereyensis varies significantly with intertidal height ($p < .001$). The overall vertical frequency curve was the same for each season ($p > .05$), and the frequency at each height also remained the same throughout the year

Figure 10. Size frequency distributions of *Archidoris montereyensis* on the grid site at Bamfield, 1970.



0 2 4
NO. OF INDIVIDUALS
LENGTH OF NUDIBRANCHS (cm)
8
7
6
5
4
3
2
1
1970
M24
Ju3
Jl18
A16
S16

Figure 11. Comparison of the sponge cover (bars) with individual size range (lines) and population density of nudibranchs between Lantzville and Bamfield in the summer of 1970.



SPONGE COVER: % TOTAL AREA
60
50
40
30
20
10
0
NUDIBRANCH SIZE (cm)
8
7
6
5
4
3
2
1
.6/m 2
1.1/m 2
LANTZVILLE
BAMFIELD
HEAVY
MODERATE
SPARSE

Figure 12. Seasonal vertical distribution of Archidoris montereyensis at Lantzville. Curves show percent of population occurring at each intertidal height.

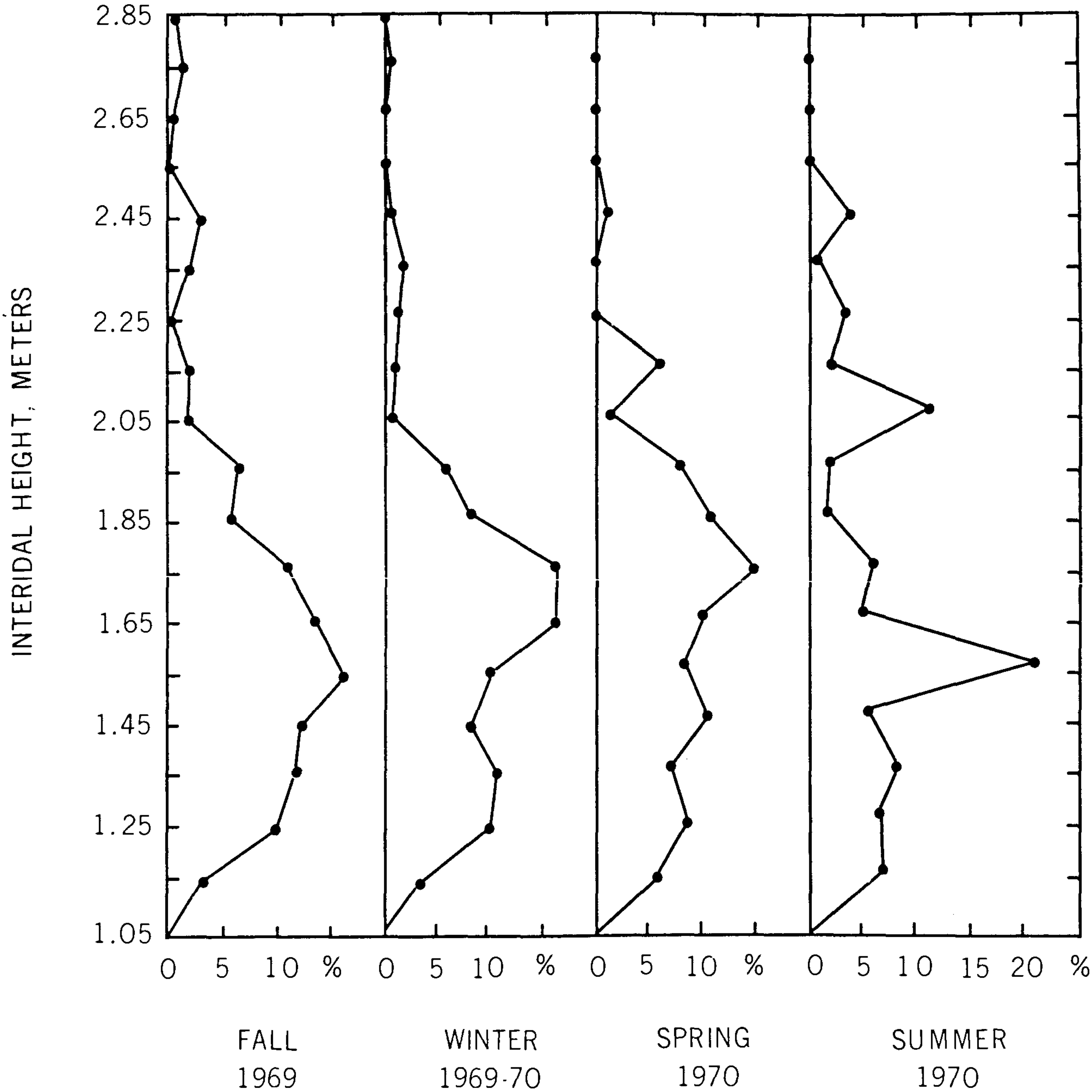

INTERIDAL HEIGHT, METERS
2.85
2.65
2.45
2.25
2.05
1.85
1.65
1.45
1.25
1.05
0 5 10 %
0 5 10 %
0 5 10 %
0 5 10 15 20 %
FALL
1969
WINTER
1969-70
SPRING
1970
SUMMER
1970

Table 2. Analysis of variance (F test) of the % frequency of *Archidoris montereyensis* at 10 intertidal heights and 4 seasons.

Source of variation	Means of squares	Degrees of freedom	F ratio	Critical values of F ratio	Probability
Between samples	2446.444	39			
intertidal heights	10515.063	9	338.4993	338.499 >4.02	P ≤0.001
seasons	28.500	3	0.9175	.918 <2.84	P ≥0.05
seasons and heights	25.565	27	0.8230	.823 <1.76	P ≥0.05
Within samples	31.064	40			

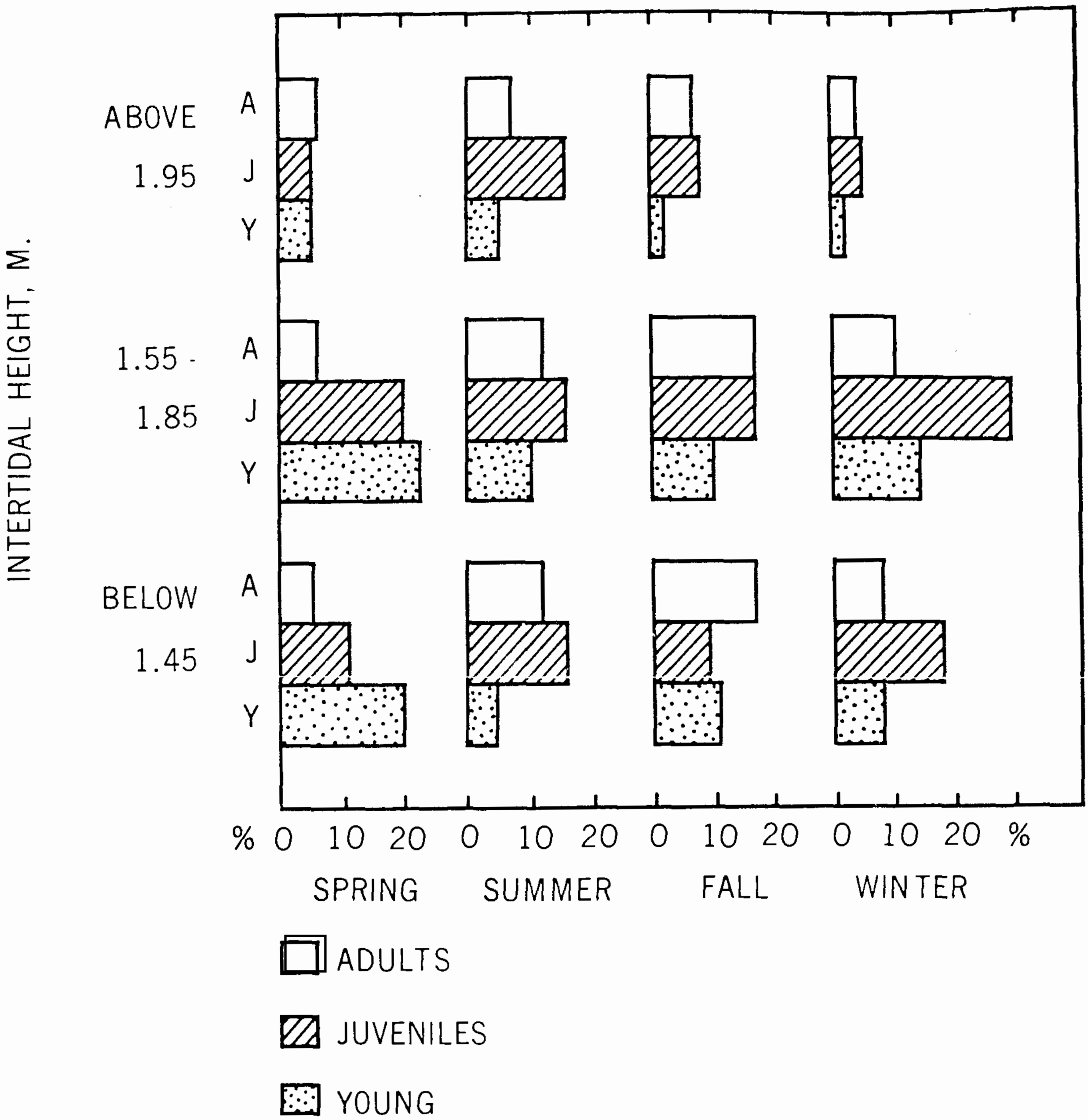
($p > .05$). This indicates that for the year studied there was no seasonal change in the vertical range of the population nor in the relative distribution within this range. Peak numbers were never at the lowest portion of the grid sites. Thus, no downward shift took place.

To check whether the population continued below the vertical height accessible at low tide, scuba dives were made in June, 1969 and April, 1970. *Archidoris montereyensis* was not found on the shifting sand below the grid sites. At Blunden Point, where the rocky reef extended to a depth of 4 meters below zero datum, *A. montereyensis* was found occupying a narrow zone near the top of the reef, which corresponded to the intertidal heights of the grid sites. No *A. montereyensis* were observed in the subtidal areas.

The Bamfield population likewise showed no downward shift as numbers diminished. The smallest population completely sampled (August 16, 1970) did not have any nudibranchs on the lowest 2 meters.

The population at Lantzville was broken down into three size classes, and examined for each season at three heights (Fig. 13). This was to see if size was related to season and vertical position in the intertidal zone. In the

Figure 13. Frequency at different seasons (1969-70) of Young (Y), Juveniles (J) and Adults (A) at three intertidal heights at Lantzville. Bars are percents of the total population present in a given season.


INTERTIDAL HEIGHT, M.
ABOVE
1.95
1.55 -
1.85
BELOW
1.45
A
J
Y
% 0 10 20 0 10 20 0 10 20 0 10 20 %
SPRING
SUMMER
FALL
WINTER
ADULTS
JUVENILES
YOUNG

spring, the bulk of the nudibranchs (45%) were young, in the summer 50% were juveniles, the fall population was comprised of 42% adults, and in the winter 51% of the population were juveniles. In proportion to the number of nudibranchs occurring at each height, a chi-square analysis (Table 3) indicated that in the spring there were more young at the bottom of the grid site than at the top. The fall data also showed this trend for young to occur on the low or the mid-portion rather than on the top. This was not the case in the summer and the winter, when the young appeared in the same proportion at all three heights. Since recruitment at these times was gradual, not sporadic as in the spring and fall, the young had time to disperse into the upper zone. The only other significant change was a greater proportion of adults on the top in the spring which, considering their small numbers at this time, probably reflects a gregarious grouping which remained for a few months. One difference which cannot be explained is the lower proportion of juveniles in the fall in the population at the bottom of the grid when compared with the top.

Table 3. Chi-square analysis of frequency differences at three intertidal heights at Lantzville. The animals were separated as to size (Young <.5 cm, Juveniles < 3 cm, Adults > 3 cm) and grouped into four seasons.

Age	Heights Compared	Spring	Summer	Fall	Winter
Young	low and medium	N	N	N	N
	low and high	P <.01	N	P <.01	N
	medium and high	N	N	P <.001	N
Juvenile	low and medium	N	N	N	N
	low and high	N	N	P <.01	N
	medium and high	N	N	N	N
Adults	low and medium	N	N	N	N
	low and high	P <.01	N	N	N
	medium and high	P <.001	N	N	N

N = no significant difference, P >.05 d.f. = 1

Individual Movements

Examination of the movement patterns of individual nudibranchs was done by measuring the net distance covered by marked animals between observations and by observation of distinctive groups. The marked adult nudibranchs exhibited considerable lateral movement but little vertical movement, averaging 108 cm net horizontal movement in two weeks, but only 18 cm vertical movement. Since *Archidoris montereyensis* was observed to move rapidly enough to cover these distances in a single high tide, it appears to lead a fairly sedentary life. However, the actual movements between observations were unknown. The nudibranchs rarely moved at all when exposed by low tides.

When there were few nudibranchs, individuals in small groups could be recognized as remaining near the same locale for several months. There were very few changes in these groups, which appeared to be formed when the animals were sexually mature. Each nudibranch probably remained in these groups as long as it was in breeding condition, laying its eggs nearby. The locales chosen for many of these groups appeared to have a protective function. Several areas were shaded and had water runoff from high tide pools. This moisture would serve to prevent desiccation during the low tides which occurred during the day in the spring and summer.

The only times nudibranchs were found out of the shelters, they were copulating rather than feeding; forays for food, if any, must have taken place at high tide. Generally, the nudibranchs returned to the same shelter but sometimes they were found in a new shelter. These groupings were always of large adults and the individuals disappeared within a few months. Young and juveniles did not form lasting groups, but individuals were often spotted several times under the same alga or in the same crack.

Reproductive Activity

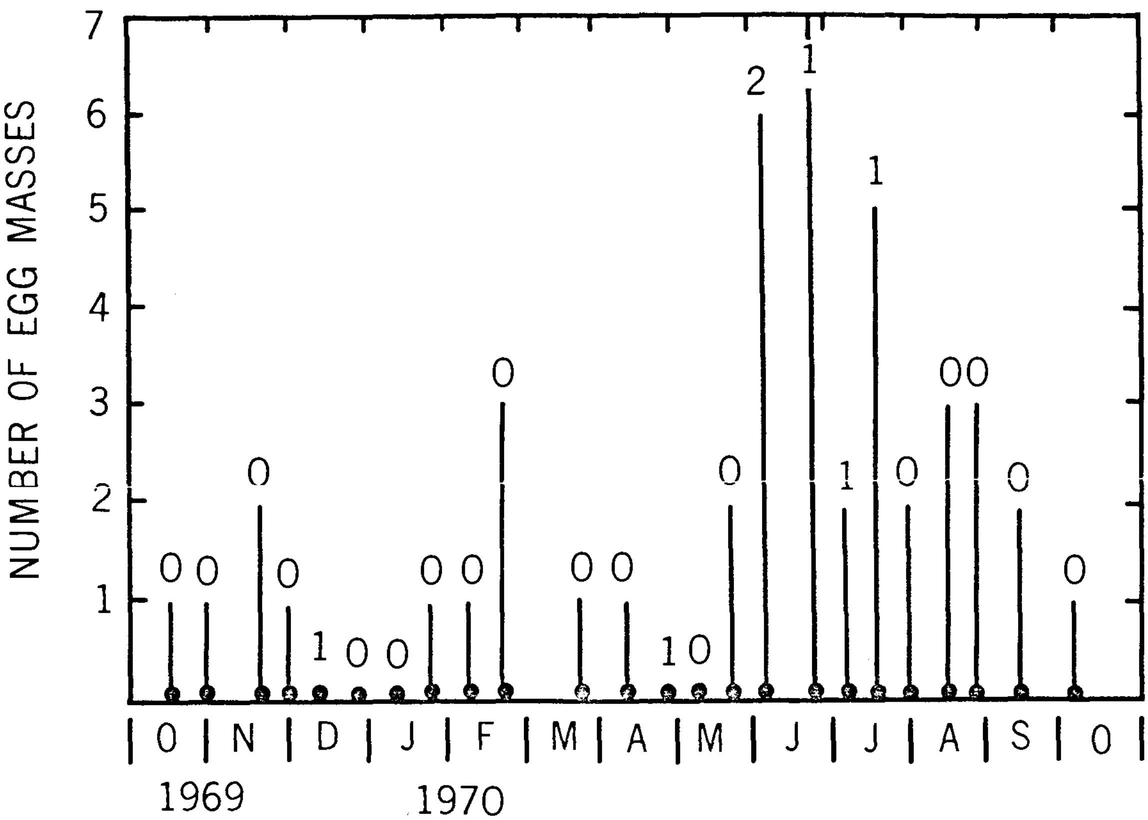
Reproduction of these hermaphroditic animals was assessed by the number of copulating pairs, spawn, and recently settled nudibranchs less than 5 mm in length. Pairing probably always took place at high tide when the nudibranchs were mobile, but it was not interrupted by low tides and a number of copulating pairs were found on the grid sites at Lantzville and Bamfield. Copulation lasted the duration of the low tide and sometimes pairs were still together the next day. Thompson (1966) found *Archidoris pseudoargus* to typically mate for several hours, but Fretter and Graham (1964) have noted prolonged mating in the same species. After copulating, a pair of A. montereyensis do not move far, and spawn, when deposited several days later, was often within 10 cm of where copulation took place. The spawn of A. montereyensis is laid in a large, coiled jelly-like ribbon on rocks where there is vigorous wave action or a strong current. It is usually pale cream in colour and very conspicuous to the naked eye.

In the laboratory, animals differing in length up to 3 or 4 cm would copulate, but in the field almost all pairs were closely matched in size. The greatest discrepancy was a pair at Bamfield measuring 4.9 cm and 7.4 cm in length. The smallest individual found copulating was 1.6 cm, but the average length was 3.6 cm at Lantzville and 5.1 cm at Bamfield.

Since copulation normally took place in less than a day, and spawn remained for several weeks, it is reasonable to expect fewer sightings of copulation than of egg masses. At Lantzville copulating pairs were found in April, June and July, 1970 (Fig. 14).

Archidoris montereyensis was found to spawn throughout the year. The Lantzville grid sites from October, 1969 to October, 1970 had spawn present every month except

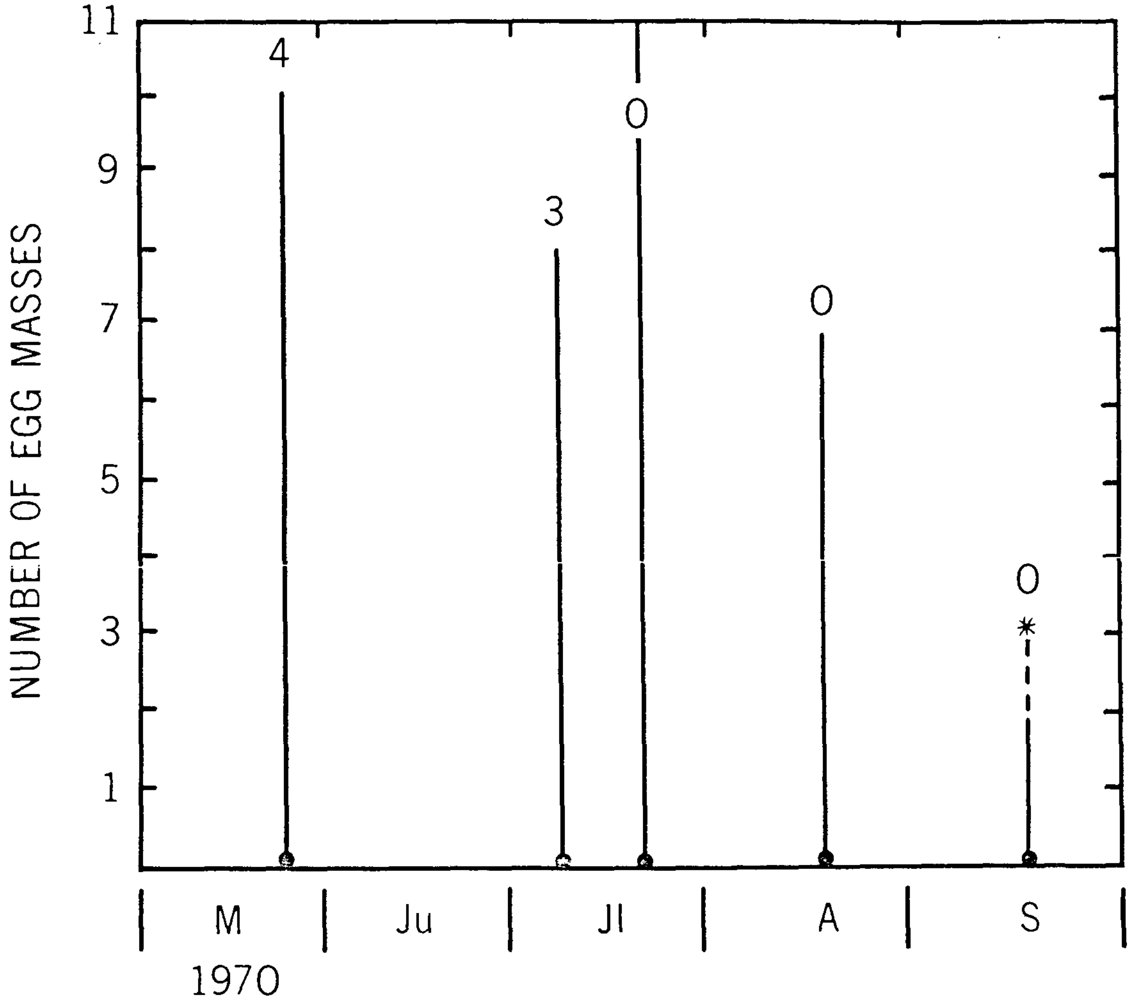
Figure 14. Spawn (bars) and number of copulating pairs (numerals) on the Lantzville grid sites. No spawn or copulating pairs were found in the earlier samples (May, June, July, 1969).


NUMBER OF EGG MASSES
7
6
5
4
3
2
1
0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 2 1 1 1 0 00 0 0
O N D J F M A M J J A S O
1969
1970

December (Fig. 14). One copulating pair was found that month, so the resulting egg masses were either laid off the grid site or destroyed. Spawning did not occur to the same extent every month. There was a peak in the number of spawn found in June, July and August, and a low but steady number of spawn throughout the rest of the year.

"Nudibranch Point" had many copulating and spawning Archidoris montereyensis in April, 1970 which suggests that massive spawning began earlier than at Lantzville. Spawning was still prevalent when the grid sites were set up in May (Fig. 15). The trend at the Bamfield site correlates with that found at Lantzville as there were a large number of nudibranchs copulating and spawning in the summer, and this was reduced in the fall. For the September data, the dotted line in Figure 15 represents a pro-rated estimate as the lower 1/3 of the grid site was not accessible because of surf. Qualitative observations made during the winter and spring of 1971-72 suggest that the life cycle at Bamfield shows greater seasonal regularity than at Lantzville, since spawning was not seen to occur during this period, and the average size of the nudibranchs became progressively larger from early winter to late spring, although considerable variation

Figure 15. Spawn (bars) and number of copulating pairs (numerals) found on the Bamfield grid site. September data is pro-rated (see text).



NUMBER OF EGG MASSES
11
9
7
5
3
1
4
3
0
0
0
*
M
Ju
Jl
A
S
1970

still existed.

Growth Rates and Longevity

Growth rates could not be determined individually except where marked animals were used. Small individuals could not be marked since the surface area was too small to permit discrete staining patterns. Adults tended to disappear, probably dying, so that the growth rates obtained were only for a short period. The average growth rate for marked adults at Lantzville, October - January, 1969 - 70, was 0.4 cm per month (Table 4). The fastest growth rate was 0.6 cm per month, the slowest was 0.3 cm per month.

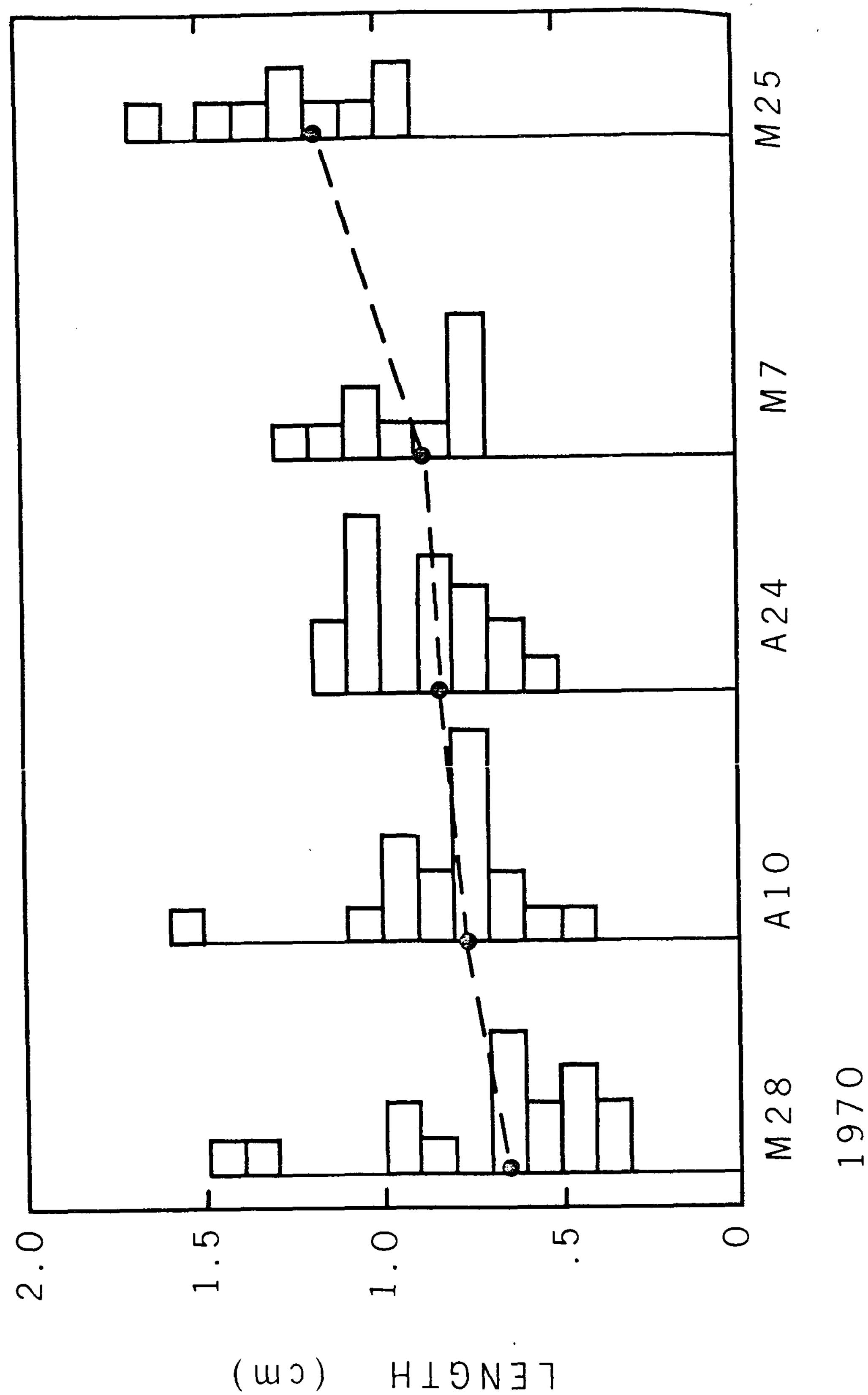
Growth rates of small individuals were estimated by following cohorts as long as they remained distinguishable. A cohort at Lantzville grew from a mean length of 0.65 cm to 1.28 cm from March - May, 1970, a rate of 0.31 cm per month (Fig. 16). This rate is a minimum estimate since some new young were discovered, and some of the larger nudibranchs disappeared. A similar estimate on Grid 1 between June 30 and October 15, 1969, yielded an average growth rate of 0.69 cm per month, for young growing from a mean length of 0.75 cm to 3.17 cm. Growth appears to take place in *Archidoris*

Table 4. Length (cm) of individually marked nudibranchs on the grid sites at Lantzville.

Grid	Oct. 15 1969	Oct. 28	Nov. 15	Nov. 22	Dec. 11	Dec. 22	Jan. 8 1970
1	--	4.0	4.1	4.3	--	--	5.5
	--	3.6	3.9	4.2	--	--	--
	--	3.0	3.8	3.8	--	--	--
	--	4.2	--	4.6	--	--	--
	--	3.4	3.7	*	3.8	4.0	--
2	--	2.0	2.3	--	--	--	--
3	4.0	4.1	4.4	--	--	--	--
	1.0	--	--	--	--	--	--
4	--	3.3	--	--	--	--	--

* Nudibranch in crack-measurement incomplete.

Figure 16. Estimation of growth rate in a cohort of young nudibranchs. Line connects mean lengths of each sample. Data are taken from Grid I, Lantzville.


M25
M7
A24
A10
M28
1970
2.0
1.5
1.0
.5
0
LENGTH (cm)

montereyensis all year around and at approximately the same rate for small and large individuals, although more data would be needed to detect any small differences due to age or season.

If we make no allowances for the effect of age or season on growth rates, in one year a nudibranch could grow to a length between 3.72 and 7.28 cm. Since at Lantzville, the largest nudibranch found was 5.7 cm, and nudibranchs 3 cm long were spawning, Archidoris montereyensis appears to reach sexual maturity in less than one year.

An estimate of the life span of Archidoris montereyensis was made from data obtained at Lantzville. Only young nudibranchs and no spawn were present in June and July, 1969 (Fig. 8). By October, 1969, spawning adults, presumably the now mature June-July young, were present. This generation disappeared by March, 1970, as can be seen from the sizes of nudibranchs on the individual grid sites (Appendix I). Young which settled by November, 1969, began spawning in March, 1970, and nearly all of the adults disappeared in March, although a few were present until July. A March recruitment underwent a large summer mortality, but the survivors were spawning by late summer. These three recruitments were the only ones which could be followed clearly, but since recruitment took place all year, there was considerable overlap in generations and the various size classes were coexisting almost all year around.

It appears that, if we consider Archidoris montereyensis to be a month old before being spotted on the grid sites (a maximum estimate according to growth rate data), they were capable of spawning between 5 and 7 months after metamorphosis, and most of the animals disappeared shortly thereafter although some remained as long as 10 months. Since none remained any longer than 10 months, and extrapolation of growth rate data shows them to be capable of growing as large as they did in that time, the data are consistent with an estimated life span of a year or slightly less for A. montereyensis.

Comparisons of individual sizes for the same date in the Bamfield and Lantzville populations (Fig. 11) revealed that Bamfield had much larger specimens than were ever found at Lantzville, due probably to greater food supply which will be discussed in the next section. Since the animals are larger at Bamfield, and since the population of adults had been considerably reduced in numbers by August (Fig. 9) with no evidence of downward migration, it appears that the large individuals obtained their size due to a more rapid growth rate than that at Lantzville rather than from a longer life span.

Relationships of Archidoris montereyensis To Its Food Supply

Feeding Behaviour

Archidoris montereyensis feeds exclusively on sponges. The radula is used to rasp as the nudibranch moves over the sponge surface. From my observations and the literature, the main prey appears to be *Halichondria panicea* although I have found it eating *Haliclona permollis* and *Suberites sp.* in the field. It has also been observed feeding upon *Tedania sp.*, *Mycale adhaerens*, and *Stylissa stipata* (G. A. Robilliard, pers. comm.). *A. montereyensis* near Argyle Lagoon, San Juan Island, Washington, which were feeding on *Haliclona sp.* were coloured bluish-green with an overcast of yellow, probably due to the pigments of this sponge. Diet has been found to affect the coloration of nudibranchs (Labbé, 1931; Swennen, 1961; Roginskaya, 1963).

Archidoris montereyensis is almost invariably found in an area where *Halichondria* is present, although the nudibranchs are not always upon the sponge. *A. montereyensis* are often found on bare rock when not feeding, and spawn is deposited on the rock surface. It appears that sponge does not present as good a substrate for attachment as bare rock.

A. montereyensis usually begins feeding at the edge of a sponge patch, and, as it rasps away the sponge, it moves on to the bared substrate. Where the sponge cover is thick, A. montereyensis eats its way down into the sponge, and rasps a tunnel underneath (Fig. 17). This results in the animal being hidden completely, and may be the reason that small specimens are rarely seen in areas of heavy sponge cover. Feeding appears to be sporadic at least in large nudibranchs, and they may move from one part to another before the first is completely consumed. Field observations suggest that grazing has a marked effect on Halichondria, as areas supporting an A. montereyensis population have large grazed patches in contrast to areas without A. montereyensis. Long (1968) considers A. montereyensis to be the major predator of Halichondria panicea.

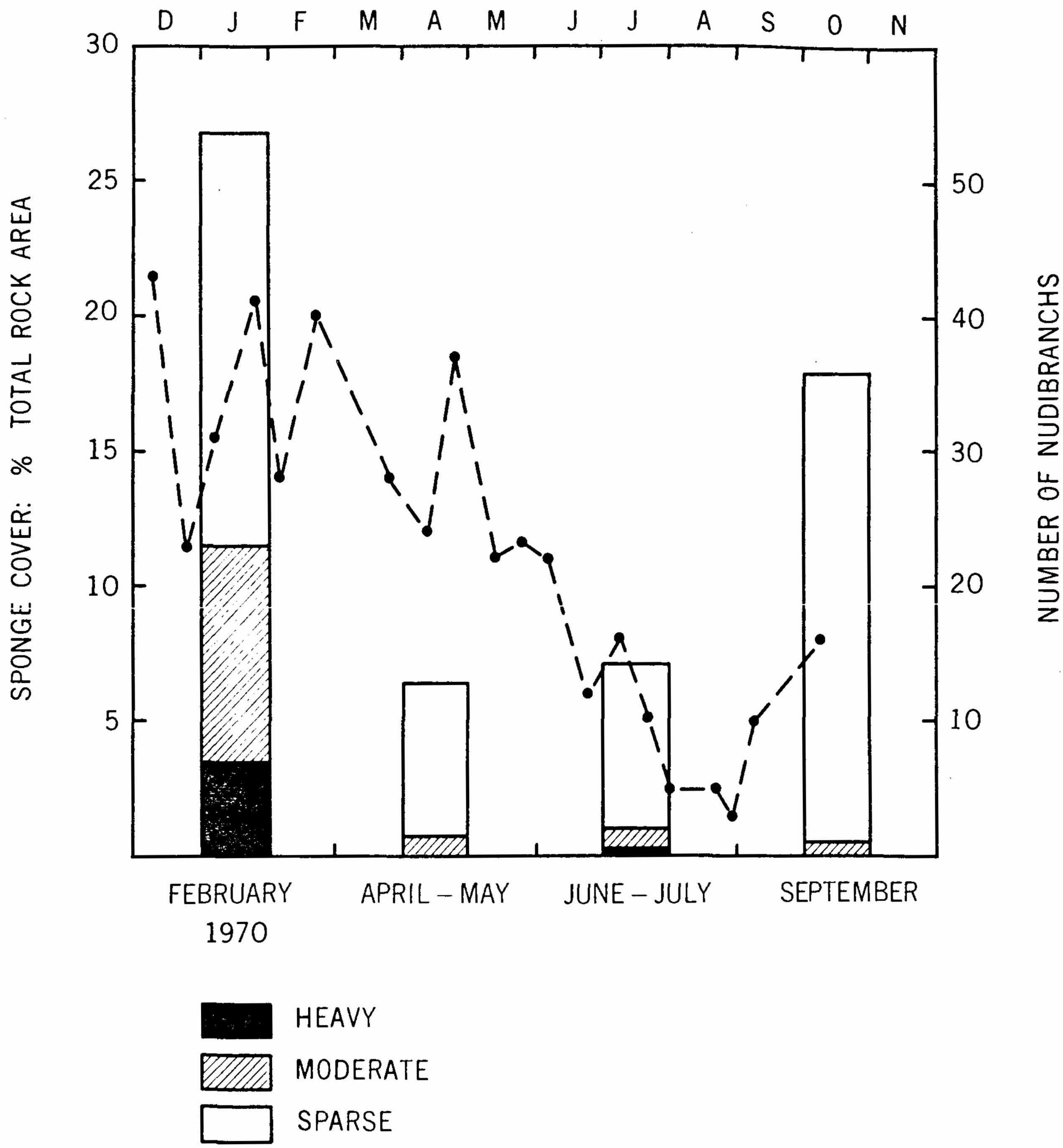
Distribution and Food Supply

The results of the sponge survey at Lantzville (Fig. 18) indicate that in 1970 the sponge cover at Lantzville, which consisted of Halichondria panicea and a few small patches of Haliclona permollis, was always very light. Between 73% and 93% of the gridded area had no visible sponge. Scrapings of these areas, when examined under a microscope,

Figure 17. Two *Archidoris montereyensis* feeding on *Halichondria panicea* at Bamfield. Grazed areas (G) are evident, and one nudibranch (N) is eating a tunnel under the sponge. Photo by Lea Seeton.


N
G

Figure 18. Seasonal variation in sponge cover and numbers of Archidoris montereyensis at Lantzville. Sponge cover is classified as heavy, moderate, sparse, or absent (see text). Each bar represents one set of measurements, sometimes spanning a two month period, on the four grid sites.


D J F M A M J J A S O N
30
25
20
15
10
5
50
40
30
20
10
SPONGE COVER: % TOTAL ROCK AREA
NUMBER OF NUDIBRANCHS
FEBRUARY
1970
APRIL – MAY
JUNE – JULY
SEPTEMBER
HEAVY
MODERATE
SPARSE

occasionally revealed a thin layer of sponge. The population curve declines later than the sponge decline in the spring and begins to increase in the fall when sponge is more plentiful.

In the fall the grid sites were covered with a sparse layer of bright yellow sponge. The sponge cover increased during the winter and very early spring, but declined in the late spring and summer. This corroborates with deLaubenfels' (1932) observation of a decrease in Halichondria panicea in the summer along the central California coast.

Bamfield had considerably more sponge on the grid sites than at Lantzville (Fig. 11). This difference in food supply, as mentioned earlier, probably causes the difference in size found between the nudibranchs at Bamfield and at Lantzville (Fig. 11). Although there is no obvious seasonal correlation between numbers and sponge cover at Lantzville, the fact that nudibranch numbers are at their lowest when sponge is scarce and increase in the fall when sponge increases as well as the fact that Lantzville had a lower average population density than Bamfield, suggests that there is a relationship between food supply and nudibranch population size.

A check was made at Lantzville to see if there was any correlation in dispersion between sponge and nudibranchs. In 1970, 12.9% of the squares contained sponge. A total of 75 nudibranchs were observed, of which 19 (25%) occurred in squares containing sponge. A chi-square test (Table 5) was carried out comparing the number of nudibranchs observed with the number expected if nudibranch distribution was random with respect to sponge. The test showed a highly significant correlation between nudibranchs and sponge distribution ($p < .005$).

Field Experiments on Food Supply

Fence Experiment:

Marked differences in movement patterns were observed between *Archidoris montereyensis* placed on *Halichondria panicea* and those placed on bare rock (Fig. 19). On the side of the fence which retained its sponge cover, *A. montereyensis* was found either in the same place or a short distance from the starting area. At the end of four high tides, these individuals showed no net horizontal movement away from the starting place, and a net downward, vertical movement of 3.7 cm.

On the side of the fence denuded of sponge, horizontal and vertical movement was more pronounced. Net movement during the first high tide was horizontal, but during the next three high tides was downward in the intertidal zone. None of the nudibranchs moved upward. On both sides

Table 5. Chi-square analysis of the distribution of *Archidoris montereyensis* and sponge on the grid sites at Lantzville.

	Number of Nudibranchs OBSERVED	Number of Nudibranchs EXPECTED
Sponge present	19	9.68
Sponge absent	56	65.32

Expected value, sponge present = % squares containing sponge x total number of nudibranchs

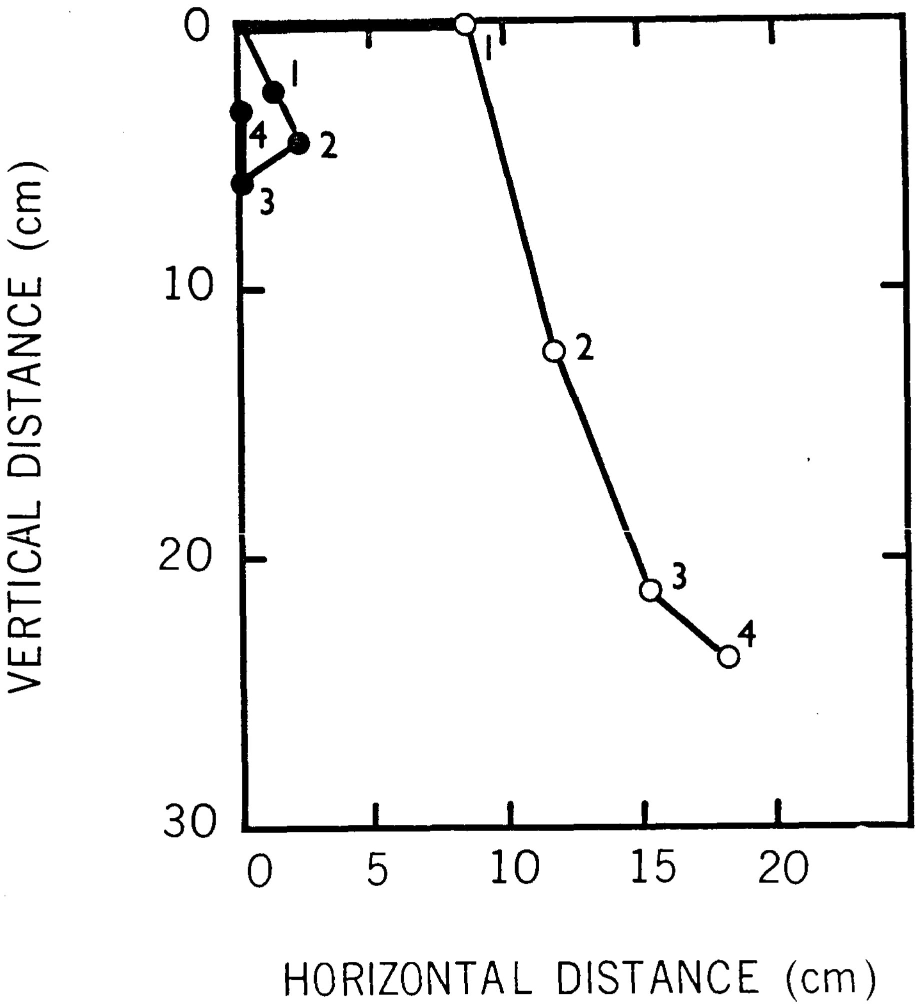
= 12.9% x 75

= 9.68

$\Sigma \frac{(O-E)^2}{E} = 10.65$ d.f. = 1

$P < 0.005$

Figure 19. Distribution pattern of _Archidoris montereyensis_ transplanted to sites where sponge was present (●) and removed (○). Numbers mark net positions of nudibranchs after consecutive high tides.



VERTICAL DISTANCE (cm)
HORIZONTAL DISTANCE (cm)
0
10
20
30
0
5
10
15
20
1
2
3
4

of the fence, the movement patterns of individuals were similar to the net movement patterns shown in Figure 19. None of the nudibranchs managed to cross the fence barrier.

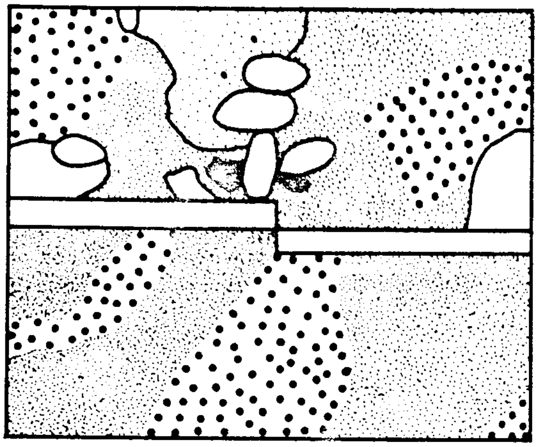
Losses of nudibranchs during the experiment were surprisingly high. Only those lost after the first high tide were replaced. Poor initial attachment was not the only factor involved, since six nudibranchs disappeared after surviving one or more high tides. This may be a reflection of the high natural mortality rate.

Cage Experiment:

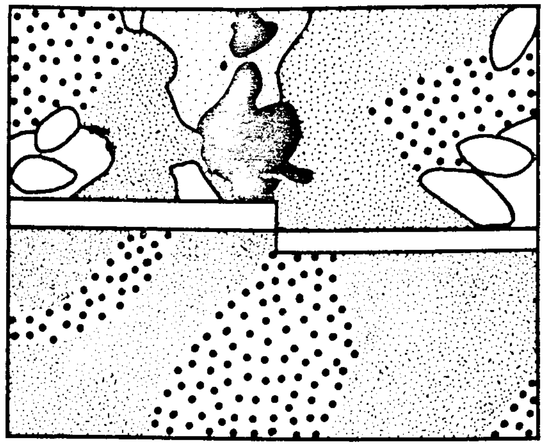
The five nudibranchs enclosed in a wire cage to test the effect of feeding on the sponge cover remained attached throughout the experiment and evidence of grazing was apparent after the first high tide. Their positions and areas of sponge depleted by grazing are shown in Fig. 20.

The volume of sponge consumed was estimated by multiplying the area of the patches by a depth of .64 cm, which was 3/4 of the average depth determined by the random depth samples (average .85 cm, range 0-1.8 cm). The full depth was not used because the sponge was not always rasped down to

Figure 20. Diagrams of cage experiment after consecutive high tides. Areas of deep ( ), moderate ( ), shallow ( ) and absent (□) sponge cover are outlined. Solid (■) areas show where <u>Archidoris montereyensis</u> has been feeding. Reduced to 1/5 original size. Five oval outlines (⬭) indicate nudibranchs.



TIDE 1



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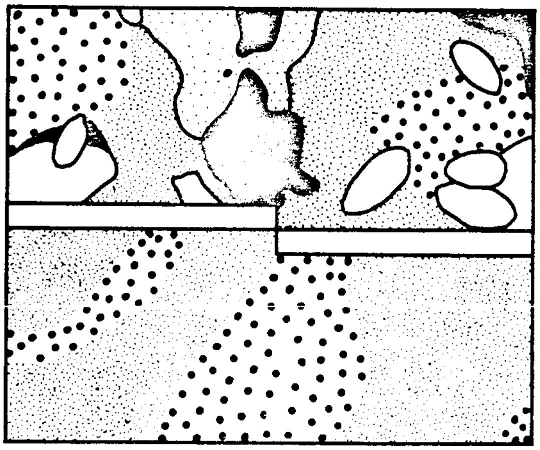

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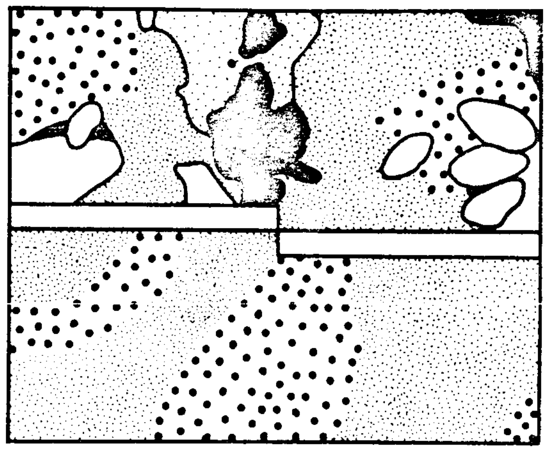
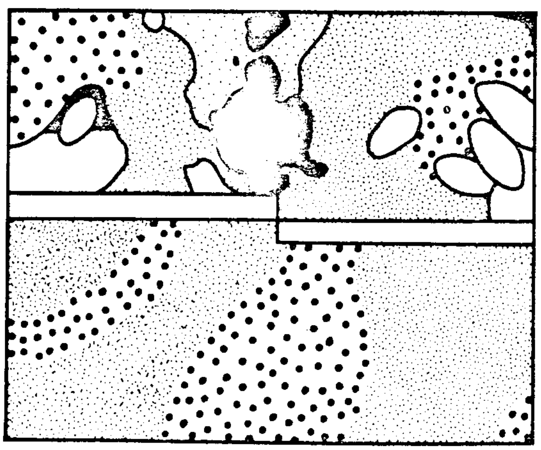
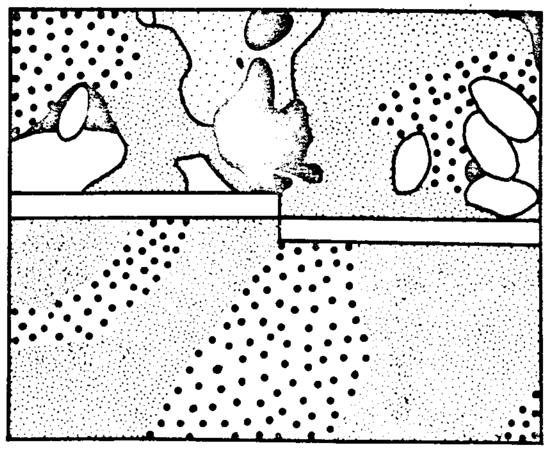


TIDE 4



TIDE 5



TIDE 6

the substrate. The volume of Halichondria panicea eaten was high during the first three high tides, and then decreased considerably (Table 6). There was evidence of some sponge eaten during the sixth high tide but it could not be measured because the bodies of the nudibranchs concealed most of the portion they had eaten. Nudibranchs moving away from an area often revealed a large grazed patch. The growth rate of H. panicea during this time is evidently not fast enough to replace the sponge grazed by the nudibranchs. In the cage experiment, the control section showed no change in depth or area covered by the sponge.

The only volume of sponge which could be attributed to a particular nudibranch was that eaten by #3. This nudibranch remained near the same area during the three days the cage was examined. It ate an estimated total volume of 5.61 cm^3 in three days, excluding the portion covered by its body, which could not be estimated.

From the activities of the nudibranchs after each high tide (Table 6), it appears that #3 and #4 were consuming sponge rather than searching for a mate. Nudibranchs #1, 2 and 5 were all feeding the first day and

Table 6. Activities and sponge consumption of 5 nudibranchs in cage experiment at Bamfield.

Nudibranch number	1	2	3	4	5	cm^3 sponge
Size in cm	4.2	4.9	3.2	4.0	5.5	consumed
September 15 morning	f	f	f	f	f	2.84
September 15 evening	m	m	f	m,f	m	19.23
September 16 morning	c	c	f	m,f	m	9.29
September 16 evening	f	m	f	m,f	m	0.45
September 17 morning	f	c	f	f	c	1.59
September 17 evening	f	c	f	f	c	0.00

f - evidence of feeding

m - moved position

c - copulating

sponge was rasped away around their anterior ends. Later, all three were seen copulating but no spawn was laid. Nudibranch #1 resumed feeding after copulation was completed.

The total volume of sponge eaten was approximately 33.4 cm^3, which means the nudibranchs ate an average of 2.23 cm^3 of sponge/nudibranch/day. This is an underestimate, as the amount of sponge under the nudibranchs at the time of sampling was not measured. In the laboratory, captive nudibranchs ate a much smaller quantity of *Halichondria panicea*. This was probably due to the fact that the sponge was difficult to maintain in an aquarium and quickly became coated with a bacterial film.

The Influence of Physical Factors on Population Size

Storms

Severe storms, prevalent in the winter, considerably changed the environment of *Archidoris montereyensis*. Storms affect the temperature and salinity of the ocean and at low tide the nudibranchs may be exposed to rain, snow, ice and severe frost. Abrasive effects occur from sand and debris washed up by the waves and by strong wave action. After storms, the number of nudibranchs was found to be diminished. A decline between December 11 and 22, 1969, occurred during a storm period. Observations made after storms showed that much of the algal cover was removed. During storms and on hot sunny days, nudibranchs were observed to be in cracks or under algae. On cloudy days or calm nights they were observed in the open, often feeding, copulating or spawning. Since under the algae there is less likelihood of snow, rain, frost or desiccation and therefore the climate would not be as severe, it appears that the removal of algae by storms would be disadvantageous to the nudibranchs.

Sand abrasion often causes great damage to intertidal organisms. Large portions of the Lantzville grid sites would be completely buried in sand after a storm. The bottom 30 cm of grid III was buried during the fall of 1969. Portions of the grid not actually buried were blasted clean by the churning, sand-filled waves. In less severe storms, a thin coating of sand would be stuck to the mucous coating of the nudibranchs and on the surrounding sponge and alga.

Temperature and Salinity

Surface temperature and salinity were measured at Lantzville for eight months. The pattern was found to be essentially the same as that obtained by the Fisheries Research Board at Departure Bay (Hollister, 1971a,b), so their data was considered to represent conditions at the Lantzville grid sites. At Lantzville, winter conditions are characterised by low temperatures and high salinity; the reverse is true for the summer. In 1969, the transition from winter to summer conditions occurred in May. Between May and mid-July temperatures rose and salinities fell. Temperature reached a high of 20°C, salinities a low of 16‰. Between mid-July, 1969 and January, 1970, temperatures declined to 6°C and salinity rose to 29‰. The period during the summer, May - September, 1969, was characterised by large temperature and salinity fluctuations. These were not so evident during May - September, 1970. The extremes of temperature and salinity were therefore not as great, temperature reaching a high of 19°C, salinity a low of 23‰.

At Bamfield, surface temperature and salinity data were obtained from Western Canadian Universities Marine Biological Society data taken at Bamfield Inlet (unpublished).

Greater extremes of temperature and salinity are to be expected in the inlet than at the actual sample site due to less turbulence and greater fresh water runoff. Unlike Lantzville, salinities show no marked seasonal difference. Salinities ranged from 24 - 32‰ all year round with occasional extreme lows to 15‰. Temperature changed considerably with the season, rising from an average low of 7°C in January, 1970, to an average high of 16°C in June - August.

When the total numbers of *Archidoris montereyensis* found on the grid sites at Lantzville (Fig. 7) are examined in relation to the water temperature and salinity conditions it appears that there may be a rough correlation. When temperatures are low and salinities high, *A. montereyensis* is most numerous. When salinities are low and temperature high, *A. montereyensis* is scarce.

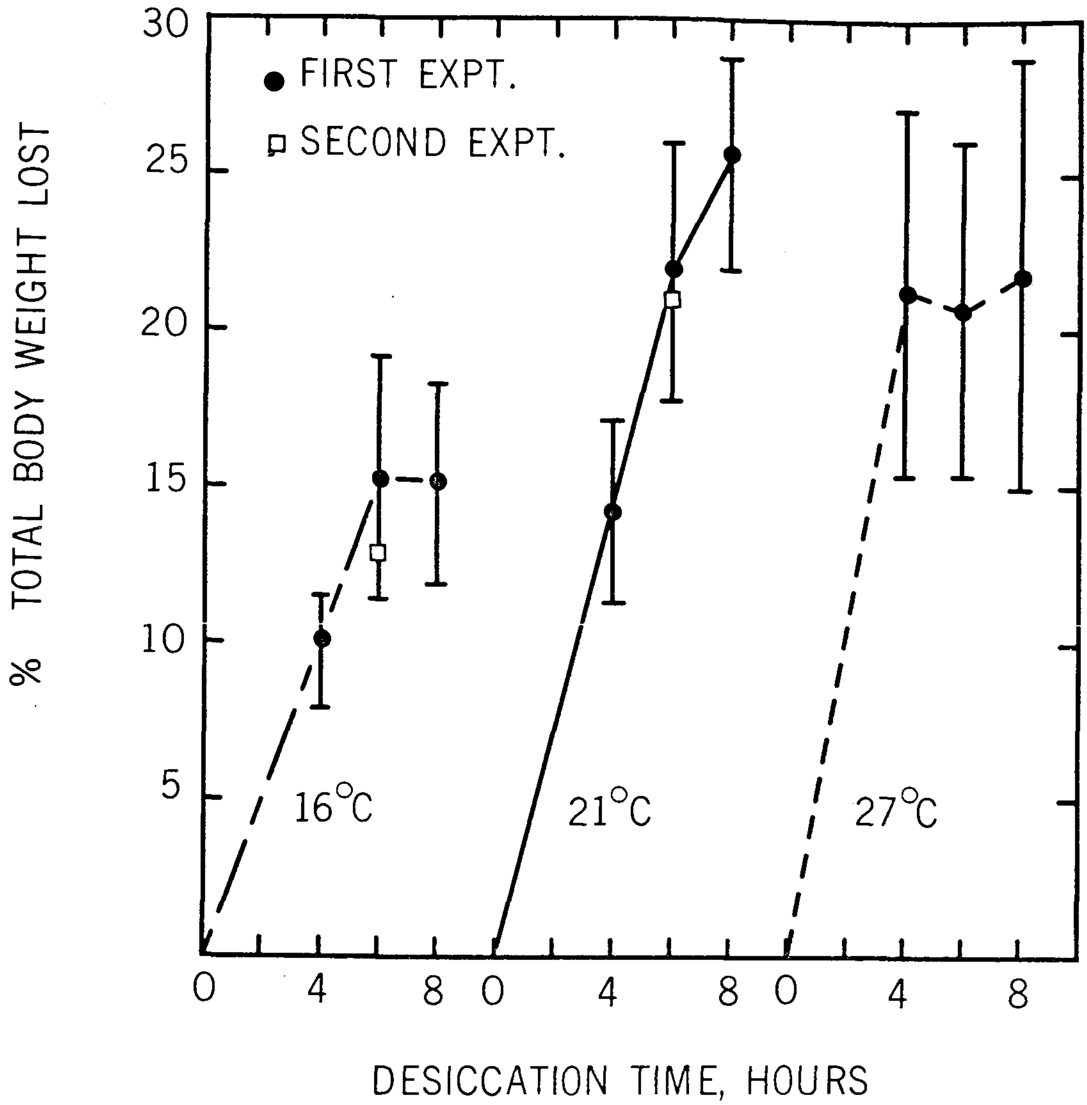
At Bamfield the population was not studied for an extended period of time, but numbers also declined in the summer of 1970. Unlike Lantzville, Bamfield did not have low salinities during this period of decline, so it appears that high air and water temperatures rather than low salinities are correlated with a population low.

Desiccation - Temperature Experiments

A decline in numbers during the summer was evident in 1969 and 1970, but was particularly severe in 1969, when the population numbers at Lantzville dropped from 239 to 43 individuals between June 1 and June 30. It was noted during field trips that at this time the low spring tides, which occurred in mid to late morning, coincided with high air temperatures. The nudibranchs were exposed, often to the direct sun's rays, for periods of 6 - 6½ hours and air temperatures of 18 - 23°C at a relative humidity of 73 - 79‰. To test the role of these physical conditions in causing the population crash, the laboratory experiments bracketed the field temperatures and exposure times.

Results of the first desiccation experiment of April 28, 1970 indicate a general trend of increased percent body weight loss with increasing temperature and exposure time (Fig. 21). The weight loss at the smallest exposure time (4 hours) and lowest temperature (16°C) was significantly lower than at any of the other exposures (Table 7). However, at 16°C it appears to make no difference whether the animals were exposed for 6 or 8 hours, and at 27°C the animals exposed for 6 and 8 hours did not lose significantly

Figure 21. The percent body weight loss of *Archidoris montereyensis* in relation to desiccation time and temperature. 95% confidence intervals are shown around the means. N = 10 for each point.



FIRST EXPT.
SECOND EXPT.
% TOTAL BODY WEIGHT LOST
30
25
20
15
10
5
16°C
21°C
27°C
0
4
8
0
4
8
0
4
8
DESICCATION TIME, HOURS

Table 7. Results of student's t-test comparing the means of the % weight lost during the first desiccation experiment. Three exposure times were used at each of three different temperatures measured in °C.

		16° 4 hrs	16° 6 hrs	16° 8 hrs	21° 4 hrs	21° 6 hrs	21° 8 hrs	27° 4 hrs	27° 6 hrs	27° 8 hrs
16°	4 hrs	--								
16°	6 hrs	P <.01	--							
16°	8 hrs	P <.01	N	--						
21°	4 hrs	P <.05	N	N	--					
21°	6 hrs	P <.01	P <.05	P <.05	P <.01	--				
21°	8 hrs	P <.01	P <.01	P <.01	P <.01	N	--			
27°	4 hrs	P <.01	N	N	P <.01	N	N	--		
27°	6 hrs	P <.01	N	N	P <.05	N	N	N	--	
27°	8 hrs	P <.01	N	N	P <.05	N	N	N	N	--

N = not significant (P >.05).

more weight than they had for those exposure times at 21°C (Table 7). This lack of increased weight loss at 27°C may have been a result of a swift death at this high temperature. The mucous-covered epidermis of the nudibranchs became brittle and hard; perhaps a resulting loss of permeability prevented water from escaping. At 21°C the nudibranchs secreted large amounts of greenish coloured mucous and thus weight loss was greater. The control animals showed negligible weight loss. A two-way analysis of variance (F test) showed that time and temperature were both variables affecting the percent weight lost ($p < .001$) but that there was no synergistic effect ($p < .05$). Mortality is shown in Table 8. After four hours exposure there were survivors at all three temperatures, but after six and eight hours there were only survivors among the group at the lowest temperature (16°C). Individual <u>Archidoris montereyensis</u> survived up to an 18% loss in body weight, but some died after an 8% weight loss. None of the control animals died.

In the second experiment of July 9, 1970, which was performed to replicate the conditions closest to those found in the field, the mean weight loss fell within the range of the previous experiment (Fig. 21). Mortality, however, did not follow the same pattern. One rather than eight nudibranchs died at 16°C and four compared to ten at 21°C (Table 8). Death did not occur before 13.9% weight loss, and some nudibranchs survived as much as a 26.4% weight loss. The length of the individuals did not appear to affect survival. Control animals showed no weight loss or mortality.

These experiments underlined the extreme variability of individuals to withstand desiccation and high temperatures. This individual variability plus the lack of specimens available for sufficient replication of the experiments make it impossible to draw conclusive results from the data. However, these experiments show that temperatures and exposure times similar to field conditions during the large population decline can cause significant mortality.

Table 8. % mortality occurring after desiccation at three exposure times at each of three different temperatures.

Temperature °C	Time hours	% Mortality 1st experiment	% Mortality 2nd experiment
16°	4	40	
	6	80	10
	8	40	
21°	4	40	
	6	100	40
	8	100	
27°	4	80	
	6	100	
	8	100	

DISCUSSION

Life Cycle

A reasonably complete life cycle can be drawn from the information obtained in this study of *Archidoris montereyensis*. The larvae settle in the intertidal zone sporadically both in time and space. The newly settled young show rapid growth and probably reach sexual maturity in about six months. The rather sedentary adults reciprocally copulate and lay egg masses nearby a few days later. The veligers hatch in 23-28 days (Hurst, 1967), although I have observed considerable destruction of the egg masses. The length of larval life appears to be approximately two months. *A. montereyensis* appears to be an annual, dying from post-reproductive mortality, and there is evidence that it does not attempt to migrate to the subtidal after spawning.

I will now discuss my evidence for these features of the life cycle of *Archidoris montereyensis*. The relative absence of young in the intertidal zone gave rise to the theory that some nudibranch species settled in the subtidal zone and only appeared in the intertidal as adults (Garstang, 1890; Eliot, 1910; Costello, 1938). However, the appearance of young *A. montereyensis* at the same intertidal height as adults leads me to agree with the alternate theory that larval settlement occurs in the intertidal zone (Alder and Hancock, 1845-55; Miller, 1961; Potts, 1970). In the case of *A. montereyensis*, the small size of the young, and their tendency to burrow into sponge probably caused them to be overlooked by most collectors. Due to fast growth rates, *A. montereyensis* rapidly reaches adult proportions and then would be apparent to the observer in places where they had not been noticed several months previously. I suspect another reason why spawning nudibranchs are the only ones noticeable in the intertidal zone is that immature nudibranchs are cryptic, hiding in cracks, under algae, and in sponge. Only adults which were copulating or spawning and did not interrupt these acts at low tide, or had not yet moved away to a sheltered place were visible. Since spawn is quite noticeable, collectors tend to search for nudibranchs near spawn and because adults have rarely moved very far away, they are often discovered. My spawning data showed summer to be the time of greatest reproduction in *A. montereyensis* and these months tend to be those most often collected in; indeed, most collections are made extensively only in the summer months and tend to give a very biased view of the yearly occurrence of any nudibranch group.

The sporadic nature of larval settlement in time is suggested by the size frequency data at Lantzville. It is clear from these data that there was some settlement taking place all year around, but the size of settlement varied considerably. In the spring of 1969, there was a huge settlement which was not repeated the next year. Also, the size and timing of the fall settlement was not the same in 1969 and 1970. There were two periods of time when no young appeared on the grid sites, although these were of short duration, and the October, 1969 absence was not repeated in October, 1970, suggesting there is no pattern to these absences. Evidence that *Archidoris montereyensis* settles sporadically in space comes from the striking settlement at Lantzville in the spring of 1969. Nudibranchs covered the rocks at Lantzville in numbers which were not found in the areas searched from Point No Point to Lantzville on the coast of Vancouver Island that spring, or the next.

I shall now discuss my evidence concerning the length of larval life in *Archidoris montereyensis*. There is considerable difficulty in determining how long the larvae remain in the planktonic stage because metamorphosis has not yet been induced in the laboratory, and field populations do not undergo distinct, regular fluctuations. McGowan and Pratt (1954) suggest that larval life is only a few hours; however, I have evidence that it is longer. Some of my evidence derives from possible explanations of periods when no young are present, other evidence comes from correlations of spawning peaks and settlement times.

If larval life is only a few hours long, then it is difficult to explain the lack of young in October, 1969 and the summer of 1970. However, the lack of young can be explained if we assume Archidoris montereyensis has a longer larval life. If the lack of settlement in July-August, 1970 reflects the scarcity of spawn in late April and early May, it suggests a larval stage of at least two months, plus one month for enough growth to take place to allow the young to be spotted in the field. This would correlate with the October, 1969 lack of settlement also, as the population in July had no nudibranchs larger than 1.8 cm and no spawn was found with this immature population. However, the lack of spawn in December-January, 1969-1970, shows no corresponding lack of young.

McGowan and Pratt (1954) suggested a larval life of only a few hours because in the laboratory *Archidoris montereyensis* veligers settled to the bottom of their dishes and died in this time. However, Thompson (1958, 1959) and Hadfield (1963) found that some nudibranch veligers are capable of feeding and growing, lengthening the planktonic phase to several months. Unfortunately, in the only study of a related species, *A. pseudoargus*, no larvae were found in plankton hauls, and no suitable larval diet was found (Thompson, 1966). Settlement has only been induced in a few opisthobranchs (Thompson, 1958, 1962; Tardy, 1962). In all cases, the adult opisthobranch diet triggered metamorphosis.

My population data also suggests that the veliger stage is several months long, because spawning was at its peak in the early summer and an increase in recruitment did not occur until the fall. Although my data does not provide conclusive evidence of a long veliger stage, it is consistent with this hypothesis. If the veliger stage is only a few hours long, settlement would have been expected to appear right after the 20-28 days required for eggs to hatch, and to be noticed shortly thereafter. There was no evidence for such an early settlement. There are, however, many other factors which could explain a lack of early settlement. For example, production of larvae could be less because egg masses were destroyed, or settling conditions could be unfavorable at a particular time of year, or losses in the planktonic phase may be greater. If predation is causing differential losses in the planktonic stage, the predators remain unknown. Thompson (1966) tested veligers of Archidoris pseudoargus for possible predators. He found them to be relatively safe from predation by some hydroids, small anemones and bryozoans, and suggests that larger suspension feeding organisms, like the barnacles suggested by Hadfield (1963), were their chief predators.

Some workers (Swennen, 1961; Potts, 1970), assuming that larval life is very short, consider that only the eggs laid at the end of a long breeding season contribute to new settlement. I believe that it is unlikely that all the eggs laid during a breeding peak would be unviable in perpetuating the population, and only those few laid at the end of the peak would be successful. Why then would there be such a phenomenon as a breeding peak? A lengthy planktonic phase is the most reasonable explanation for delayed settlements after breeding peaks.

If the veliger stage is several months long, tides and currents could cause considerable dispersion of veligers

(Crisp and Southward, 1953). *Archidoris montereyensis* from other populations may at times exert considerable influence on the settlement at the grid sites. This may have been one of the causes of the sporadic settlement both on the grid sites and elsewhere. Larvae of other invertebrates have been shown to settle gregariously (Knight-Jones, 1954; Crisp and Meadows, 1962) and local currents may have carried nudibranch veligers to one area where they settled simultaneously.

The rapid growth rate of *Archidoris montereyensis*, .31 - .69 cm per month, would be expected for an annual. The maximum length possible for *A. montereyensis* to attain is unknown; the largest specimen I have found was 11.3 cm long.

The question of whether nudibranchs have a post-reproductive mortality has long been in debate. My findings show that *Archidoris montereyensis* does not have a long natural life span, but disappears shortly after reaching reproductive maturity (Appendix I). Since I found evidence that migration does not occur (discussed later), post-reproductive mortality seems the most likely cause of their disappearance. Furthermore, senescent individuals, distinguished by their wrinkled, shrunken appearance, were seen occasionally on the grid sites at Lantzville. Thompson (1966) has found a pattern of senescence and death to follow spawning in *Archidoris pseudoargus*. This pattern has also been found in the life cycles of other nudibranchs (Behrentz, 1931; Costello, 1938; Thompson, 1961, 1964; Potts, 1970).

The question has arisen (Potts, 1970) as to whether nudibranchs show a plateau in their growth rate before dying. Comfort (1957) suggests that in wild populations of annual and biennial molluscs there is no plateau in the growth curve because death occurs in adults when growth is still taking place. On the other hand, Potts (1970) found in his study of *Onchidoris fusca* and in examining the size frequency data of other nudibranch populations (Garstang, 1890; Miller, 1962; Thompson, 1964) that plateaus in growth rates appeared to occur. He suggested that these plateaus are reached because nudibranchs are not limited by food or predators and so can live out a full life span. The population data for *Archidoris montereyensis* is not as straightforward as those for other nudibranchs which have been studied, because they breed all year round. However, the fact that individual size was much larger at Bamfield than at Lantzville (7-8 cm vs 4-5 cm) suggests that there is a limiting factor on maximum size although this may not correlate with age but with food supply. To further support this is the fact that reproduction commenced before the maximum length was reached. This suggests that individuals in neither group reached a maximum possible length before dying. Also, measurements of marked animals showed an individual still growing rapidly between 4.0 and 5.5 cm. Since A. montereyensis probably dies after a spawning period and small individuals at Lantzville were reproductively mature, the onset of reproductive maturity appears to be not necessarily a function of size but of age, although it may be influenced by temperature (Swennen, 1961). Since the smaller individuals were found at Lantzville where there was very little sponge compared with Bamfield, it appears that the availability of sponge limits the growth rate and therefore the maximum size attainable by A. montereyensis before reaching the age of spawning and death.

There is evidence from examination of the seasonal intertidal positions of the nudibranchs on the grid sites at Lantzville and Bamfield, and from scuba dives, to suggest that vertical migration did not take place on the grid sites at Lantzville. Because of the physical nature of the Lantzville sites, it is likely that any attempted downward migration would result in death as nudibranchs tried to cross the shifting sand, and none were seen attempting to do so. This barrier to migration would not normally be present, and Archidoris montereyensis are often found subtidally but at no particular season or state of maturity.

I hypothesize that at Lantzville, Archidoris montereyensis is an annual because (1) specimens remained up to ten months but no longer on the Lantzville sites, (2) growth rates were rapid enough for maturity to be reached in one year or less, and (3) there was no evidence of migration after spawning. This means that A. montereyensis would then have a short life span for a mollusc (Comfort, 1957), but this agrees with the annual life spans obtained from some other opisthobranchs (McMillan, 1947; Garstang, 1890; Guberlet, 1928; Roginskaya, 1963; Potts, 1970; Thompson, 1964, 1966). Miller (1962) classified nudibranchs into rapidly maturing semi-annuals and slow growing nudibranchs living one or more years, and related these differences to their diet. He found sponge eaters to live 2 - 2¼ years which is a longer estimate than mine, although he was not dealing with A. montereyensis, but a related form, A. pseudoargus. Thompson (1966) concluded that A. pseudoargus was an annual, and that Miller's results were an artifact obtained from pooling growth and breeding data from several localities.

Population Dynamics

The results of the Lantzville grid survey have shown that _Archidoris montereyensis_ fluctuates sporadically in numbers throughout the year. In view of the great differences between 1969 and 1970, a long term study would be necessary to confirm any yearly population trend. However, it appears that an increase in numbers in the fall and a decline in the summer, with the populations maintaining a higher density throughout the winter and spring than in the summer, may represent a regular pattern. However, it is the non-seasonal fluctuations in numbers that form the predominant pattern. I would like to discuss several hypotheses for the causes of these fluctuations. As mentioned in the preceding section, settlement is intertidal and mass migration does not occur after spawning, so migration is not a factor causing fluctuations. Major factors which have already been discussed are post-reproductive mortality, which appears to be genetically determined in _A. montereyensis_, and the sporadic nature of larval settlement. Two other factors which I shall discuss here are the relationship of _A. montereyensis_ to its food supply, and the influence of physical stresses on the population.

Food supply has often been found to limit population size (Lack, 1954; Wynne-Edwards, 1962). Miller (1962) classifies nudibranchs into two categories, those with a non-fluctuating food supply, and those with a seasonal food supply. The latter he considers limited by their food supply. Sponge eaters he considers to have a food supply which shows little seasonal variance in abundance. This may be so in Bamfield where *Halichondria panicea* is always plentiful, but at Lantzville, where *H. panicea* is scarce, seasonal variations are more evident and it is possible that the consequences on *Archidoris montereyensis* are more drastic.

Opisthobranchs have been shown to be voracious feeders (Garstang, 1890; Barnes and Powell, 1954; Potts, 1970; Crane, 1971; Robilliard, 1971). Grazing pressures exerted by *Archidoris montereyensis* may affect the food supply in areas where sponge is scarce since the cage experiment showed that natural densities of *A. montereyensis* were capable of consuming large quantities of *Halichondria panicea* relative to the biomass present. The large settlement at Lantzville in May and June, 1969 may have depleted the available sponge which was not adequate to withstand this sudden influx of grazers. Food shortage may thus have contributed to the high nudibranch mortality which followed. The smaller numbers present after the June, 1969 decrease may be more representative of an endogenous population. Also, the influence of grazing pressure at Lantzville in the winter and spring, 1970 may have caused the scarcity of sponge in the spring. The low in the nudibranch population in the summer of 1970 was followed by an increase in sponge cover in the fall.

The few nudibranchs which were present in the summer were spawning, and there is some doubt as to whether nudibranchs feed much during the spawning period (Thompson, 1962, 1964). I found that nudibranchs resumed feeding after copulation, but it is possible that they cease feeding later in their breeding cycle. My experiments were not designed to show any negative correlation between feeding and reproduction, nor did they separate grazing from other factors affecting sponge density. _Archidoris montereyensis_ as well as many other species of nudibranchs, when brought into the laboratory, will lay egg masses long after the food supply has been diminished. The animals are probably using up their body reserves as their overall size decreases during this period. This may explain how spawning may be at a peak, as in the summer of 1970 at Lantzville, and yet the sponge remained scarce.

In an area like Lantzville, where sponge is in short supply, nudibranch pressure may be great enough to reduce the sponge supply to the point where food becomes a limiting factor to population size and individual growth. Andrewartha and Browning (1961) discuss the possibility of food being present in an area and yet unattainable, which would lead to a "relative" rather than an "absolute" shortage of food. The grid sites at Lantzville had areas of sponge which remained untouched by nudibranchs even during the summer when sponge cover was scanty. It appears that the nudibranchs were suffering from a relative scarcity of sponge since they could not locate all the available food due to its patchy distribution. Evidence that they were suffering from a shortage of food comes from the smaller size and density of nudibranchs at Lantzville when compared to Bamfield, and the rough correlation of numbers with seasonal sponge fluctuations. In contrast, from my observations of the large sponge cover at Bamfield, it appears that the depletion by grazing of a few sponge patches would have little effect on the nudibranch population.

Thompson (1964) hypothesized that nudibranchs with a seasonal food supply may actively seek out an alternate food source. This may be true for *Archidoris montereyensis* when *Halichondria panicea* is scarce. The results of the field experiment at Bamfield in which sponge was removed suggests that *A. montereyensis* would move horizontally and downward in the intertidal zone when faced with a food shortage. It would be to their advantage to have a refuge in the subtidal zone where different species of sponge were available and conditions more stable. Alternate subtidal sponges would be of no advantage to the Lantzville population as they were forced by the sand barrier to remain intertidal. However, due to the sponge's patchy distribution, it is possible that individuals were affected by a scarcity of sponge at different times, and they moved down to the sand barrier only to return to where the scant sponge cover remained.

Another apparent cause of population fluctuations is the physical stresses which are sporadic in occurrence or vary in intensity with the seasons. Andrewartha and

Birch (1954) and Newell (1970) note a number of these factors which affect marine populations by causing mortality and by triggering the onset of the breeding season. Factors which may be applicable to this study are fluctuations in water temperature and salinity and fluctuations in aerial temperature and desiccation stress. Sensitivity to low salinities and high temperatures have been considered by Swennen (1961) to be a limiting factor to nudibranchs. However, little can be concluded about the effects of salinity and water temperature on *Archidoris montereyensis*. The fact that *A. montereyensis* shows a decline in numbers at Bamfield where salinity did not fluctuate very much, suggests that, for the Bamfield population, salinity was not a major limiting factor. Since *A. montereyensis* spawned all year round at Lantzville, the water temperature could not have become too low for spawning, as was found in *Adalaria proxima* (Thompson, 1958a, b). In the summer, when water temperatures were highest, although populations declined at Bamfield and Lantzville, spawning continued.

Evidence which suggests that aerial temperature and desiccation influences *Archidoris montereyensis* numbers was provided by the large population decline of June, 1969 at Lantzville which coincided with low tides and hot weather. This, combined with the behavioural tendency of *A. montereyensis* to seek dark, damp areas in the summer led me to perform the experiments testing the effects of aerial exposure under various temperature regimes. Since weight loss in the experiments varied considerably with each individual, as did the amount of weight loss tolerated before mortality occurred, it appears that *A. montereyensis* is variable in its response to these physical stresses. However, the high mortality shows that aerial exposure at high temperatures may have considerable influence on the population. The fact that mortality was less in the experiment performed in June than the one in April even though weight loss remained the same suggests that some acclimatization to high temperatures takes place during the summer.

Desiccation under laboratory conditions, similar to those found in the field, caused extensive mortality and indicates that the field conditions could result in a decline in numbers which would tend to be seasonal but which would vary in time and severity according to climatic conditions. In years in which spring low tides coincided with cool, cloudy weather nudibranchs would suffer little or no loss in numbers, but during summers, like that of 1969 when spring tides coincided with clear sunny days and temperatures from 18 - 23°C, desiccation and/or high temperatures would have a considerable effect. Nudibranchs move into dark damp places, under algae or in cracks which cuts down on desiccation, but the number and availability of suitable large hiding places appears to limit the number of survivors as evidenced by the fact that only individuals hiding in the algae which were therefore small, survived the population decline of June, 1969.

Other periodic declines were caused by the effects of storms. When, as happened at Lantzville, severe storms cause sand to blast the rocks, the mortality is high. The effects of sand sticking to the mucous of the nudibranchs and waves dislodging them are probably not as severe, although the high disappearance rate of nudibranchs during the fence experiment at Bamfield suggests that dislodging by wave action may have considerable influence. Hadfield (1963) mentions that storm tossed nudibranchs may be carried on debris a considerable distance.

In summary, it appears that density independent factors such as the chance timing of physical stresses co-inciding with larval settlements may limit the population size. If these density independent factors do not occur, other density dependent factors may become important. One of these may be the availability of food, another the number of suitable microhabitats available for shelter during low tides, although the latter would to some extent depend on the occurrence of high temperatures at critical times. Thus a favorable settlement may result in a high density of nudibranchs until the food supply was depleted unless a chance physical stress limited their numbers. Physical stresses may also act synergistically with nudibranch grazing pressure to limit the amount of sponge in the summer and thus indirectly cause the observed seasonal decline in nudibranchs.

Archidoris montereyensis, when dislodged by storms, may be carried by tides and currents to a considerable depth. This may account for their infrequent subtidal appearances. The species is found subtidally in all sizes at all times of the year (G. A. Robilliard, pers. comm.), but in much smaller numbers than in the intertidal zone. Some are probably there because they have been dislodged by storms, but this may not be the only cause of their subtidal appearance; another may be lack of food in the intertidal zone. While it is possible a subtidal population is endogenous, the small numbers suggest _A. montereyensis_ is predominantly an intertidal form. Subtidally, alternate sponges to _Halichondria panicea_ appear to be eaten since _H. panicea_ is usually intertidal, although it has subtidal records in Naples and off Maine (W. D. Hartman, pers. comm.). Since settling has not yet been induced in _A. montereyensis_, it is not yet known if _H. panicea_ triggers metamorphosis, and this represents an interesting area for further research.

The majority of subtidal sitings of _Archidoris montereyensis_ are probably a result of confusing this species with _Anisodoris nobilis_ which is similar in appearance to _A. montereyensis_ and is usually found subtidally. The problem of identifying which of these species is present without dissection is notorious. O'Donoghue (1921 b), in attempting to clarify systematic characters, made a mistake in listing the differences in tentacles, and several popular marine natural history guide books (Guberlet, 1962; Flora and Fairbanks, 1966) have a photograph of _Archidoris montereyensis_ over a description of _Anisodoris nobilis_. The presence of the white _Archidoris odhneri_ in our local waters also adds to the problem of mis-identification.

CONCLUSIONS

The general trend for nudibranchs to have a short life span ranging from less than a year to one or two years places them in an unusual category among molluscs, most of which live long lives (Comfort, 1957). As a rapidly reproducing, short lived group they have evolved into a variety of forms each adapted to fit a particular food supply. Most nudibranchs have been found to be specific in their food choice. _Archidoris montereyensis_ is no exception since it is usually found on _Halichondria panicea_, but it may at times utilize other sponges.

Nudibranchs have evolved to exploit food supplies which because of their annual nature or their sensitivity to physical factors are not constant in abundance. Because they can grow swiftly and produce large numbers of eggs they take full advantage of this type of resource. How nudibranchs survive the periods when food is sparse is not fully known. Some appear to be able to use alternate food supplies. *Archidoris montereyensis* may survive because of individuals in the subtidal which produce veligers which will recolonize the intertidal zone. Some species may depend upon a few individuals existing on remnants of the food supply (Miller, 1962). This appears to be the case for *Archidoris* at Lantzville. The remarkable reproductive potential of nudibranchs means that a few individuals are capable of reinstating the original population size. The advantages of having a short life span and great reproductive powers are obvious when an animal has become specialized on a food supply whose distribution and abundance is variable. The multitude of species of nudibranchs are an indication of the success of this evolutionary strategy.

The fact remains, that all nudibranchs are relatively scarce in numbers. Why this holds true for species like Archidoris montereyensis which have chosen a relatively stable food supply is not known. It is true that sponges, barnacles, and anemones, the principal foods of the nudibranchs discussed in this paper, all undergo a certain amount of seasonal fluctuation but except at Lantzville where food appears to affect the population, the numbers of nudibranchs are often smaller than the food supply appears to be able to support, as found with Onchidoris fusca (Potts, 1970). This is the case with A. montereyensis in Bamfield where the sponge cover of Halichondria panicea remains dense all year round, yet A. montereyensis are scarce. It is apparent in these situations that factors other than post-reproductive mortality and food supply limit population growth. Nudibranchs seem to be relatively safe from predators due to their various defence adaptations, and from competitors due to their specialized exploiting of foods. In some species, especially those feeding on hydroids, competition may be important, but not in A. montereyensis. This study has revealed certain physical factors which may cause mortality. There are undoubtedly still other factors which account for the high mortality rate in settled nudibranchs. One of the main sources of fluctuation is the sporadic settlement of young, which suggests that lack of survival of spawn and veliger larvae is one of the major causes of nudibranch scarcity.

SUMMARY

1. Two populations of the nudibranch Archidoris montereyensis were studied from May, 1969 to October, 1970 on four fixed field sites at Lantzville, B. C. (in the Straits of Georgia), and one site at Bamfield on the exposed coast of Vancouver Island. The population size fluctuates sporadically, although all size classes are present at Lantzville at all times of the year. Breeding occurs all year round at Lantzville but there is considerable destruction of egg masses. Peak egg production in 1970 occurred in the summer at Lantzville and Bamfield.

2. Settling of veliger larvae takes place in the intertidal zone. It is sporadic both in time, abundance, and in the area of its appearance, although the sponge Halichondria panicea is always present. Rapid growth, averaging 0.69 cm/month for small individuals, takes place in all size ranges at all times of the year.

3. Vertical migration does not occur in A. montereyensis as young settle in the intertidal and there is no evidence of downward movement on the grid sites at any time of the year. Scuba dives at Lantzville and Bamfield show that there is no A. montereyensis below the grid sites

following a spawning period which suggests no post-reproductive migration takes place.

4. It is concluded that _A. montereyensis_ is an annual because no individuals remain on the Lantzville sites longer than ten months, senescent individuals were observed suggesting innate post-reproductive mortality, growth rates were rapid enough for a mature size to be reached in less than a year, and there is evidence that vertical migration does not occur.

5. Experiments performed in the field indicate that natural densities of _A. montereyensis_ consume an average volume of 2.23 cm^3/nudibranch/day relative to the standing crop of sponge, although with considerable daily fluctuation and, when sponge is removed, the nudibranchs tend to move downward in the intertidal. This would be to their advantage as there are other sponges under more stable conditions in the subtidal. Data from the grid sites show that although _A. montereyensis_ eats a variety of sponge, it is usually associated with _Halichondria panicea_. At Bamfield where sponge was plentiful, the nudibranchs were larger and more abundant than at Lantzville where sponge appeared to be scarce. The possibility of there being a

relative rather than an absolute shortage of food at Lantzville is discussed.

6. Physical factors were investigated as possible causes of observed fluctuations in numbers. Storms cause some mortality in winter. No close correlation was observed between the fluctuations of water temperature and salinity and population numbers. Extremely high aerial temperatures coinciding with low daytime tides were followed by a population crash in June, 1969. Laboratory experiments confirmed that aerial exposure at high temperatures can cause considerable mortality.

7. It appears that the nudibranch population will increase following sporadic settlements either until chance physical factors reduce their numbers, or until they have increased enough to deplete their food supply, which is itself subject to physical stresses. The size and timing of settlements are therefore important in determining the number of nudibranchs in an area, and factors which may affect these are discussed.

8. Natural history information is given for the nudibranchs *Onchidoris bilamellata*, *Diaulula sandiegensis* and *Aeolidia papillosa* on the grid sites at Lantzville (Appendix II).

APPENDIX I

Population data for *Archidoris montereyensis* on individual grid sites at Lantzville, 1969-70.

Table A1. Size frequency distributions on grid site I.(cm)

DATE	0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0-4.5	4.5-5.0	5.0-5.5	5.5-6.0
May 17/69	53	46	16	6	2	1	-	-	1	-	-	-
May 30	23	86	22	6	6	2	3	1	-	1	-	-
June 30	6	30	2	-	-	-	-	-	-	-	-	-
July 15	5	23	10	1	-	-	-	-	-	-	-	-
Oct. 15	-	-	1	1	1	6	8	1	1	1	1	-
Oct. 28	-	-	-	-	3	3	4	3	7	-	-	-
Nov. 15	3	4	2	2	2	1	4	6	5	3	1	2
Nov. 23	-	1	2	2	1	-	3	4	2	5	-	-
Dec. 11	2	4	6	1	3	1	4	1	4	2	1	-
Dec. 22	-	1	3	2	3	-	2	2	3	1	-	-
Jan. 8/70	2	-	6	3	2	3	3	3	-	-	1	-
Jan. 27	7	2	8	1	3	4	2	2	1	-	1	-
Feb. 5	1	2	4	2	2	3	-	-	1	1	-	-
Feb. 19	-	6	3	3	1	3	1	1	-	-	-	-
Mar. 28	5	9	2	-	-	-	-	1	-	-	-	-
Apr. 10	1	12	1	2	-	-	-	-	-	-	-	-
Apr. 24	-	10	7	-	1	1	-	-	1	1	-	-
May 7	-	6	4	-	1	1	1	-	1	1	-	-
May 25	-	2	6	1	-	-	1	3	-	2	-	-
June 4	2	3	3	-	2	-	3	4	1	1	-	-
June 20	1	3	-	1	-	1	2	1	-	-	-	-

Table A1. (continued)

DATE	0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0-4.5	4.5-5.0	5.0-5.5	5.5-6.0
July 7	1	1	5	-	1	2	1	1	1	-	-	-
July 16	-	-	4	-	-	1	-	1	1	-	-	-
July 31	-	-	1	1	-	-	-	-	-	-	-	-
August 17	-	-	2	-	1	1	-	-	-	-	-	-
August 28	-	1	-	1	-	-	-	-	-	-	-	-
Sept. 12	-	5	-	1	-	-	1	-	1	-	-	-
Oct. 7	3	4	2	1	-	1	-	-	1	-	-	-

Table A2. Size frequency distributions on grid site II. (cm)

DATE	0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0-4.5	4.5-5.0	5.0-5.5	5.5-6.0
June 2/69	3	14	8	2	-	-	-	-	-	-	-	-
June 30	-	1	-	-	-	-	-	-	-	-	-	-
July 15	-	2	-	-	-	-	-	-	-	-	-	-
Oct. 15	-	-	-	-	-	-	-	-	-	-	-	-
Oct. 28	-	-	-	1	1	-	-	1	1	-	-	-
Nov. 15	-	2	2	1	2	1	-	-	-	1	1	-
Nov. 22	-	1	1	-	2	-	-	-	-	1	-	-
Dec. 11	0	1	1	1	-	-	-	1	-	-	1	-
Dec. 22	1	1	1	-	-	-	-	1	-	-	-	-
Jan. 8/70	-	2	3	-	-	-	-	1	-	-	-	-
Jan. 21	-	3	2	-	-	1	-	-	-	-	-	1
Feb. 5	1	2	3	2	1	-	-	-	-	-	-	1
Feb. 19	1	6	5	4	1	-	1	-	1	-	-	-
Mar. 28	-	3	2	2	-	-	3	-	-	-	-	-
Apr. 10	-	3	3	2	-	-	-	-	-	-	-	-
Apr. 24	1	3	4	1	1	-	1	1	2	-	-	-
May 7	1	2	-	-	-	1	-	-	-	-	-	-
May 25	2	3	-	1	-	-	1	1	-	-	-	-
June 4	1	1	-	-	-	-	-	-	-	-	-	-
June 20	-	-	-	1	-	-	1	-	1	-	-	-
July 7	-	-	-	-	-	-	1	1	-	-	-	-

Table A2. (continued)

DATE	0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0-4.5	4.5-5.0	5.0-5.5	5.5-6.0
July 16	-	-	-	-	-	-	-	-	-	-	-	-
July 31	-	-	-	-	-	1	-	-	-	-	-	-
August 17	-	-	-	-	-	-	-	-	-	-	-	-
August 28	-	-	1	-	-	-	-	-	-	-	-	-
Sept. 12	1	-	-	-	-	-	-	-	-	-	-	-
Oct. 7	-	2	1	-	-	-	-	-	-	-	-	-

Table A3. Size frequency distributions on grid site III. (cm)

DATE	0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0-4.5	4.5-5.0	5.0-5.5	5.5-6.0
June 1/69	-	2	3	8	5	3	-	-	1	1	-	-
June 30	-	1	-	1	-	-	-	-	-	-	-	-
July 15	-	-	-	-	-	-	-	-	-	-	-	-
Oct. 15	-	1	-	-	1	-	-	-	-	-	-	-
Oct. 28	-	-	-	-	-	1	-	-	1	-	-	-
Nov. 15	2	7	7	1	-	-	1	-	1	-	-	-
Nov. 22	1	8	1	1	-	-	-	-	-	-	-	-
Dec. 11	-	2	5	1	1	-	-	-	-	-	-	-
Dec. 22	-	1	-	-	-	-	1	-	-	-	-	-
Jan. 8/70	-	-	1	-	1	-	-	-	-	-	-	-
Jan. 21	-	-	-	1	-	-	-	1	-	-	-	-
Feb. 5	-	1	1	-	-	-	-	-	-	-	-	-
Feb. 19	-	1	2	-	-	1	-	-	-	-	-	-
Mar. 28	-	-	1	-	-	-	-	-	-	-	-	-
Apr. 10	-	-	-	-	-	-	-	-	-	-	-	-
Apr. 24	-	-	-	1	-	-	-	-	-	-	-	-
May 7	-	-	-	-	1	-	-	-	1	-	-	-
May 25	-	-	-	-	-	-	-	-	-	-	-	-
June 4	-	-	-	-	-	-	-	-	-	-	-	-
June 20	-	-	-	-	-	-	-	-	-	-	-	-

Table A3. (continued)

DATE	0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0-4.5	4.5-5.0	5.0-5.5	5.5-6.0
July 7	-	-	-	-	-	-	-	-	-	-	-	-
July 16	-	-	-	1	-	-	-	-	-	-	-	-
July 31	-	-	-	-	-	1	1	-	-	-	-	-
August 17	-	-	-	-	-	-	-	1	-	-	-	-
August 28	-	-	-	-	-	-	-	-	-	-	-	-
Sept. 12	-	1	-	-	-	-	-	-	-	-	-	-
Oct. 7	-	-	1	-	-	-	-	-	-	-	-	-

Table A4. *Size frequency distributions on grid site IV.* (cm)

DATE	0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0-4.5	4.5-5.0	5.0-5.5	5.5-6.0
June 2/69	-	10	5	1	2	1	1	-	-	-	-	-
June 30	1	1	-	-	-	-	-	-	-	-	-	-
July 15	-	-	-	1	-	-	-	-	-	-	-	-
Oct. 15	-	-	-	1	-	1	-	-	-	-	-	-
Oct. 28	-	-	-	-	1	-	1	-	-	-	-	-
Nov. 15	-	-	-	1	-	-	-	-	-	-	-	-
Nov. 22	-	-	-	-	1	1	-	-	-	-	-	-
Dec. 11	-	-	-	-	-	-	-	-	-	-	-	-
Dec. 22	-	-	-	-	-	-	-	-	-	-	-	-
Jan. 8/70	-	-	-	-	-	-	-	-	-	-	-	-
Jan. 21	-	-	-	-	-	-	-	-	-	-	-	-
Feb. 5	-	-	-	-	-	-	-	-	-	-	-	-
Feb. 19	-	-	-	-	-	-	-	-	-	-	-	-
Mar. 28	-	-	-	-	-	-	-	-	-	-	-	-
Apr. 10	-	-	-	-	-	-	-	-	-	-	-	-
Apr. 24	-	-	-	-	-	-	-	-	-	-	-	-
May 7	-	-	1	-	-	-	-	-	-	-	-	-
May 25	-	-	-	-	-	-	-	-	-	-	-	-
June 4	-	-	-	-	-	1	-	-	-	-	-	-
June 20	-	-	-	-	-	-	-	-	-	-	-	-
July 7	-	-	-	1	-	-	-	-	-	-	-	-

Table A4. (continued)

DATE	0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0-4.5	4.5-5.0	5.0-5.5	5.5-6.0
July 16	-	-	-	-	1	1	-	-	-	-	-	-
July 31	-	-	-	-	-	-	-	-	-	-	-	-
August 17	-	-	-	-	-	-	-	-	-	-	-	-
August 28	-	-	-	-	-	-	-	-	-	-	-	-
Sept. 12	-	-	-	-	-	-	-	-	-	-	-	-
Oct. 7	-	-	-	-	-	-	-	-	-	-	-	-

APPENDIX II

Other Species of Nudibranchs

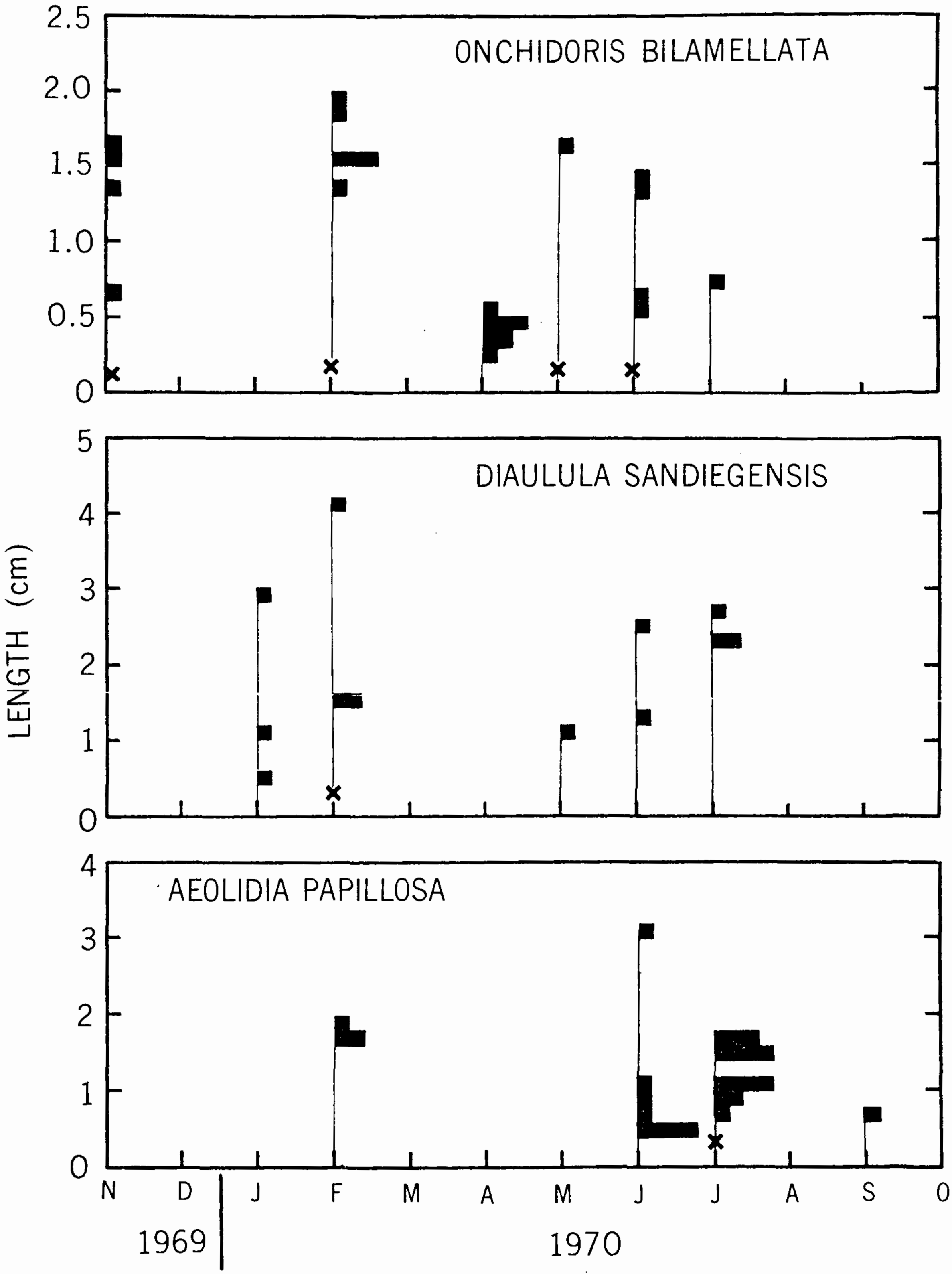
The grid site at Bamfield did not reveal any other species of nudibranchs although Rostanga pulchra, Cadlina marginata, Dirona albolineata and Hermissenda crassicornis were all common in the area. A scuba dive below the grid site in May, 1971, revealed one Cadlina marginata, three large Anisodoris nobilis and two Archidoris odhneri.

Several species of nudibranchs appeared sporadically on the grid sites at Lantzville. Since nudibranch life cycles are largely unknown, the size, date of appearance, and spawning were recorded (Fig. A1).

It is probable that a continuous population of Onchidoris bilamellata (= fusca), a predator of barnacles, was present near the study area but since they were not specifically sought after, and because they often inhabited the barnacle zone above the area in which Archidoris montereyensis appeared, they were often overlooked. Spawn was seen beside large groups which had gathered for copulation. Not all the Onchidoris found on the grid sites were counted, but a random sample was measured. A scuba check of the area at the bottom of the grid sites in April, 1970, revealed many small specimens under 0.5 cm. This number of young would not have been spotted at low tide because of their cryptic coloration. In Onchidoris only one long breeding season was noted with small individuals in evidence in April and June. O'Donoghue & O'Donoghue (1922) found spawn on Vancouver Island from May - June. In the laboratory I noted that O. bilamellata alternates periods of spawning and eating. It appears that this is an annual nudibranch as suggested by Potts (1970), with adults disappearing after a long spawning period and young growing up in the summer and fall ready to breed in the fall.

A few Diaulula sandiegensis were found on the grid sites. Its food source appears to be Haliclona in the intertidal but it is not known what it eats in subtidal areas (G. A. Robilliard, pers. comm.). The only large specimens found were copulating in February. Since Diaulula is often found on the under surface of

Figure 1A. Size frequency distributions of three species of nudibranchs found on the Lantzville grid sites in association with Archidoris montereyensis. The appearance of spawn is marked (x). One square represents one individual.


ONCHIDORIS BILAMELLATA
DIAULULA SANDIEGENSIS
AEOLIDIA PAPILLOSA
LENGTH (cm)
2.5
2.0
1.5
1.0
0.5
0
5
4
3
2
1
0
4
3
2
1
0
N D J F M A M J J A S O
1969
1970

large rocks in the area, it is possible that there were hidden under the rocks which appeared in the sand at the bottom of the grid sites. Individuals appear to be growing during the spring and summer, but small specimens were present in the winter also, which suggests that spawning takes place at times other than February. It appears that Diaulaula breeds in February and probably earlier as there were young present in January. Immature individuals were found to increase in size during the spring and summer.

Aeolidia papillosa, a predator of sea anemones, was sometimes found on the lower portion of the grids in cracks and crevasses. Most specimens were small, but a large one was found in June and spawn was found in July. Since small specimens were present in June, breeding had probably also occurred earlier. My data gives me no reason to differ from the hypothesis of Hecht (1896), Swennen (1961), Miller (1962) that Aeolidia papillosa is an annual with one long breeding season a year.

Hermissenda crassicornis, normally a common nudibranch in the Strait of Georgia, was not found on the grid sites. A scuba dive in April, 1970, revealed that they were abundant on the subtidal portion of Blunden Point. Dirona albolineata was also found subtidally during this dive, although it was never seen on the grid site.

In November, 1969, two small Cadlina pacifica were found on the grid sites. They were 1.0 and 1.2 cm in length. One small Acanthodoris nanaimoensis, 0.9 cm long, was taken in October, 1970.

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