AN ANALYSIS OF THE DISTRIBUTION OF A COMMENSAL POLYNOID ON ITS HOSTS

by

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A DISSERTATION

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Presented to the Department of Biology
and the Graduate School of the University of Oregon
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NOT APPROVED

(Adviser for the thesis, Peter W. Frank)

I would like to acknowledge the help and guidance of Dr. Peter W. Frank in developing this problem with Arctonoe.

To Patsy and Robert for braving cold Pacific waters;
To Ann for bravely typing;
And to all the _Cryptochiton_ that have ever lived
for bravely being what they are.

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INTRODUCTION

"...In displacing other shells, I found in nearly every one a similar tenant: the secret was discovered, the worm was a parasite, that lived in peace and good fellowship with the Keyhole....At least four out of every six contained a parasite, and, what is rather strange, the worms were nearly all of one size."

From the first written account of contact between Western Science and *Arctonoe vittata*.--J. K. Lord, 1866.

The observed distribution of an animal population in its habitat is the resultant of a large number of factors such as reproductive habits, gregariousness or its lack, catastrophes, resource distribution, habitat selection, etc. It is also influenced by the manner and time of sampling. Distribution is an aggregate phenomenon. Ideally, one might determine the true distribution of the population, then resolve the various forces responsible for it, and finally determine the selective value of this pattern of distribution to the individuals which make up the population. Such an account is probably not complete for any population. Another, less heroic approach is to study population distributions as phenomena with a certain demographic logic of their own. This has been the rationale of the present study.

The distribution of many organisms is difficult to analyze because accurate and natural definitions of the unit regions in which the population is distributed are hard to make. Depending on the size of the sample unit, the individuals of a population will, with sufficiently large sample size, show aggregation and with smaller sample size demonstrate random or regular distribution (Greig-Smith, 1964; Slobodkin, 1961). In addition, the pattern of distribution is likely to change in space and time and vary with age or size class distribution of the population.

Intuitively, one feels that hosts of commensals and parasites offer themselves as "natural" sample units for studying distribution. As all or most of the needs of the commensals are found on the host, the host is the basic unit of the habitat for the commensal. For this reason, changes or variations in the distribution of commensals are likely to be ecologically interesting. Williams (1964) presents the distribution by occupancy classes of a number of ectoparasites and argues that there is some mathematical pattern to them, since several observed distributions seem close to a log series. However, the biological implications of a log series are not at all clear. It is ecologically interesting to determine if the observed occupancy is random, and if not, how it deviates. Such deviation indicates constraints on the dispersion (Connell, 1963). When compared to a Poisson distribution, selected examples from Williams are observed to deviate in the direction of aggregation (Table 1). Aggregation is considered to be the mode of distribution not only for ectoparasites, but for most organisms in nature (Allee et al., 1949). Even in territorial animals, it is often groups that are isolated from each other. A certain amount of aggregation is held to have survival value for most organisms (Allee, 1931; Odum, 1951).

Table 1.--Comparisons of observed distributions of various ectoparasites to the Poisson distribution. Calculated from data in Williams (1964).

Number per host	Observed	Expected	Observed	Expected	Observed	Expected
0	242	95	160	11	1127	1022
1	116	161	19	34	243	408
2	53	137	11	51	97	81
3	38	78	6	51	32	11
4	28	33	5	38	19	1
5	7	11	4	23	7	+
6	9	3	4	11		
7	5	1	3	5		
8	3	+	2	2		
9	20		2	1		
10+			6	+		
Ectoparasite	Fleas		Mites		Hippoboscid flies	
Host	*Brandicota bengalensis*		*Liponyssus bacoti*		Quail	

There is a lack of documentation for the regular spatial distribution of individual animals. (Connell (1963) reports on regular dispersion in an amphipod, and the manner in which this pattern is built up. In addition, he summarizes information on a few known cases of regular dispersion in other marine invertebrates. None of these organisms is a commensal or parasite which, as has been suggested, might be very suitable for a study of distribution. Reviews of commensalism and parasitism have not addressed themselves to the problem of spatial regularity in inquiline distribution (Baer, 1951; Caullery, 1952; Davenport, 1955, 1966; Dales, 1966; Lewis, 1956; Pearce, 1962).

Arctonoe vittata (Grube, 1855) is a scaleworm which is commensal with several large molluscs and echinoderms along the Pacific Coast of North America. Most of the literature on *Arctonoe* is taxonomic, and little is said about the ecology other than to mention the host and location of collection (Baird, 1863; Berkeley, 1924; Chamberlin, 1920; Hartman, 1936, 1944, 1948; Hartman and Reish, 1950; Moore, 1904, 1908, 1909; Okuda, 1936, 1950; Seider, 1924; Skogsberg, 1952; Treadwell, 1926, 1937). However, a few casual observations have implied that *A. vittata* may have the very regular distribution of one worm to a host (Lord, 1866; Pettibone, 1953; Ricketts and Calvin, 1962). These observations were not, however, based on extensive or careful sampling of the various hosts of *A. vittata*. Consequently, statements about the true nature of the distribution could not be made with certainty.

The goal of the present study was to obtain a clear picture of the pattern of occupancy of *A. vittata* against the background of its population ecology. The distribution of the commensal in terms of occupancy and size was extensively sampled. This information was combined with growth and recruitment data to work out a general picture of the dynamics and relations of the commensal and host populations. The state of knowledge about the commensal at the beginning of the study can be summed up in the following statement: If one were to collect a host keyhole limpet, *Diodora aspera*, as often as not there would be a large *A. vittata* in the mantle cavity, and occasionally one might observe the same worm on *Cryptochiton stelleri*. Unanswered were the following questions: Is the distribution always one worm per host? If so, how do the worms become distributed in this manner? Is a host infected just once or several times in its life? How old do host and commensal grow? Is the commensal a fluctuating or a constant feature of the marine community? If it is a constant feature, what is the recruitment and turnover by which it maintains itself? Are there aspects of the demographic ecology of *A. vittata* which suggest a general population ecology of commensalism?

METHODS AND STUDY AREAS

Information was gathered by field censuses and recapture studies of marked hosts. In the field census surveys, collections were made of hosts and an enumeration taken of the commensals on the hosts. The worms were then preserved. This procedure provided information on commensal distribution and worm settlement. The reproductive condition of the preserved worms was determined. From the recapture studies with marked hosts in the field, experimental data were gathered on the nature of recruitment and growth rates of host and commensal, and on vagility of commensals.

Intensive census work was carried out at Cape Arago, Oregon (43^{o} 20' N. lat.). In this region Diodora aspera and Cryptochiton stelleri were the only abundant hosts, although Solaster stimpsoni Dermasterias imbricata were occasionally collected. The conclusions of the present study are based chiefly on work with the two molluscan hosts in the Cape Arago region. Six subtidal and three intertidal collecting stations were established. Figure 1 is a map showing their location. Each station was a locale within which the substrate, aspect, and vegatation did not vary greatly and which supported a large host population. Sample size varied between 10 and 50 hosts, since it was difficult to collect and process more than this at one time. At the collecting stations hosts were picked up haphazardly and not according to some randomized scheme. All hosts discovered were collected until

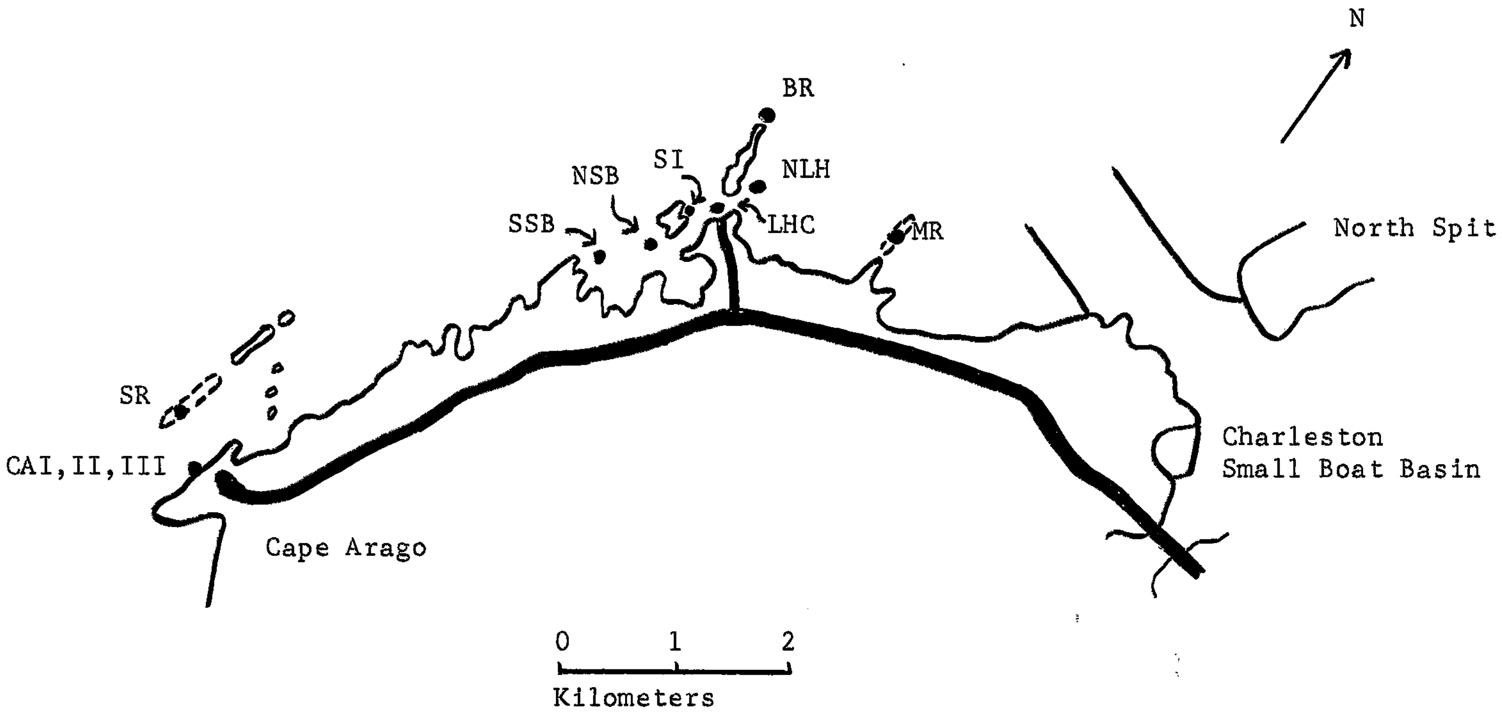


Figure 1.--Collection and return stations in the Cape Arago region of the Oregon coast. Subtidal stations: Mussel Reef (MR), Baltimore Rock (BR), South Sunset Bay (SSB), North Sunset Bay (NSB), Cape Arago State Park (CAI,CAIII), Simpson Reef (SR). Intertidal stations: Cape Arago Light House Channel (LHC), South Light House (SLH), Squaw Island (SI), Cape Arago State Park (CAII).

the number desired was obtained. A more elaborate method could not have been carried out by a single diver, nor was it important enough to do so for the type of information desired.

Supplementary collections were made along the Pacific coast to determine to what extent the information gathered at Cape Arago was typical of the commensal over more of its geographical range. At San Juan Island, Washington (48° 33' N. lat.) *Solaster stimpsoni*, *Evasterias imbricata*, *Diodora*, and *Cryptochiton* were sampled for *A. vittata*. *Parastichopus californicus* was common in the area and host to the sibling species *A. pulchra*. This host-commensal pair was sampled also. *Diodora* and *Cryptochiton* were sampled on the exposed Washington coast at Neah Bay (48° 22' N. lat.), Cape Alava (48° 10' N. lat.), and La Push (47° 55' N. lat.). *Megathura crenulata* was common at Pacific Grove, California (36° 36' N. lat.) and host to either *A. vittata* or *A. pulchra*. *Diodora* was too rare to be sampled in numbers, but *Cryptochiton* was abundant and sampled. Further south, at Punta Banda, Mexico (31° 51' N. lat.) *A. vittata* was not found at all, although *A. pulchra* was common on *Megathura*, *Dermasterias*, and a holothurian, probably a form of *P. californicus*. Collections were made between June 1964 and May 1967. Other commensals sampled for comparison of distribution on hosts were *Pinnixa faba* on *Schizothaerus nuttalli*, and *Podarke pugettensis* on *Solaster* and *Patiria miniata*.

Hosts were collected by SCUBA or free diving and on low tides of less than -0.15m. Above this tide mark hosts were typically not found. All hosts were wrapped immediately in polyethelene bags upon removal from the substrate. Isolation of the hosts by bagging was necessary to avoid loss of the worms. Worms were removed in various ways. Large worms could usually be forced off with a probe. Smaller worms, which were damaged or missed by this method, could be removed by a high speed jet of sea water generated by a submersible pump (IP 599, sold by W. W. Grainger, Inc.). A nozzle of 2mm bore was used to produce a vigorous stream of water which would remove all the worms. Before worms were removed from molluscan hosts, the hosts were set on their dorsa. In a few moments most hosts would relax and expose the gill and mantle cavities to inspection. The simplest method, used in the later surveys of the study, was to add a few grams of $MgSO_4$ to the sea water in the collecting bags. After 15 minutes, the worms were floating about in the bag or could easily be removed from the host without the usual struggle. This last method was less troublesome than the probe and water jet.

The numbers and length in millimeters of the commensals on each host were recorded. The worms were narcotized with $MgSO_4$ and measured on a plastic scale while immersed in sea water. Usually the size of the host was determined. Diodora was measured with vernier calipers to the nearest tenth millimeter for the greatest distance along the posterior dorsum from the top aperture to the shell edge. The disk diameter of Solaster, the arm length of P. miniata, and the shell length of S. nuttalli were likewise measured to the nearest millimeter. Cryptochiton was shaken of water and weighed on a balance to ± 5g. Other hosts were not measured.

The worms collected in these censuses were preserved in FAA (10% formalin; 2% acetic acid; 48% ethyl alcohol; 40% water). They were subsequently examined for gut content and reproductive condition. The condition of the gonad in a worm was determined from a transverse section about 2mm thick in the region of the 20th segment. The distinction between eggs and sperm was quite easy to make. With a binocular microscope the relative amount of gametic material was determined visually.

Marked Diodora and Cryptochiton were used in certain field experiments. The limpet was marked by a modification of the technique of Frank (1965). An absolutely dry shell surface was a prerequisite for a successful tag. Many of the limpets, especially the larger subtidal forms, have a very porous shell because of the activities of boring organisms, and some individuals were impossible to mark. After the shell was abraded clean, it was dried with a small hair drier for several minutes until the shell was chalky white. It was possible to mark the shell directly with ink, dye, or pencil and cover this with methacrylate glue (Dekophane), which was then dried rapidly with the hair drier. When the tag was dry and hard, the limpet was returned to running sea water to recover. The chiton was marked by inserting a monofilament nylon line of 2.3kg test through a shallow hole in the dorsum made with a #22 hypodermic needle. This technique is a modification of that of Ebert (1965). It is, however, not necessary to mount the needle in a drill. An analysis of the success of these two marking methods is presented in Appendix 1.

To obtain information on recruitment independent of that gathered in the field censuses, marked hosts were cleared of worms by the probe and water jet method and returned to suitable field locations in the Arago region. After a period of time, recoveries were made of the hosts, and the new worms, if any, were measured and counted. The field locations for the returns were both subtidal and intertidal. The latter were generally more accessible during inclement weather. In order to assure that the locations were good habitats, return stations were selected which originally had large populations of hosts. Two major intertidal stations (Fig. 1: CAII, SI) and one subtidal station (Fig. 1: CAI) were set up for Diodora. Between August 1963 and July 1966, 330 recoveries were made from these locations. The period of exposure to reinfestation varied between 1 month and 1 year, and the schedule of collection varied. All marked chitons used in this phase of the study were concentrated at one protected rocky intertidal station (Fig. 1: LHC). Between August 1964 and February 1966, 345 chiton recoveries were made. From October 1964 to October 1965, monthly collections were carried out in which marked hosts were recaptured and new hosts marked and released. Worms which were removed from marked hosts were measured and counted as described for the field censuses. In addition, measurements at successive recaptures were kept for the marked hosts. From this information inferences about commensal recruitment, and growth rates of commensal and host could be made.

In a limited number of cases, marked hosts were returned with a worm which could be recognized again. At a later recovery it was possible to say whether or not the worm which had been returned with the host had remained. Worms were removed in the usual manner and placed in a dish of sea water with nylon bolting cloth or sand fixed to the bottom. Such a substrate provides the worms with a purchase and they will remain motionless. The size of the worm was then measured and the pattern of the dorsal pigmentation described. This is useful as individual variation in the pattern of pigmentation exists. The inquiline climbed on its host when the two were reunited in a bag of sea water. After the commensal was secure in the mantle cavity, the water was poured out of the bag, and commensal and host were wrapped up in the bag and taken back to the field immediately. Subsequently the host could be recovered and the identification procedure repeated. The two worm identifications were then compared. In most of this work *Diodora* was employed.

RESULTS

Habitat and Habits of Hosts

All of the hosts of *A. vittata* and *A. pulchra* collected in the present study may occur in the sublittoral fringe and can be collected on minus tides. However, the bulk of the population of each species lies in the sublittoral zone, which was explored to a depth of about 20m. *Cryptochiton* was common at Pacific Grove, California, Cape Arago, Oregon and San Juan Island, Washington. Its abundance in all these collecting areas is estimated to be roughly the same. This species was concentrated in the upper parts of the sublittoral zone in which the growth of brown algae was most extensive. In some locations, the chitons appeared concentrated in depressions in which algal detritus had accumulated. At Simpson Reef and other locations at Cape Arago, *Cryptochiton* was concentrated on the tops of relatively flat rocky masses located in the *Laminaria* zone. It is a reported macroherbivore (Tucker and Giese, 1962) and was often seen with algal fragments protruding from its mouth. It was absent on rare or the vertical sides and sloping faces of these rock masses which extend below the *Laminaria* zone to a depth of more than 20 meters. These faces were covered with a rich growth of sedentary animals, but few plants other than occasional red algae. Found here were bryozoans, hydroids, entopracts, various tunicates, fields of holothurians, numerous anthozoans, fixed scallops, clusters of giant barnacles, and numerous sponges. The commonest large motile invertebrate here was Diodora. This limpet, however, was rare in the upper flat parts of the reef where Cryptochiton was common. When it occurred in the upper zone, it was in cracks and crevices. In no other collecting area was Diodora as abundant as at Simpson Reef. This distribution of Diodora and Cryptochiton is shown in Fig. 2. The vertical range of this limpet was much more restricted at San Juan Island. At False Bay on the island, Diodora was definitely restricted to the first few meters in which there was a heavy growth of algae. This is quite at variance with the situation at Cape Arago, where most occurred below this region. Margolin (1964) in describing the mantle response of Diodora to various echinoderms, argues that since Diodora is restricted to the intertidal, Pisaster ochraceus is likely to be its most important predator. Furthermore, other echinoderms such as Pyncnopodia helianthoides and Strogylocentrotous purpuratus are not likely to be predators because they occur below Diodora. This situation is perhaps true of the San Juan region but not of the open coast, where the range of these and other predators overlaps with that of the limpet.

Dermasterias was nowhere really abundant, but present at all four major collecting locations along the coast. Solaster occurred in fairly large numbers only off San Juan Island. There a number of the starfish were seen eating an abundant small holothurian, probably Cucumaria lubrica. In these subtidal locations where Solaster might be found, Parastichopus, a possible food item (at least when small), was very abundant, at least 10 times as common as the starfish. It is interesting to note that in the laboratory Parastichopus demonstrated an

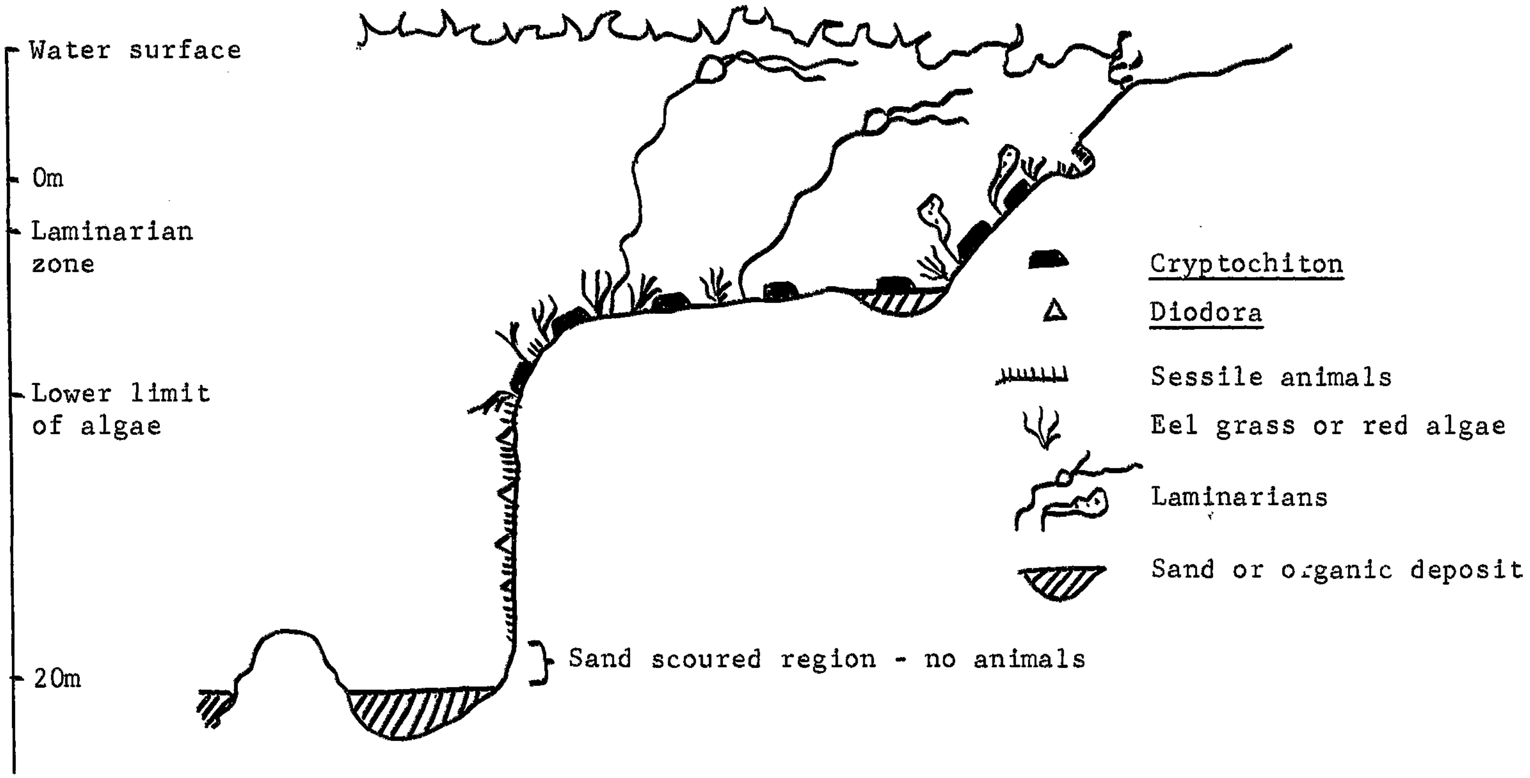


Figure 2.--Habitat of Diodora and Cryptochiton in the Cape Arago region of the Oregon coast.

avoidance reaction to the starfish. The holothurian found at Punta Banda may be a different form from the northern species. It was a bit smaller, the papillae did not appear as prominent, and it balled up when handled more frequently than the other stichopoids collected in this study did. Megathura, found at Pacific Grove and Punta Banda, occurred roughly in the sorts of places one would look to find Diodora. It also has a commensal copepod similar to Anthesius nortoni, which occurs on Diodora, but with a cross of pigmentation on the dorsum.

Distribution of the Commensal on Its Hosts

Multiple occupancy of hosts was found to be rather common on both Diodora and Cryptochiton (Tables 2 and 3). This was contrary to expectation. However, from a tabulation of the size of the second largest worm in all cases of multiple occupancy, an almost invariable rule emerged: The size of the second largest worm never exceeded 20mm. In other words, all worms larger than 20mm are distributed in an apparently regular manner of one worm to a host. However, because of the radically different infestation rates of these large worms, it is necessary to examine occupancy on the two different hosts separately before a conclusive statement on the nature of occupancy can be developed.

The overall infestation frequency of A. vittata greater than 20mm on Diodora (Tables 2 and 4) was 0.84 worms per host. It would be unreasonable, because of crowding, to expect five or more A. vittata on a single Diodora, but, in most cases, two or three could easily have fit into the host space. A binomial expansion $(p + q)^n$, with $n = 2$ and $np = 0.84$ therefore will give an approximation of the number of doubles

Table 2.--Distribution of the number of *A. vittata* per host *Diodora* from the Cape Arago region of the Oregon Coast, 1964 to 1966. Entries are the number of hosts with the indicated number of commensals.

		Number of commensals per host								Total number of hosts
Date	Place[a]	0	1	2	3	4	5	6	7	
Aug. 1964	SR	1	35	14	2	0				52
Oct. 1964	SI	4	17	3	0					24
April 1965	CAI	0	13	0						13
May 1965	CAII	16	61	3	0					80
June 1965	CAII	26	29	1	0					56
July 1965	CAI	0	19	1	0					20
Aug. 1965	BR	1	9	9	2	1	0			21
Aug. 1965	NSB	0	0	4	6	6	0	2	2	20
Oct. 1965	MR	0	5	9	7	2	0			23
Feb. 1966	MR	1	19	6	1	0				27
July 1966	SR	0	3	16	12	11	4	5	0	51

[a] See Figure 1.

Table 3.--Distribution of the number of *A. vittata* per host *Cryptochiton* from the Cape Arago region of the Oregon Coast, 1964 to 1965. Entries are the number of hosts with the indicated number of commensals

Date	Place[a]	Number of commensals per host 0	1	2	3	4	5	6	7	Total number of hosts
July 1964	SI	59	9	0						68
Aug. 1964	SR	8	8	0						16
Oct. 1964	NLH	0	6	4	0					10
Nov. 1964	LHC	11	9	2	0					22
Jan. 1965	LHC	23	13	1	0					37
March 1965	NLH	10	1	1	0					12
April 1965	LHC	18	6	0						24
May 1965	SI	199	44	0						243
May 1965	LHC	38	8	0						46
June 1965	LHC	11	2	0						13
July 1965	CAII	55	9	0						64
July 1965	LHC	26	4	0						30
Aug. 1965	NLH	12	7	2	1	0				22
Aug. 1965	SSB	7	10	8	6	0				31
Aug. 1965	NSB	0	2	6	2	4	0	1		15
Oct. 1965	NSB	0	6	10	8	1	0			25
Oct. 1965	SSB	0	15	12	1	0				28

[a] See Figure 1.

that might be expected in a space of this capacity (Greig-Smith, 1964). This expectation is 68 doubles for the aggregate of the worms in Table 2. Although this expectation is not logically exact because the value of n must vary between one and five, it is certainly in the right range. If multiple occupancy of the large worms occurred, it would be apparent in a sample of this size. It does not occur and I conclude that the regularity is real.

Cryptochiton differs from *Diodora* in two significant ways important to an analysis of occupancy. It is larger, and the frequency of worm infestation is much lower, 0.16 worms per host (Tables 3 and 5). The biological condition which must be met in order that the Poisson distribution, $\frac{E^X}{X!} e^{-E}$, may be used as a model for randomness is that the number of individuals occurring in the sample space does not approach the number which could occur (Greig-Smith, 1964). One can argue that this condition is met by the large worms on *Cryptochiton*. Between five and ten worms could easily fit on a typical chiton from the Cape Arago region. If a binomial of the fifth power and np = 0.16 is compared to a Poisson distribution with E = 0.16, they are found to be virtually identical (Table 6). This indicates that the conditions for invoking a Poisson model are met in this situation. The variance: mean ratio test has been used to assess the statistical confidence with which one can say that the large worms on *Cryptochiton* are distributed in a regular manner (Greig-Smith, 1964). All the census data have been pooled in Table 3 (N = 706). This procedure is likely to result in over-representation of the zero occupancy class (Williams, 1964) which

Table 4.--Distribution of the size of *A. vittata* from host *Diodora* in the Cape Arago region of the Oregon Coast, 1964 to 1966. Entries are the number of worms in the indicated size class.

		Size class of commensal (mm)							
Date	Place[a]	00-09	10-19	20-29	30-39	40-49	50-59	60-69	70-99[b]
Aug. 1964	SR	10	8	1	7	13	23	7	5
Oct. 1964	SI	2	4	1	1	9	5	1	0
April 1965	CAI	0	0	5	1	4	3	0	
May 1965	CAII	1	2	4	8	24	17	11	0
June 1965	CAII	0	2	3	9	9	6	2	0
July 1965	CAI	0	3	1	2	9	3	3	0
Aug. 1965	BR	14	4	2	0	2	3	11	1
Aug. 1965	NSB	51	5	0	0	2	6	9	3
Oct. 1965	MR	16	13	0	1	3	4	9	6
Feb. 1966	MR	5	3	2	4	4	5	5	6
July 1966	SR	86	27	3	1	3	27	15	3

[a] See Figure 1.

[b] Last size class spans 30 mm.

Table 5.--Distribution of the size of *A. vittata* from host *Cryptochiton* in the Cape Arago region of the Oregon Coast, 1964 to 1965. Entries are the number of worms in the indicated size class.

		Size class of commensal (mm)					
Date	Place[a]	00-09	10-19	20-29	30-39	40-49	50-59
July 1964	SI	0	1	2	3	3	0
Aug. 1964	SR	0	1	3	3	1	0
Oct. 1964	NLH	6	7	0	1	0	
Nov. 1964	LHC	3	5	4	1	0	
Jan. 1965	LHC	0	8	4	2	0	1
March 1965	NLH	1	2	0			
April 1965	LHC	0	0	1	2	2	1
May 1965	SI	1	10	16	10	5	2
May 1965	LHC	0	3	2	2	1	0
June 1965	LHC	1	1				
July 1965	CAII	0	1	3	5	0	
July 1965	LHC	0	1	1	1	1	0
Aug. 1965	NLH	12	0	0	2	0	
Aug. 1965	SSB	16	0	3	5	0	
Aug. 1965	NSB	32	6	1	2	1	0
Oct. 1965	NSB	34	14	5	0	1	0
Oct. 1965	SSB	17	17	2	3	3	0

[a] See Figure 1.

would only make the null hypothesis of randomness more difficult to reject. The value of the ratio is 0.846, which is significantly different from 1 by a t-test ($P < 0.005$).

Table 6.--A binomial model of occupancy for the commensals on Cryptochiton compared with the Poisson distribution of the same average occupancy ($np=E=0.16$ worms per host). The chiton is considered to be a sample space which could hold a maximum of five worms ($n=5$). The average size of chiton and worm would actually allow a greater capacity than this, and thus, a closer approach to the Poisson distribution

Number of worms per host	Probability	
	Binomial	Poisson
0	0.850	0.852
1	0.140	0.136
2	0.010	0.012

It is quite reasonable to state that on both of these hosts the large worms are distributed in a regular manner of one worm to a host. Because of the low infestation rate on Cryptochiton, it was necessary to argue for and apply a statistical test to be able to assert, with some confidence that the failure to observe multiple occupancy was not due merely to sampling error. The high frequency of infestation on Diodora speaks for itself: If multiple occupancy of large worms existed, it is almost unimaginable that it was not observed.

Numerous worms smaller than 20mm were collected from the hosts, and these were often distributed multiply. What is the nature of the distribution of these worms? A Poisson model of randomness is appropriate for reasons similar to those advanced in analyzing the large worm distribution on Cryptochiton. A far greater number of small worms could have occurred than were found on any host. The maximum number of small worms observed on a host was five. It is likely that about fifty could easily be accommodated in the available space. The sample of Diodora on July 1966 (Table 2) had a considerable number of small worms which were responsible for the multiple occupancy of that sample. The representation in the various occupancy classes was sufficient for a chi square goodness-of-fit test to be applied (Table 7). The P value is between 0.50 and 0.30. The null hypothesis cannot be rejected, and the allotment of the small worms cannot be distinguished from a random one. Variance: mean statistics have been calculated for a number of samples in which the small worms were not abundant enough to allow a goodness-of-fit test (Table 8). It is interesting that in all these cases the null hypothesis cannot be rejected at the 0.01 level of significance, but in almost half it could be rejected at the 0.05 level. The direction of deviation from randomness is toward regularity. With one exception, in which it is very nearly equal to 1, the variance: mean ratio is always less than 1.0. Although the worms less than 20mm in length are often multiply distributed on these hosts, their distribution may, in nature, tend toward regularity. Yet often it is not distinguishable from a random allotment of the small worms to the hosts.

Negative Worm-Worm Interaction

Regularity and isolation of the large worms is the striking feature of their distribution. It appears that the presence of one large worm is incompatible with the presence of another on a single host. One would expect that there is a negative worm-worm interaction

Table 7.--Goodness-of-fit analysis of all worms less than 20mm in length from a sample of 51 Diodora collected in July 1966. from Simpson Reef at Cape Arago

<table>
<tr><th>Number of worms per host</th><th>Observed</th><th></th><th>Expected</th><th></th></tr>
<tr><td>0</td><td>3</td><td rowspan="2">19</td><td>5.4</td><td rowspan="2">17.5</td></tr>
<tr><td>1</td><td>16</td><td>12.1</td></tr>
<tr><td>2</td><td>12</td><td></td><td>13.6</td><td></td></tr>
<tr><td>3</td><td>11</td><td></td><td>10.2</td><td></td></tr>
<tr><td>4+</td><td>9</td><td></td><td>9.6</td><td></td></tr>
</table>

$\text{Chi}^2 = 1.326$ $0.30 < P < 0.50$

Table 8.--Variance:mean analysis of all worms less than 20mm long from 9 samples of hosts.

Host[a]	Date	Location[b]	Number of hosts	Average number of small worms per host	$S^2/\bar{X}$
C	Aug. 1965	NSB	15	2.7	1.064
C	Aug. 1965	SSB	23	0.7	0.765
D	Aug. 1965	NSB	20	2.8	0.887
C	Oct. 1965	NSB	25	1.9	0.387*
C	Oct. 1965	SSB	28	1.2	0.510*
D	Oct. 1965	MR	23	1.3	0.728
C	July 1965	CAI	18	1.3	0.351*
D	July 1965	CAI	36	1.3	0.517*
D	July 1965	SR[c]	51	2.2	0.958

*Statistically significant at the 0.05 (but not at the 0.01) level.

[a] C = Cryptochiton; D = Diodora.

[b] See Figure 1.

[c] See also Table 7.

of some sort among the commensals. Indeed, when placed in finger bowls, the worms may act aggressively toward each other. Often one worm will attack another by biting with its proboscis. The attacked worm will usually retreat. Worms may jerk away from each other without any attack taking place. However, I have never observed large worms attack markedly smaller ones, although I have often given them the opportunity. Scaleworms have been noted for their fierce behavior. "Polynoidae are voracious feeders, devouring any animal they can capture. In captivity they attack one another" (Essenberg, 1917). MacGinitie and MacGinitie (1948) report on the scaleworms Hesperonoe adventor and H. complanata which drive off "any intruder" from the burrow of their host. In the finger bowl environment, I have never been able to encourage A. vittata to attack other species of the same size, chiefly Idothea sp. and nereid worms. Similar experience of inter-specific behavior is reported by St. John (1966).

Although what the worms do to each other in the privacy of their own hosts to bring about the observed regular distribution is not clear, certain field data, in addition to the basic census data, suggest that there is an important negative interaction between the large worm on a host and small recently settled worms. In October 1965, 36 marked host limpets were collected from CAI and 23 from MR (Fig. 1). Those from CAI had been cleared of all worms and returned to the collecting station 1 or 2 months earlier. The hosts from MR had not been previously disturbed. All the MR animals save one had a large worm when collected. From evidence which will be presented on worm growth and vagility, one can conclude that these large worms had been present on the hosts for at least 2 months. All worms taken from the CAI sample had been recruited within the last 2 months or less. When the worms from the two samples that are likely to have been of recent recruitment are compared (Table 9), a striking difference is apparent. The newly recruited worms from the experimental sample are typically much larger than those from the MR sample. On the bases of time of exposure and time of worm growth, the opposite would be expected. The smaller size of the newly recruited worms from the MR sample is apparently associated with the presence of the large worms.

Table 9.--Frequencies of worms from marked Diodora compared to those from previously undisturbed hosts. Worms in the first three size classes represent possible new recruitment in the preceding 2 months. Entries are numbers of worms. Modal size of new recruits is greater where large worms are not present.

	Worm size (mm)				
Worm category	0-15	16-30	31-45	46+	Remarks
Largest	7	19	2	0	From marked hosts exposed 2 months N=23 CAI[a]
Next largest	11	0			
Largest	1	1	1	20	From previously undisturbed hosts N=23 MR[a]
Next largest	17	1	0		

[a] See Figure 1.

An effect consistent with this inference can be observed between samples from Diodora and two other hosts, Cryptochiton and Solaster. On these latter hosts infestation by the large worms is comparatively low. Contemporaneous samples from Diodora and Cryptochiton are compared for the relative abundance of the first two 10mm size classes in Table 10.

In August there was no real difference, but in October the larger of the small size classes was more abundant on Cryptochiton. This is contrary to what one would expect on the basis of the infestation frequencies of the large worms (p. 16). Since infestation of the large worms is lower on Cryptochiton, there is reason to believe that mortality would be greater for all worm sizes on this host. It seems reasonable to associate the relative reduction in numbers of the larger of the small worms on Diodora with the presence of large worms (more than 20mm in length) on this host. No other apparent factor presents itself. Table 11 presents the comparative size frequencies of commensals on Diodora and Solaster collected at San Juan Island, Washington in March 1966. Where large worms occur (Diodora), the smaller worms are very infrequent and compose a relatively small proportion of the sample.

Table 10.--Comparison of the frequencies of the larger small worms (10-19mm size class) on Diodora and Cryptochiton from Sunset Bay, Oregon in 1965. The larger worms were relatively more abundant on Cryptochiton in October.

Month	Host	Number of worms in size class 00-09mm	10-19mm	Frequency of 10-19 size class
August	Diodora	51	5	0.08
	Cryptochiton	48	6	0.11
October	Diodora	69	18	0.21
	Cryptochiton	53	31	0.37

Table 11.--Comparison of abundance of A. vittata on Diodora and Solaster from San Juan Island, Washington in 1966. Entries are numbers of worms. Smaller worms are more abundant on Solaster from which large worms are absent.

	Worm size (mm)						
Host	00-09	10-19	20-29	30-39	40-49	50-59	60+
Diodora	1	1	3	1	11	6	1
Solaster	1	12	6	2	0		

Of course, this evidence is only circumstantial. However, it does seem that a good case can be built for asserting that a negative worm-worm interaction is responsible for maintaining the isolation of the large worms. These worms are clearly distributed in a regular manner. If the largest worm on a host is longer than 20mm, the second--if present--never is this long. This is surprising, as multiple occupancy is rather common and large worms often exceed 40mm (Tables 4 and 5). More than just one worm at a time should be large on a host. In itself, this strongly implies some aggressive interaction among the worms. What form such behavior may take is not clear merely from the distribution of the worms or from the way they behave in the laboratory. It will depend, in part, on the manner in which the worms are recruited onto the hosts. As will be shown, most recruitment is by small, recently settled worms, and on Diodora, at least, adult worms typically live more than 1 year. On this host, the small worms must often contend with a large resident worm which, as has been shown, may be associated with a reduction in numbers of the smaller worms. The large worms could devour, drive off, or retard the growth of the smaller worms. The field evidence cannot really distinguish among these possibilities. It is of note that the small worms themselves show some tendency toward a regular distribution (Table 8). The regular distribution can, in fact, be established without a large worm being originally present on the host. If the inference of regularity in the distribution of large worms on Cryptochiton is accepted, then negative interaction among the worms on this host very likely follows. As resident worms are relatively scarce, this interaction must often involve competition among a cohort of recently settled worms. The regular distribution was also obtained experimentally in the absence of large worms on marked Diodora. Following 8 months' exposure to recruitment, of a sample of 33 previously cleared limpets 29 had one worm and 4 had none. The modal size class of the worms was 20 to 29mm. The negative interaction is not just between large and small worms, but seems to include worms of all size classes.

Recruitment of the Commensal

The abundance of small worms in numerous samples (Tables 4 and 5) suggested that commensalism must begin very early in the life of A. vittata. The smallest worms collected from the hosts were only 1.5mm in length, which is equivalent to a dozen segments. This size is about the same as the largest planktonic post-larval polynoids reported in Nordisches Plankton. In addition, it is the same size as the earliest Harmothoe imbricata taken in bottom samples from Danish waters (Thorson, 1946). A. vittata this size and slightly larger have long delicate setae, which presumably are used for swimming.

Furthermore, these small commensals could swim when removed from their host, a feat which larger worms were never observed to do. Worms of several segments could seek out a host and settle directly upon it. Such behavior would be consistent with the known selective powers of other invertebrate larvae (Wilson, 1958). Both large and small worms responded positively to "host factor" in a modified Y-tube (Appendix 2). They would seem to be able to locate a host chemotactically.

Marked hosts were used to investigate recruitment experimentally in the field. Hosts were cleared of all worms, tagged, and returned to a suitable location. Collections were made at intervals of a month or more and the newly recruited worms were removed and counted. Such work indicated that most recruitment was, as expected, through settlement. However, a certain amount of recruitment was due to infestation by large worms which did not represent recent settlement. In Tables 12 and 13 the frequency and size of the newly recruited worms is given for the number of months preceding recapture of the marked host. Both Diodora and Cryptochiton were employed. The bulk of the worms in the first 3 months are less than 20mm. This is the expectation if recruitment is by recently settled worms. In Table 11, about a seventh of the worms recruited to Diodora in the first 3 months seem too large to represent very recent settlement. Such worms were not found on the marked Cryptochiton. These worms are as large or larger than the strong modal class obtained in 8 months on Diodora. Either there is great variation in early growth or worms which have not recently settled can infect hosts.

Table 12.--Reinfestation of marked Cryptochiton. Entries are the number of worms removed from hosts after the indicated months of exposure.

Number of months preceding recapture	Size of new worms (mm)					
	00-19	10-19	20-29	30-39	40-49	50-59
1	4	2	0			
2	8	14	2	0		
3	7	12	8	0		
4	0	2	3	0		
5	1	4	0			
6						
7		0	1	1	0	
8		0	1	1	1	0
11				0	1	0

Table 13.--Reinfestation of marked Diodora. Entries are the number of worms removed from hosts after the indicated months of exposure.

Number of months preceding recapture	Size of new worms (mm)					
	00-09	10-19	20-29	30-39	40-49	50-59
1	10	8	2	2	3	0
2	9	16	2	2	3	0
3	5	7	1	0		
4	0	4	9	2	1	0
6	0	1	2	1	0	
8	1	4	19	4	0	
10		0	2	0		
11			0	2	0	1
12				0	3	1
21			0	3	1	4

These data raised the question of whether or not initial recruitment of the small worms was by direct settlement on the hosts. The small worms might settle on the substrate and then crawl about until a host was located. If some were tardy in finding a host, an explanation of the large newly recruited worms would exist. To decide if the worms settle directly on the hosts or on the substrate and then seek out the host, a number of recaptures of marked hosts were made after only 1 week of exposure to recruitment. If worms 5mm or larger were recruited, this would be evidence for believing that the worms typically settle on the substrate and seek out a host. Assuming that they settle at a size of 1.5 to 3.0mm, it would seem unlikely that in a week's time they would grow much larger than 5mm. Table 14 lists the sizes of the worms recovered in this experiment. Some of these are larger than the modal size class obtained after 1 month of exposure and thus a maximum of 1 month for growth on the host. Some of these worms were probably already on the substrate when the marked hosts were put out.

Table 14.--Sizes of worms collected from marked hosts after 1 week of exposure to recruitment. The smallest worms collected during the whole study were 1.5mm in length. Worms of about this size were expected in this experiment.

Host	Worm sizes (mm)
Diodora	18, 15, 15, 6, 4, 3, 3
Cryptochiton	7, 6, 6

Although it seemed quite likely that the source of an occasional large worm in recruitment was freeliving A. vittata, direct observation of these was never made. Considerable effort was expended in searching for freeliving worms. A few instances of freeliving A. vittata have been reported, yet they seem to be somewhat equivocal (Berkeley and Berkeley, 1941; Ricketts, 1963; Hartman, 1939). Ricketts' account suggests that the worms may have fallen from hosts on the underside of rocks. Hartman mentions two specimens 25mm in length which were taken in a surface tow! But this was not a direct observation of the author. The Berkeleys' report is of dredged material, believed to be freeliving because aberrant in appearance. There is certainly no large freeliving population of A. vittata in the field. Yet there can be almost no doubt that some large individuals are at least transiently freeliving.

Some of the large, newly recruited worms may have recently abandoned other hosts. This possibility was investigated experimentally in the field. Individually identifiable worms were returned to marked limpet hosts. A third of the hosts were returned without any worms on the suspicion that they might pick up straying worms. The worms were put out in batches of about 20 animals spaced 30cm or less from each other on the substrate and left for a period of 1 month. About half the hosts were recovered (Table 15). Of the large worms taken from these hosts, 32% were new to their hosts and thus demonstrated vagility. Two of these gained worms were very distinctive in appearance, and were quite clearly the same worms which had been put out in marked hosts at the beginning of the period. These two hosts were collected and the original worms were gone. It is concluded that these two worms switched over from one marked host to another. The total overall gains and losses of worms in Table 15 are about the same, which suggests that the gained worms may be the lost ones. In any case, the large worms do exhibit vagility on the keyhole limpet under experimental field conditions.

Table 15.-- Worm vagility experiments. Individually identifiable worms were returned to the field in marked hosts. After a month, the hosts were collected and the worms identified to determine if the original worm had remained with its host.

		Frequency of observable event				
		No change		Change of worm		
Date	Place[a]	No worm[b]	Same worm	Worm loss	Different worm	Worm gain
July 1965	CAI	2	12	2	0	2
Feb. 1966	SI	0	7	1	0	0
March 1966	SI	0	4	1	0	0
March 1966	SI	2	8	1	1	1
April 1966	SI	2	8	5	3	2
Totals		6	39	10	4	5

[a] See Figure 1. Work at SI was carried out in a large tide pool in the low intertidal. *Diodora* occurred in this pool, but all were removed at the beginning of the experiment.

[b] For hosts returned without a worm.

On the other hand, no indication was ever obtained that large worms would recruit to *Cryptochiton*. This is apparent in Table 12 and is the striking difference in recapture data between the limpet and chiton host. In the modified Y-tube situation (Appendix 2), positive responses were obtained toward both the chiton and limpet by worms from either host. No obvious behavioral difference toward either host seems to explain the apparent rejection of Cryptochiton by vagrant large worms in the field. Figure 3 is the history of 18 worms on marked Cryptochiton which were followed in the field for several months. The chitons were checked on low tides to determine if the original worm was still present. Nearly half of the worms disappeared during the period of observation, but a certain amount of worm fidelity is indicated. The rate of worm loss is probably consistent with the suboptimality of Cryptochiton as a host which is indicated by the low infestation rates of large worms (16-22).

Recruitment of the small worms is definitely seasonal. The incidence of worms less than 20mm is greatest in the summer and fall. To establish this statement, both marked host returns and the frequencies of small worms less than 20mm in census data must be examined. The incidence of large and small worms in all collections of unmarked Cryptochiton and Diodora from the Cape Arago region is presented in Table 16. The table is partitioned by time of year (summer to winter and winter to summer) and by habitat (intertidal and subtidal). There is a solid indication of seasonal settlement for the small worms from subtidal Diodora. The seasonal difference in this case is tenfold. The same abundance of small worms is indicated for summer to winter collections of subtidal Cryptochiton. More data on the low subtidal infestation rates will be presented later. However, the seasonal distribution of early recruitment in the intertidal can be demonstrated when the recapture data for the marked Cryptochiton in LHC (Fig. 1) are examined (Table 17 and Appendix 3). Unmarked chitons were collected monthly, cleared of worms and marked. Marked chitons were

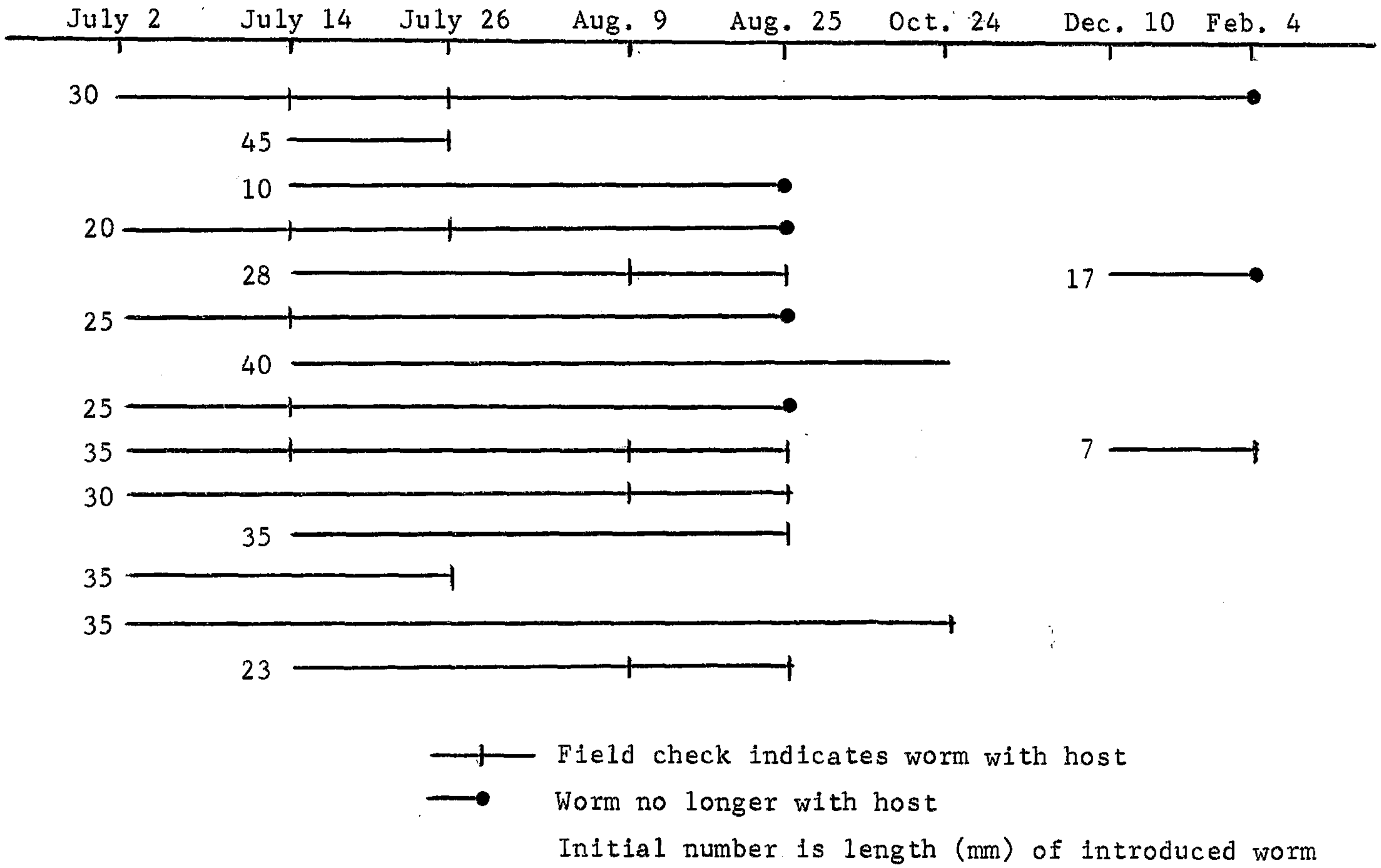


Figure 3.--Histories of 16 *A. vittata* in marked *Cryptochiton* at the Light House Channel between July 1965 and February 1966. Worms were introduced to marked chitons from other *Cryptochiton*.

Table 16.--Seasonal settlement as indicated from field census data. Total of all hosts collected in the Cape Arago region from July, 1964 to July, 1966.

a) Partition of the relative abundance of large and small, recently settled A. vittata by host, habitat, and time of year

Habitat	Time	Diodora Relative No. worms per 100 hosts Small[a]	 Large	 Actual No. hosts	Cryptochiton Relative No. worms per 100 hosts Small[a]	 Large	 Actual No. hosts
Intertidal	Jan. to June	7	72	165	7	14	377
	July to Dec.	24	76	163	8	14	207
Subtidal	Jan. to June	9	87	116	(25)	(0)	12
	July to Dec.	101	95	273	118	25	155

b) Habitat and host pooled

Habitat	Time	Both hosts Relative No. worms per 100 hosts Small[a]	 Large	 Actual No. hosts
Intertidal and Subtidal	Jan. to June	6	23	770
	July to Dec.	32	26	798

[a] Worms less than 20mm in length.

Table 17.--Seasonal settlement as indicated by data from the recapture of marked Cryptochiton. This is a summary of the worms collected by May 1965 from marked hosts released on the indicated dates. Collections were monthly. Nearly all new worms were collected from chitons which had been exposed in August and September of 1964, indicating that settlement must have occurred then. See Appendix 3 for a more extensive summary of Cryptochiton recapture data.

Date of release of marked hosts	Total of worms removed by June 1965	Total of hosts recaptured
Aug. 1964	26	63
Oct. 1964	0	3
Nov. 1964	0	23
Dec. 1964	0	19
Jan. 1965	2	25
Feb. 1965	0	15
March 1965	0	14
April 1965	0	30
May 1965	0	18

collected monthly, checked and cleared of any new worms, and then returned with the newly marked chitons. Between October 1964 and June 1965 virtually all worms were collected only from hosts which had been marked in August 1964. After June 1965 scaleworms began to appear again in the marked hosts. That new worms appeared only in the cohort of marked hosts exposed to recruitment between August and October indicates that recruitment must have occurred only then. A similar picture can be seen in the recovery data from marked Diodora (Table 18 and Appendix 4). These data must be aggregated from both sub- and intertidal collecting stations to cover the year as adequately as possible. There were not enough suitable low tides each month to maintain

Table 18.--Seasonal settlement indicated by data from the recapture of marked <u>Diodora</u>. This is a qualitative interpretation of Appendix 4. The most intensive recruitment occurred within the summer and fall (July to October). 0 = no evidence for settlement; + = no settlement; ++ = some settlement; +++ = much settlement.

Time of recapture	Summer 1963	Summer Fall 1964	Winter 1964 1965	Spring Early Summer 1965	Summer Fall 1965	Winter 1965 1966	Spring Early Summer 1966
Summer Fall 1964	++	+++					
Winter 1964 1965		0	+				
Spring Early Summer 1965			++	+			
Summer Fall 1965				++	+++		
Winter 1965 1966					++	+	
Spring Early Summer 1966						0	++

an intertidal Diodora station on a monthly basis in addition to a Cryptochiton station and inclement weather prevented monthly collection of any subtidal Diodora station in the winter months. The relative intensity of recruitment is shown in the table. The greatest recruitment was within the period from July through October, with virtually none in the winter period.

The frequency of sexually mature worms during the year is further evidence of the seasonal nature of settling and spawning in these commensals (Fig. 4). In the fall, the frequency of mature worms falls nearly to zero, indicating that most of the worms are spawned out. There is no marked decline in abundance of the large worms during this time, which suggests that they can spawn more than once, unlike some other annelids (Dales, 1951). Shedding of gametes was observed in the laboratory. The gametes pass out of the nephridial pores. There is no indication of epitoky or rupture of the body wall which might result in the death of the adult when liberating gametes. The time of the rapid decline in the frequency of sexually mature worms was not the same every year. This may mean that the timing of spawning is not constant every year, or it may be an indication of basic heterogeneity in spawning among the worms (Clark, 1964). The variation may arise from the fact that worm samples represent different subpopulations. Capacity for spawning ceases by the end of August. August is also about the peak of settlement, but small worms were collected in numbers into October. This could indicate a long larval life. The eggs have a diameter of about 80μ. According to Dales (1959), this size of egg may be taken as indicating a larval life of

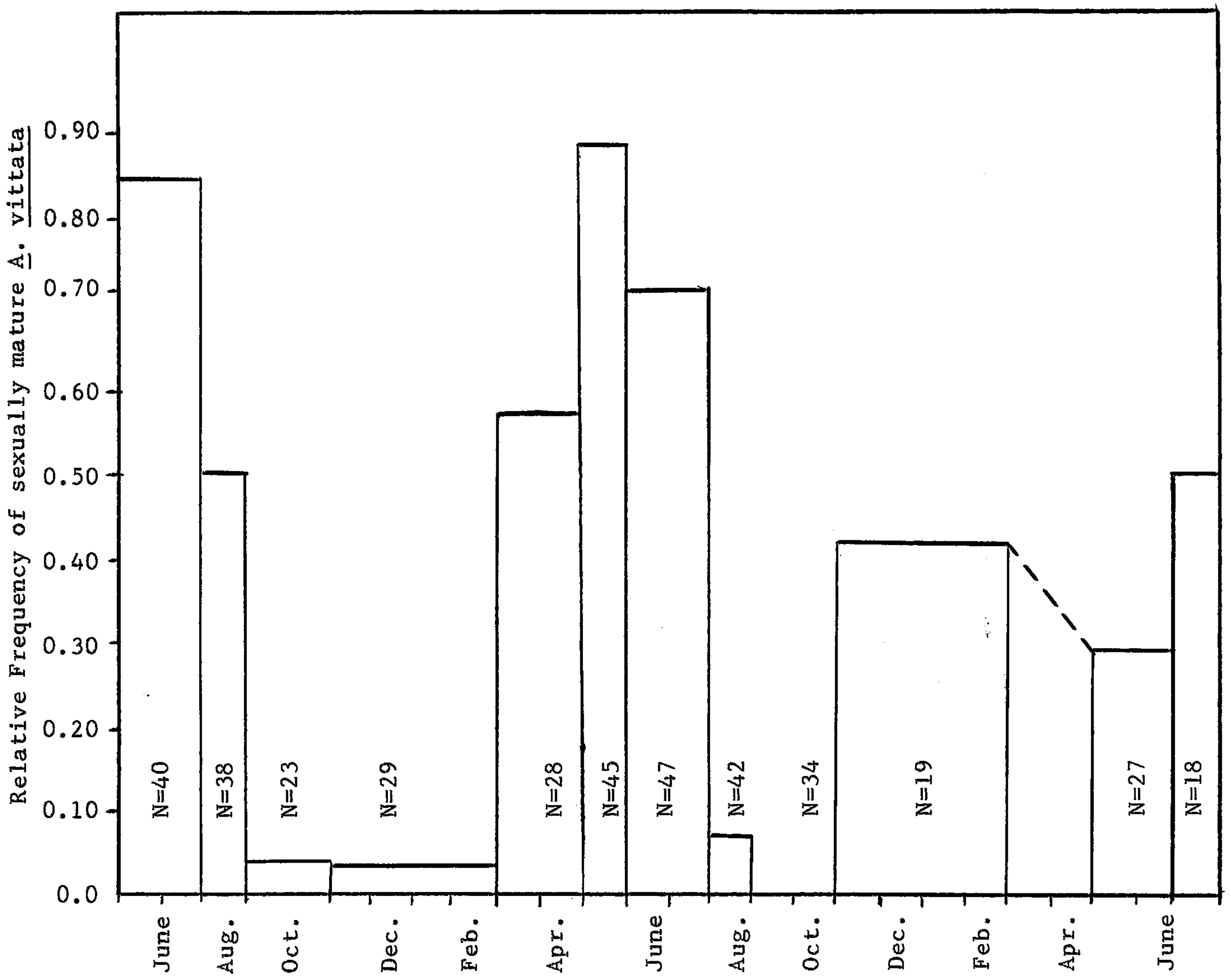


Figure 4.--Frequency of sexually mature A. vittata from Cryptochiton and Diodora in the Cape Arago region of the Oregon coast, 1964 to 1966.

a month or more. It is also possible that settlement in October represents spawning elsewhere and transport of the larvae to Cape Arago. Direct evidence is lacking, and attempts to raise the larvae and obtain an estimate of their longevity were not successful.

Large differences between the frequencies of small worms recruited to Diodora and Cryptochiton do not seem to exist, although the average number of small worms per host is slightly higher on Diodora (Tables 4 and 5). Early in the settling season the size distributions of the newly recruited worms are similar. A close examination of a mixed sample of the two hosts collected from one location on the same dive demonstrates this (Fig. 5). There is little reason to believe that there is any great difference in the size structure of the small worm portion of the populations. In this sample, the infestation frequencies of the small worms are nearly the same, 2.5 worms per chiton and 2.8 worms per limpet.

Large differences in the intensity of settlement have been observed on a subtidal-intertidal basis. Table 19 lists the frequencies of small worms for three Diodora samples collected within one week in July 1966. There is a fairly dramatic increase in the frequency of the small worms as the collecting stations become deeper and more removed from shore. Data from three Diodora recapture stations indicated similar trends (Table 20). All these recaptures were made in a 3 day period in October 1965. The CAII station is located several meters from the CAIII station and, in fact, represents its intertidal extension. Although the limpets from CAII had 1 more month of exposure to recruitment, they yielded only half as many worms.

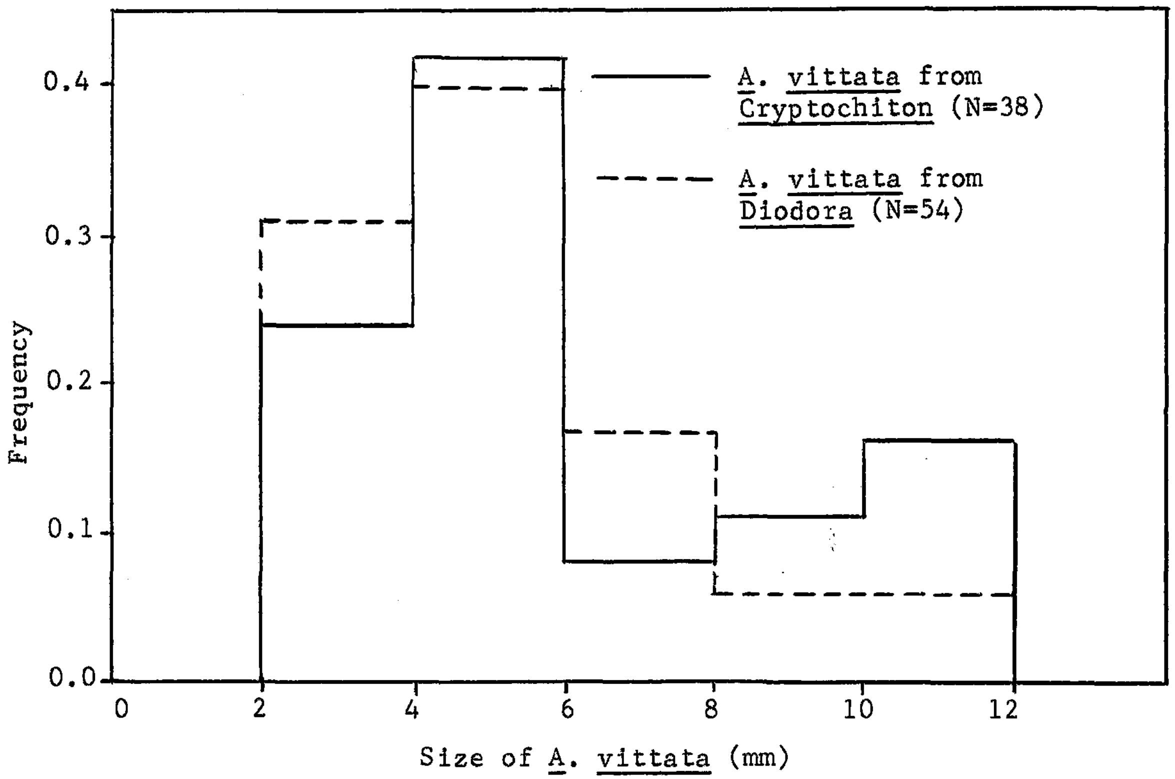


Figure 5.--Size frequency distribution of very recently settled worms on <u>Diodora</u> and <u>Cryptochiton</u> collected in August 1965.

Table 19.--Abundance of small worms (20mm or less in length) in three samples of Diodora collected during one week in July 1966.

Habitat and station[a]		Worms/Host	Ratio
Intertidal	CAII	20/41	0.49
Close subtidal	CAI	49/37	1.32
Far subtidal	SR	114/51	2.24

[a] See Figure 1.

Table 20.--Abundance of newly recruited worms on marked Diodora collected within three days in October 1965.

Habitat and station[a]	Period of exposure (months)	Worms/Host	Ratio
Intertidal, not close to good subtidal habitat; SI	2	2/19	0.19
Intertidal, extension of good subtidal habitat; CAII	2	13/18	0.72
Subtidal; CAIII	1	26/18	1.44

The SI station is at least 50 meters from water as deep as CAIII. The approach to it is a gently sloping boulder field. It has never been very productive of settling worms. The limpets collected from it had been exposed for 2 months as had the limpets from CAII. Yet only 2 worms were taken from 19 hosts. Both census and recapture data clearly show that the intensity of settlement is greater in the subtidal than in the intertidal regions. The behavior of the larvae probably would explain this difference (Wilson, 1958).

Growth Rates and Structure of Commensal Populations

From Tables 12 and 13 a growth curve for the commensal may be constructed by plotting the modal size class at each month (Fig. 6). Such a plot has validity if the hosts are infested soon after they are exposed. Settlement is restricted to the summer and fall, and nearly all hosts were marked and released in this period. In addition, reinfestation can easily occur within a week. The progressive rise of the mode suggests, in itself, that this plot is a growth curve. There is no apparent difference for worms from the two hosts in the plot. Most of the *Diodora* were subtidal; all of the *Cryptochiton* were intertidal. There is no reason for assuming different growth rates for either host or location, although the numbers are perhaps not sufficient to prove it. Recaptures at several months are not as frequent as one might wish. However, it is only these which have the largest worms. But if some worms do move from host to host, as would seem to be the case, then there is a possibility that some of the worms at 11 and 12 months are older than 1 year. The returns at 21 months set the modal and largest

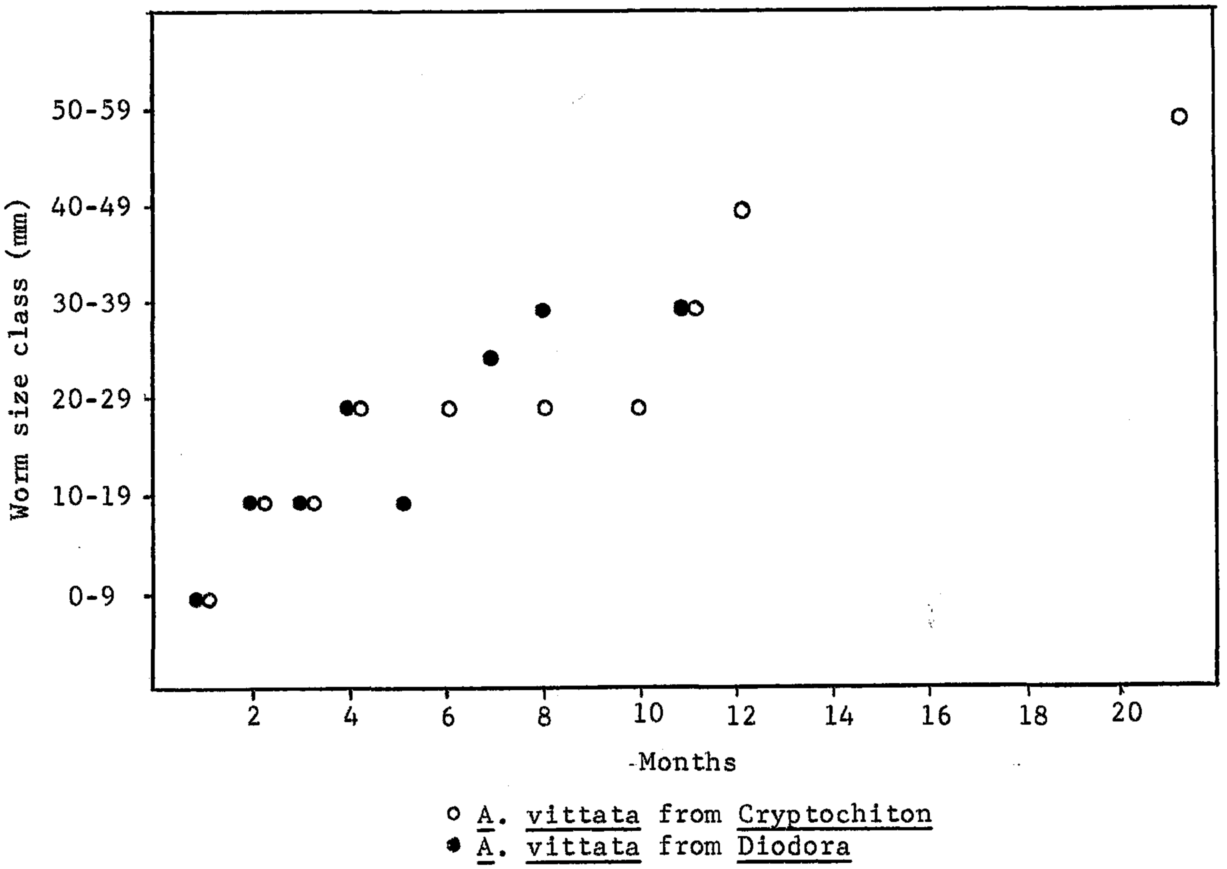


Figure 6.--Growth in A. vittata. Modal size of worms for number of months after release of hosts. Most worms were recruited soon after release of host.

size class attained at 50 to 59mm. This allows one to be comfortable in setting the size estimate of a year's growth in the 40 to 49mm class. A program to follow the growth of individual large worms over a period of a year produced only minimal results. These, however, suggest that large worms do not grow rapidly and that worms in the 40 to 49mm size class in 1 year will, at most, be in the 50 to 59mm class in the next. Segment counts of worms were made and worms were returned to the hosts to be collected in 1 year when a second segment count could be made if the worm appeared to be the same individual. Only four original worms were recovered. This was due mostly to a very bad set of tags on the hosts used in this experiment. The increments in segments were as follows: 55 to 65, 58 to 63, 57 to 58, and 57 to 59 (Arctonoe produces an indeterminate number of segments. A segment is equivalent to about 0.8mm).

The size class estimate of 1 year old animals may be used in estimating the turnover time and average age of the large worms in a population. In a sample of Diodora, all hosts with no worm or with the largest worm in the 1 year or a smaller size class represent the occurrence of a vacancy (loss of at least 1 worm) within the last year. This is the case subtidally, at least, where virtually every host is exposed to recruitment. Nearly every Diodora has a large worm (one greater than 20mm). This means that the frequency of vacancies will give a close, but maximum estimate of the death rate of the larger worms. The turnover time and average age will be estimated as the reciprocal of the frequency of vacancies occurring within the last year. Such computations for seven subtidal samples of Diodora are shown in Table 21. The range of turnover times for the large worms is 2 to 10 years. The pooled estimate is 4 years. There is variation, but it is probably safe to state that the large worms may live 4 years at the least and not longer than 10 years at the most.

Table 21.--Data for calculations of turnover time. Turnover time is the reciprocal of the fraction of large worms lost in 1 year (= death rate). The range is 2 to 10 years. The pooled estimate is 4 years. This is also an estimate of the average age of the large worms.

Date	Place[a]	Number of vacancies[b]	Number of hosts	Fraction of large worm population lost in 1 year
Aug. 1964	SR	22	52	0.42
Aug. 1965	BR	7	22	0.32
Aug. 1965	SB	2	20	0.10
Aug. 1965	CA	12	64	0.17
Oct. 1965	MR	3	23	0.13
Feb. 1966	MR	11	27	0.41
July 1966	SR	7	51	0.14
Total		64	259	0.24

[a] See Figure 1.

[b] Vacancies are hosts which have no worms or whose largest worm is in or below the 1 year size class (40 to 49mm in length).

Mortality of the small worms on Diodora is very high, as most are unfortunate enough to settle on a host already harboring a large worm which excludes the smaller worm from becoming a large one. An estimation can be made of the number of small worms lost from a host during one season. The small worms are in the 1 or 2 month class.

This indicates that replacement is between two and three times a year, assuming a 6-month recruitment period for the small worms. There are about two small worms per host during this period. Thus about 10 small worms die or disappear from their host every year. Accepting an average life span of 4 years for the large worms, the death rate for small worms is about 40 times that of the large.

The problem of the turnover time of the worms on Cryptochiton is more quickly discussed because the worms hardly ever exceed the first year size class (Table 1). The large worms thus have a turnover time of 1 year or less. Small worms become large worms on between a tenth and a fourth of the chitons. This means that the survival rate of the small worms on Cryptochiton is about the same as that on Diodora. Some source of mortality which cannot be associated with the large worms must be higher on the chiton than on the limpet host.

The above discussion assumes that the commensal populations are relatively constant in their size structure and infestation rates. Examination of Tables 2, 3, 4, and 5 shows that this is true for the period of study. In addition, no other indication from any aspect of the field work suggested that the population structure of the commensals fluctuated markedly. Diodora were found with a large worm 50 to 100% of the time. In subtidal collections the infestation was always nearly complete. These worms were typically larger by 10 or 20mm than those taken from Cryptochiton, which were only 10 to 25% infested. The intensity of settling, as far as can be determined from the collection and recovery data, has not changed radically in 3 years. Thus, the demographic features of the commensal populations in the Arago region during the period of study were generally stable. At Cape Arago A. vittata attain about 4 years of age on Diodora and occupy nearly all the available places in which to live. In the same region on the other common host, Cryptochiton, the expectancy of life is 1 year or less. On this host, though there is apparently no absolute shortage of places in which to live, mortality of small worms is about as severe as on Diodora where there does seem to be an absolute shortage of Lebensraum.

Growth Rates and Structure of the Host Populations

Growth data were collected from both hosts in the recapture studies. These have been plotted as original size against increment for various convenient periods of time. The weight increment plot for Cryptochiton is fascinating (Fig. 7). Beyond an original weight of 500g, any progressive change in the capacity for growth is masked by great individual variation which includes weight loss. This variation may be due, in part, to losses from spawning (Tucker and Giese, 1962). Measurements on three chitons gave daily changes of ±20g. Perhaps the fluid content of the animal may vary a good deal. In any case, the overall increment is positive, which is comforting since it indicates that the chitons do grow. The average increment for all chitons for a period of greater than 10 months is 35g per host. If this rate were applied to a chiton of 100g it would take over ten years to attain the modal size found in natural populations (Fig. 8). Small chitons are relatively rare. They are not represented in Figure 7 at all. Only one has been taken which could be regarded as

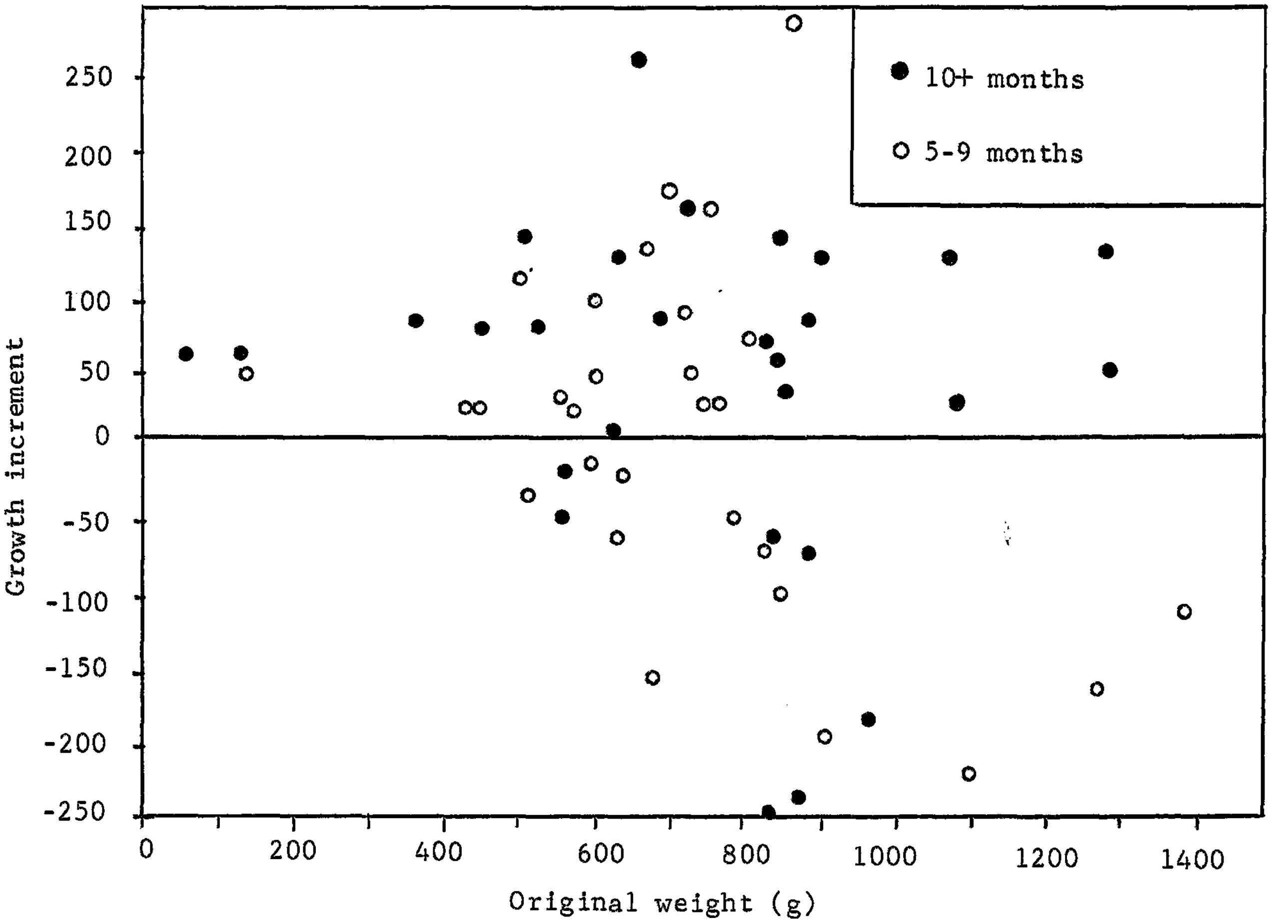
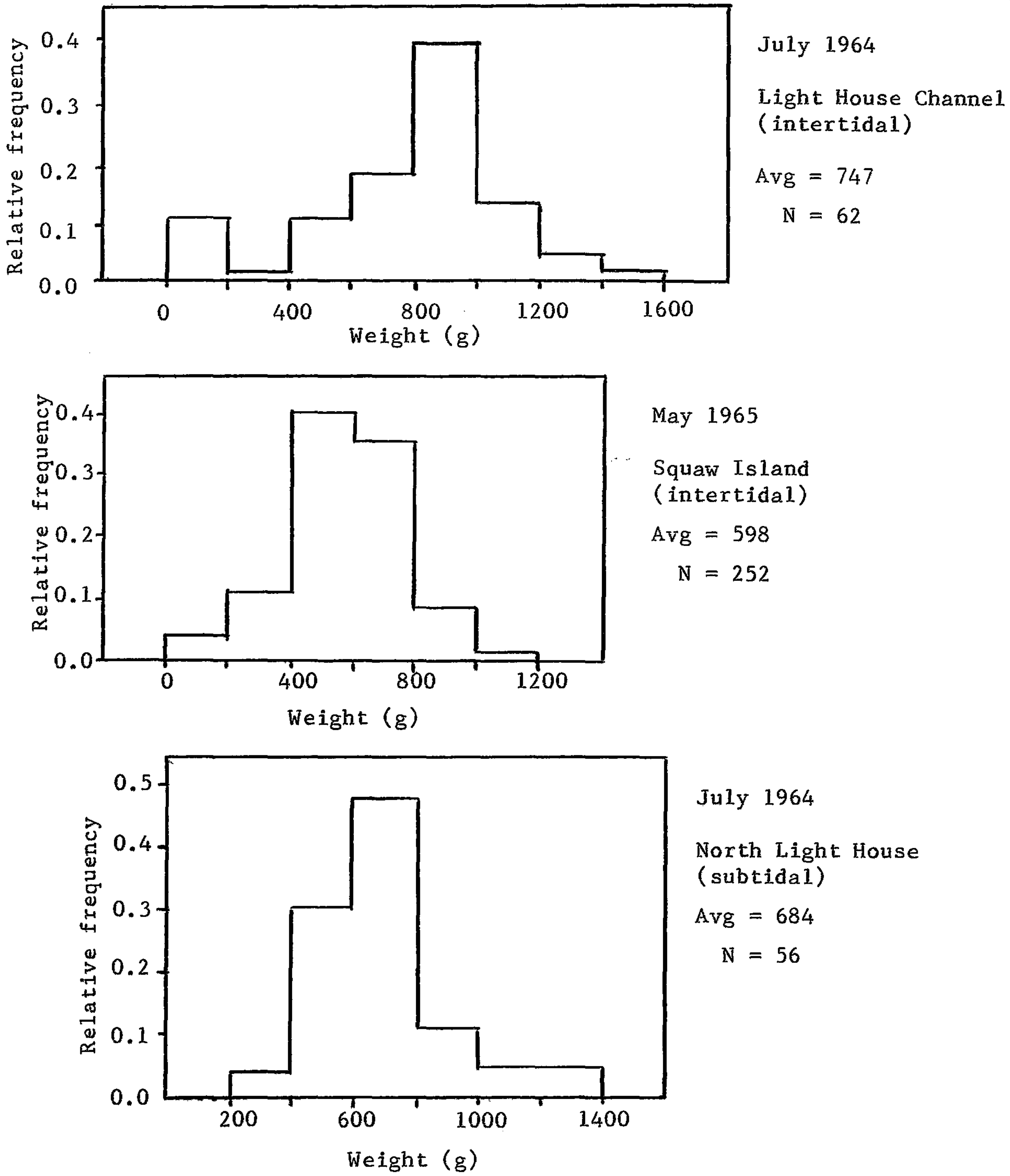


Figure 7.--Growth in Cryptochiton. The relation of growth increment and original weight for two time periods, 5-9 months and 10+ months. Weight is wet weight of chiton.



July 1964

Light House Channel
(intertidal)

Avg = 747

N = 62

May 1965

Squaw Island
(intertidal)

Avg = 598

N = 252

July 1964

North Light House
(subtidal)

Avg = 684

N = 56

Figure 8.--Size-frequency distributions of Cryptochiton. Size of chiton is wet weight.

recently settled (30mm in length). Cryptochiton less than 100g are seen occasionally in the intertidal. Allowing for the greater difficulty of discovering them, they are still probably much less than a tenth as abundant as larger chitons. Apparently only a few chitons are recruited into the population each year, and--if the population is stable--only a few can be lost each year. This situation suggests a longevous organism. However, it may be that recruitment varies greatly and good recruitment years are rare as with some other invertebrates (Cole, 1957; Buchanan, 1966; Barid, 1966; Ebert, 1967). If this is true, the expectation would still be for a very longevous animal with a life span exceeding the greatest likely period between good seasons. Cryptochiton is a long-lived organism, which has a life span greatly in excess of that of its commensal.

Although the growth plot for Diodora is quite different in appearance from that for Cryptochiton, similar conclusions may be drawn from it regarding the longevity of this host. There is progressive decline in the growth increment as the animal increases in size. At all sizes the variation in the observed increment is rather large, although above 40mm the increment is minimal and the variation reduced. The smallest limpets found in the field were 10 to 20mm from back edge of shell to top aperture. These were not too common, although they may have been more abundant in 1963 than in other years. Liberally applying the maximum rates from Figure 9, I estimate that a 20mm animal would reach 40mm in 6 years. This is a minimum time estimate as the envelope of the plot has been used. All variation in growth is, of course, below the envelope.

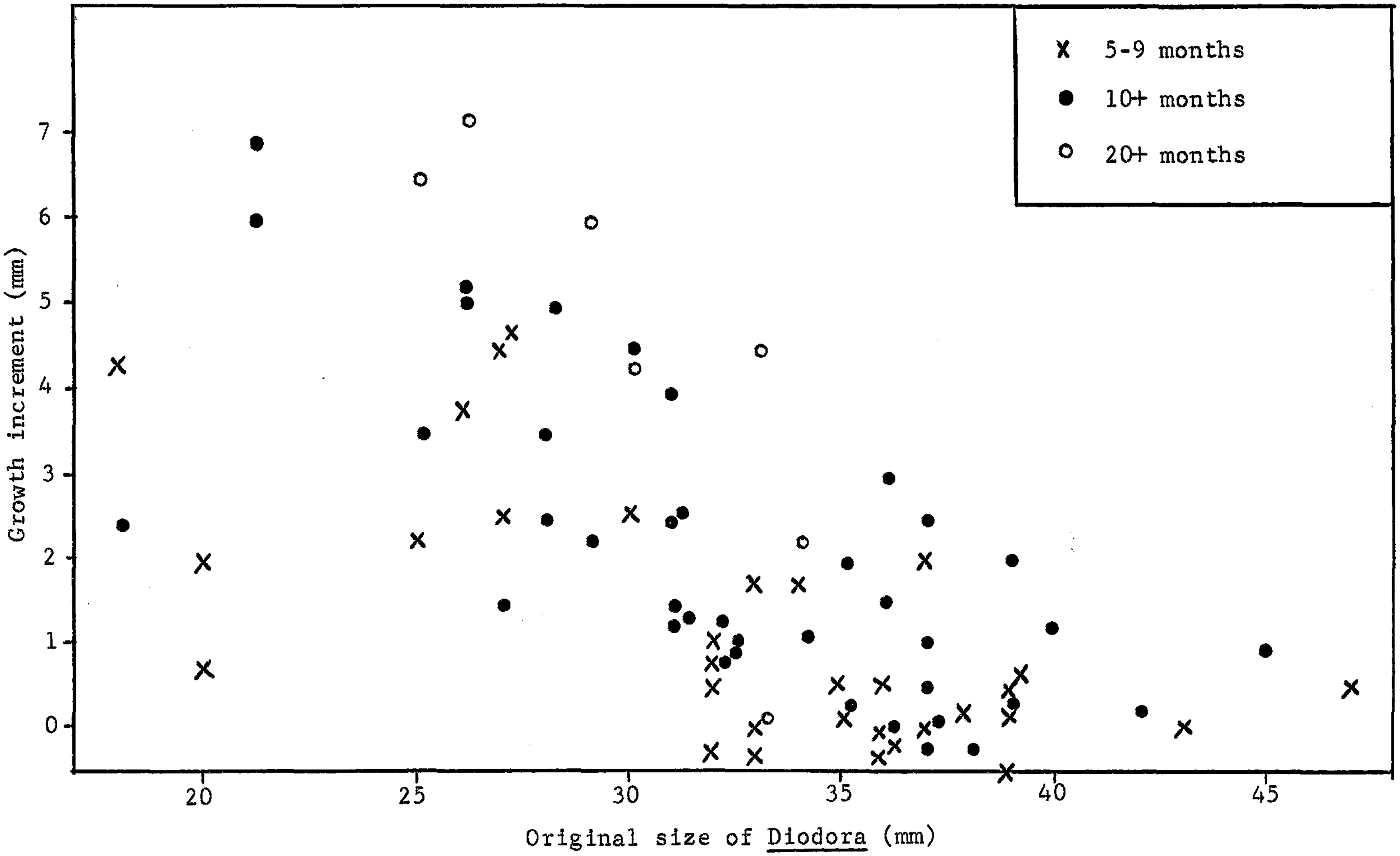


Figure 9.--Growth in _Diodora_. The relation of growth increment and original size for 3 time periods, 5-9 months, 10+ months, and 20+ months. Size is distance from top aperture to rear shell margin

The size distributions of three typical samples of this host are presented in Figure 10. Subtidal samples are skewed to the right with the modal class greater than 40mm. Intertidal samples are more symmetrical with the mode slightly less than this size. The modal age of the former is certainly greater than 10 years and that of the latter 4 years or more.

Both hosts present to the commensals well-defined places in which to live that are not likely to fluctuate greatly on a year-to-year basis. Field experience with marked hosts suggested that, in general, they were not too likely to move much either. Marked animals were never found more than several meters from their place of release. This tendency to stay in one place made it possible to recover hosts months or, in a few cases, nearly 2 years after release. In only one case were limpets observed to disperse widely. This happened when a group of Diodora was released in a high intertidal location in which limpets did not occur naturally. They tended to scatter widely toward lower levels.

In conjunction with host movements, it has been suggested that Cryptochiton may migrate into the intertidal in the spring to spawn (Ricketts and Calvin, 1962; Okuda, 1936). Field experience in this study suggests that this migration may be an illusion owing to the fact that the first good daylight tides occur in the spring before the algae have developed to their full summer cover. In the winter of 1964 and spring of 1965 Cryptochiton were collected by lantern light on low nighttime tides. In the first daylight tides of April and May the chitons were no more abundant than before. On the later summer

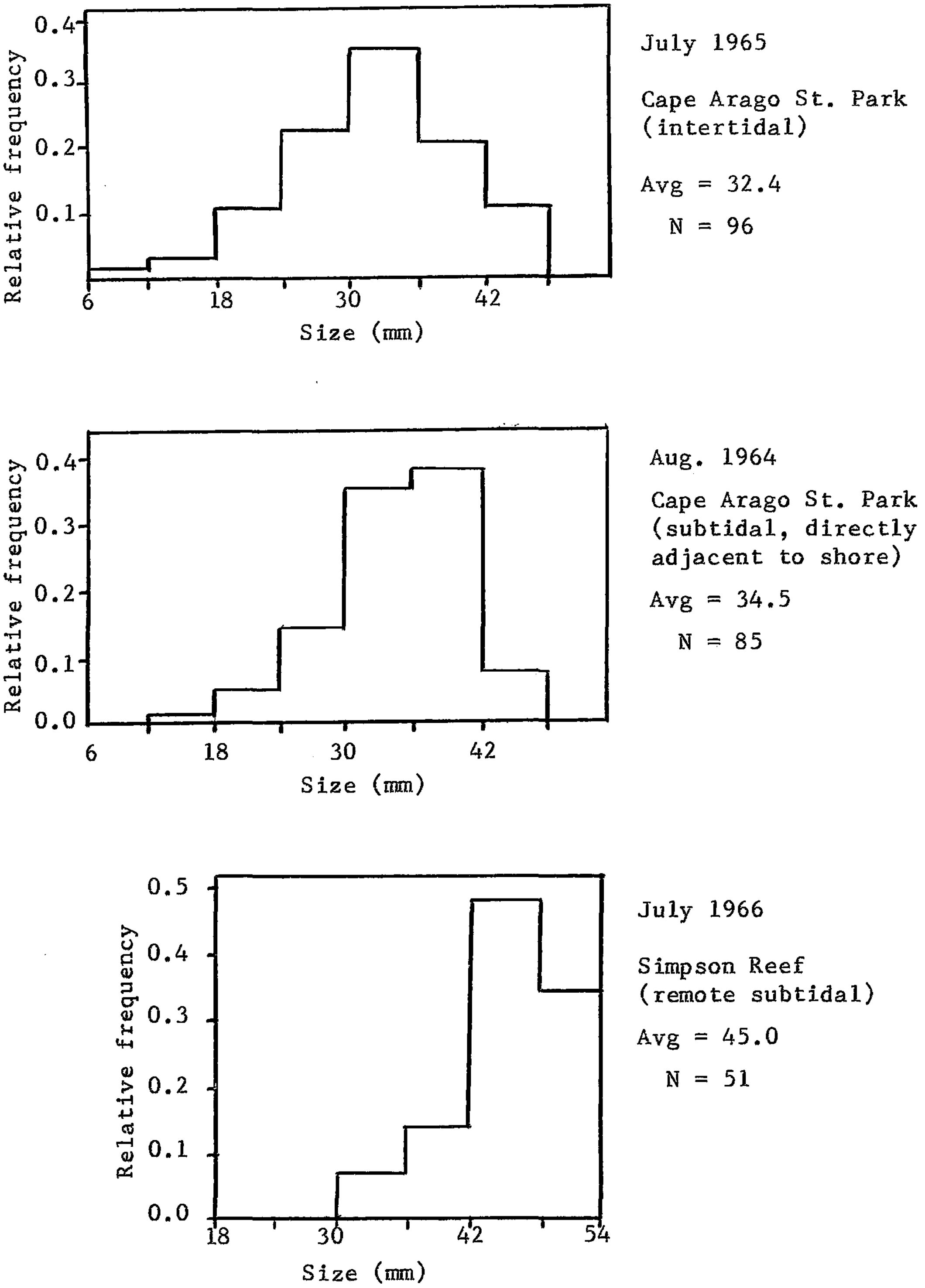


Figure 10.--Size-frequency distributions of Diodora. Size of limpet is the distance from the top aperture to the rear shell margin.

tides the chitons were somewhat harder to find beneath the heavy algal cover. Thus they appeared to have migrated out. If all the subtidal gumboot chitons were to crowd into the narrow intertidal zone each spring, their densities would be so much greater than in the winter months that there could be no doubt of it.

As the hosts provide the commensal with places in which to live, one would expect that the structure of the host population might influence that of the commensal. The average life span of a worm on Diodora is about 4 years. If this were a significant portion of the life span of the host, one would expect that some relation of age might exist between the two. It was thought worthwhile to examine this relation indirectly through size. In Table 22 correlation coefficients for size of worm on size of host for 4 samples of Diodora and 1 of Cryptochiton are presented. The length of the worm and the distance from the top aperture to the back of the shell of the limpet were used. The wet weight and cube root transformation (to approximate a linear measurement) of the chiton were used. It can be asserted that larger worms show some tendency to be found on larger limpets but not on larger chitons. The correlation of the smallest sample of Diodora (N = 25) is not significant at the 0.05 level, and that of the August 1964 sample is just significant at this level. The other two correlations are very significant. There is no indication that the correlation between chiton and commensal is significant. The hosts are more longevous than the commensals. Thus the original reason for expecting the host-commensal relation does not seem completely justified. Interestingly, the correlation of the intertidal sample (CAMC) is more significant than for the subtidal samples, and here the average age of host and commensal may be close. The most general suggestion may be that larger hosts are better hosts, and the worms grow larger on them. It may also be that the larger worms seek out larger limpets, to some extent, much as hermit crabs seek out larger shells.

Table. 22.--Correlation coefficients of the size relation of host and worm. Measurements used were length of worm; distance from top aperture to rear of shell for the limpet; weight(g) of the chiton and cube root of the weight.

Host	Date	Locale[a]	N	r	Remarks
Diodora	Aug. 1964	SR	50	0.286	$r_{50}(0.05)=0.273$
"	May 1965	CAMC	64	0.532	
"	July 1966	SR	50	0.417	
"	Feb. 1966	MR	25	0.207	$r_{25}(0.05)=0.381$
Cryptochiton	May 1965	SI	45	0.207	$r_{35}(0.05)=0.288$
"	May 1965	SI	45	0.129	cube root of weight

[a] See Figure 1.

Variation of Population Structure with Location, Host, and Species of Commensal

The extent to which the demographic variables of an organism vary as its habitat changes is an important component of its ecology, for it tempers the extent to which generalities and predictions may be made. In the present study it has been suggested that the basic pattern of occupancy for A. vittata is isolation of the large worms (longer than 20mm), which deny their hosts to smaller recently settled worms. In addition, it seems that commensals can attain a large size (+60mm) and an advanced age (+4 years) on a good host such as Diodora, though they may not do nearly so well on a poor host such as Cryptochiton. Will such a pattern be repeated in other locations, even those in which other hosts are an important part of the commensal's habitat?

This question was attacked by sampling commensals along the Pacific Coast at other stations than Cape Arago. Hosts were sampled at Friday Harbor, Washington and at Pacific Grove, California. A sister species, A. pulchra, was sampled at the above two stations and also at Punta Banda, Mexico. Samples were collected at least twice within the period of a year from these locations. All collections were from subtidal stations, except for Diodora at Friday Harbor. An additional single sampling was taken from the open Washington coast from three intertidal stations in the spring of 1967.

From the waters around San Juan Island, Washington, 91 Cryptochiton were collected. Of these, only three had commensals. Other host species collected at the same time were found to be much more heavily infested. On the other hand, from 120 chitons collected between September 1965 and March 1967 from the waters around Pacific Grove, 33 large worms were removed (Tables 23 and 24). This is an infestation of 0.28 large worms per host, which is quite comparable to that for the subtidal at Cape Arago of 0.25 worms per host (N = 117). The pattern of occupancy further conforms to that of Cape Arago in that there are no multiple occupancies of large worms. There is one striking difference between these southern worms and those from Oregon. The former are typically much larger, as large as the worms

Table 23.--Distribution of the number of A. vittata per host Cryptochiton collected in Washington and California. Entries are the number of hosts with the indicated number of commensals.

Date	Locality	Number of commensals per host 0	1	2	3	Total number of hosts
Sept. 1965 to March 1966	San Juan Is. region, Washington	88	3	0	0	91
May 1967	Open coast, Washington	80	17	0	0	97
Sept. 1965	Point Sur and Carmel Bay, California	39	9	0	0	48
Jan. 1966	Carmel Bay, California	20	9	0	0	29
Aug. 1966	" "	11	11	2	0	24
March 1967	" "	8	11	0	0	19

Table 24.--Distribution of the size of A. vittata from host Cryptochiton collected in California. Entries are the number of worms in the indicated size class.

Date	Place[a]	Size class of commensal (mm) 00-09	10-19	20-29	30-39	40-49	50-59	60-69	70-79
Sept. 1965	PS & CB	1	0	0	2	1	4	1	0
Jan. 1966	CB	0	0	3	1	2	1	1	1
Aug. 1966	CB	6	4	2	0	1	1	1	0
March 1966	CB	0	0	1	3	3	2	0	2

[a] PS = Point Sur; CB = Carmel Bay.

from Diodora at Cape Arago (Tables 4 and 24). Whether this is due to better growth or survival is not known. But since the infestation at Pacific Grove is about the same as at Cape Arago, one would suspect that growth is better in the former location. Small worms were abundant only in the August collection. There is the suggestion in Table 24 that settlement may be concentrated earlier in the summer than at Cape Arago (where abundant small worms are found in October), or that it may not be as extensive. The maximum density of small worms from Pacific Grove was 0.5 worms per host. At Cape Arago it was 2.5 worms per host.

In contrast to the situation around the San Juan Islands, Washington, the pattern of infestation on intertidal Cryptochiton collected from the exposed Washington coast was very similar to that found at Cape Arago. Of 97 chitons examined, 17 had single large worms within the size range found in Oregon. In the same period 69 intertidal Diodora were collected. The size range of these hosts was the same as that of the intertidal limpet hosts at Cape Arago. The large worm infestation was 0.84 worms per host.

Although Diodora occurs at both Pacific Grove and Friday Harbor, its habitat at Friday Harbor seems to be restricted to the intertidal, and at Pacific Grove it is very rare. In fact, only one specimen was collected from the latter location, but it was the largest Diodora collected during the whole study (56mm), and its worm was also very large (84mm; the largest worm collected was 90mm). At Friday Harbor no large subtidal concentrations of the limpet were discovered as were common in the subtidal at Cape Arago. The limpets were of a rather small size (modal class 30 to 39mm), about the minimum for the samples from the intertidal at Cape Arago. For the most part, the limpets at Friday Harbor occupied the levels above *Cryptochiton* and became rare at the level at which *Cryptochiton* became abundant. At Cape arago the two hosts overlap extensively in the intertidal, and *Diodora* often extends below the chiton subtidally, especially on vertical rock faces. The frequency of infestation with large worms was 0.68 worms per host (N = 37), about that which might be expected for intertidal limpets at Cape Arago. The pattern of occupancy was no different from that observed at Oregon (Tables 25 and 26). The one double occupancy listed in Table 25 consists of one worm 69mm and one 17mm in length.

Table 25.--Distribution of the number of *A. vittata* per host *Diodora* collected off San Juan Is., Washington in March 1966. Entries are the number of hosts with the indicated number of commensals.

Number of worms per host				Number of hosts
0	1	2	3	
10	26	1	0	37

Table 26.--Distribution of the size of *A. vittata* from *Diodora* collected off San Juan Is., Washington in March 1966. Entries are the number of worms in the indicated size class.

Size class of commensal (mm)						
00-09	10-19	20-29	30-39	40-49	50-59	60-69
1	1	3	2	10	6	4

The predaceous starfish, Solaster stimpsoni, is rather abundant at Friday Harbor in contrast to its relative scarcity at Cape Arago, where it has been collected only occasionally. It occurs in approximately the same region as does Cryptochiton. Perhaps the subtidal scarcity of Diodora may be associated with the abundance of Solaster. In any case, good samples were collected in November 1965 and March 1966 (Tables 27 and 28). Settlement in the latter part of the year is certainly indicated. The relative abundance of the small worms underscores their absence on Cryptochiton at this time. If I could find both hosts lying within a few meters of each other on the sea bottom, why couldn't or wouldn't the settling worms be able to do likewise? Solaster is certainly not an exceptionally good host. The largest worm recovered from this starfish was only 37mm in length, and the frequency of large worms decreased to Cape Arago Cryptochiton levels by April. As is the case with the worms from Cryptochiton at Cape Arago, there is not the rationale of bimodality in the size frequency distribution (Table 28) which suggests a demographic break at 20mm (as there was for worms from Diodora). In Cryptochiton, however, it could be shown that multiple occupancy of worms larger than this size did not occur. In the sample of worms from Solaster in November there is some multiple occupancy of worms in the 20mm size class. As Table 27 indicates, most of the multiple occupancy is due to the smaller worms, and the numerical distribution of all worms is not significantly different from a random one ($P > 0.10$). Yet the overall pattern does seem to be consistent with the notion that the large worms tend to become isolated. There is, after all, no magical reason

Table 27.--Analysis of the distribution of the number of A. vittata per host Solaster collected off San Juan Is., Washington. Entries are the number of hosts with the indicated number of worms.

Time	Worm category	Number of worms per host						
		0	1	2	3	4	5	6
Nov. 1965	All sizes	13	13	10	5	1	0	1
	Less than 20mm	22	12	5	3	0	1	0
	Greater than 20mm	23	17	3	0			
March 1966	All sizes	28	15	3	0			
	Less than 20mm	33	13	0				
	Greater than 20mm	38	8	0				

Table 28.--Distribution of the size of A. vittata from Solaster collected off San Juan Is., Washington. Entries are the number of worms in the indicated size class.

Time	Size class of commensal (mm)			
	00-09	10-19	20-29	30-39
November 1965	9	27	17	6
March 1966	1	12	6	2

for dividing large and small worms at exactly 20mm. If 24mm were chosen then there would be no doubles of large worms on Solaster. The arms of a Solaster may offer more refuge space and thus the contact between the worms may be less than on Diodora and Cryptochiton, and so regularity of occupancy may be established at a slightly larger size. Until evidence to the contrary is presented, the best interpretation of the data is that the same tendencies towards isolation also operate for the worms on *Solaster*.

Solaster itself has a size frequency structure that is like that of both *Diodora* and *Cryptochiton* (Table 29). The population is comprised chiefly of large animals in both fall and spring. It is suspected that this represents a population of longevous animals as was argued for the principal hosts at Cape Arago. Without a knowledge of growth, however, this must remain conjecture. The few *Solaster* collected at Cape Arago are in the size range of those gathered at Friday Harbor. The commensals from these seem to be drawn from a population with a similar infestation rate and size frequency distribution. This indicates that the quality of the starfish as a host did not decline with location as *Cryptochiton* did.

Table 29.--Distribution of the size of *Solaster* collected off San Juan Is., Washington. The measurement used was the width of the disk (mm). The entries are the number of starfish in the indicated size class.

Time	Size class of *Solaster* (mm)					
	50-59	60-69	70-79	80-89	90-99	100-109
November 1965	1	11	14	16	1	0
March 1966	0	1	12	17	11	5

A widespread, but never abundant, host is the starfish *Dermasterias imbricata*. It occurs at all the stations mentioned above. It was the most difficult to locate at Cape Arago, although it is more common at Harris Beach State Park, Oregon, 135 kilometers south of Cape Arago. It was most common at Punta Banda, where it was host to A. pulchra. At the other stations only A. vittata have been removed from it. Although only 36 have been collected from all stations, the following observations seem in order. The frequency of infestation is rather high, perhaps typically over 0.80 large worms per host. In size, the large worms are intermediate between those found on Diodora and Cryptochiton (or Solaster). If there is a large worm on a host, the others, if any, are considerably smaller. The pattern of occupancy on this host also conforms to the general pattern of regularity.

A. pulchra is very similar in size and general appearance to A. vittata. The less pigmented representatives of the two species could only be distinguished with certainty by counting and observing the tips of the superneural setae (Hartman, 1948; Skogsberg, 1942). The ranges of these two scaleworms overlapped in the area studied. At Pacific Grove they compete for the same host, Megathura crenulata. At Punta Banda no A. vittata were collected, although the southern limit is Equador (Hartman, 1939). In Tables 30 to 35 the pattern of occupancy and size frequency distribution of these commensals is presented. Size measurements of Megathura and Stichopus were not made for practical reasons; however, all populations of these hosts consisted virtually only of large individuals, as have the populations of all other hosts of this study with the partial exception of some intertidal populations of Diodora. The size structure of these populations suggest stable populations of longlived individuals. Megathura is essentially a large Diodora with a permanently reflexed mantle. It apparently replaces Diodora ecologically in the South. It seems

Table 30.--Distribution of the number of *A. pulchra* and *A. vittata* on *Megathura* collected at Pacific Grove, California in 1966. Entries are the number of hosts with the indicated number of worms. Only one entry is made for the category of no worms per host since it can not be said which species is absent.

Time	*Arctonoe* species	Number of commensals per host			
		0	1	2	3
Aug.	*A. pulchra*	2	7	2	0
Aug.	*A. vittata*		7	3	1
Dec.	*A. pulchra*	1	10	0	
Dec.	*A. vittata*		6	0	

Table 31.--Distribution of the size of *A. pulchra* and *A. vittata* on *Megathura* collected at Pacific Grove, California in 1966. Entries are the number of worms in the indicated size class.

Date	*Arctonoe* species	Size class of commensal (mm)							
		00-09	10-19	20-29	30-39	40-49	50-59	60-69	70-79
Aug.	*A. pulchra*	1	1	2	1	4	2	0	
Aug.	*A. vittata*	4	4	0	2	2	1	2	1
Dec.	*A. pulchra*				1	4	3	1	1
Dec.	*A. vittata*				2	0	0	3	1

Table 32.--Analysis of the number of *A. pulchra* per host *Parastichopus* collected off San Juan Is., Washington. Entries are the number of hosts with the indicated number of commensals.

Time	Worm category	Number of commensals per host				
		0	1	2	3	4
November 1965	All sizes	8	26	6	2	0
	Less than 20mm	24	15	3	0	
	Greater than 20mm	21	21	0		
March 1966	All sizes	32	13	1	0	

Table 33.--Distribution of the size of *A. pulchra* from *Parastichopus* collected off San Juan Is., Washington. Entries are the number of worms in the indicated size class.

Date	Size class of commensal (mm)				
	00-19	10-19	20-29	30-39	40-49
November 1965	8	15	13	7	1
March 1966	0	2	9	4	0

Table 34.--Analysis of the distribution of the number of *A. pulchra* per host on 3 of its hosts collected at Punta Banda, Mexico in August 1966. Entries are the number of hosts with the indicated number of worms.

Host	Worm category	Number of commensals per host				
		0	1	2	3	4
Megathura	All sizes	2	17	0		
Parastichopus	All sizes	7	2	5	2	1
"	Greater than 20mm	13	4	0		
Dermasterias	All sizes	0	5	6	1	3
"	Greater than 20mm	8	7	0		

Table 35.--Distribution of the size of *A. pulchra* from 3 hosts collected at Punta Banda, Mexico in August 1966. Entries are the number of commensals in the indicated size class.

Host	Size class of commensal (mm)					
	00-09	10-19	20-29	30-39	40-49	50-59
Megathura	0	2	1	6	6	2
Parastichopus	9	9	4	0		
Dermasterias	8	18	6	1	0	

likely that the growth rates of the two may be comparable (in time to reach modal size), in which case this keyhole limpet would be rather longevous.

The Megathura collected at Monterey Bay were found to harbor individuals of either species of Arctonoe but not both (Tables 30 and 31). The host was approximately equally divided between the two species. A. pulchra does not compete, at least at all successfully, for occupancy of Cryptochiton which occurs in the same habitat as Megathura or, further north, on Diodora. In a combined size distribution of these commensals from Megathura the two species cannot be distinguished as two different modes (Table 31). It is clear in Table 30 that the pattern of occupancy on this host is the same for both species--isolation of the large worms. In fact, for virtually all hosts of A. pulchra, if the occupancy of the worms is examined in terms of size, 20mm will separate single from multiple occupancy. This size was chosen from experience with A. vittata, yet it seems to apply to A. pulchra also! Most of the small A. pulchra were collected from hosts which only occasionally harbor a large worm. In addition, on Megathura, which produces the largest worms, small worms are not too common. These observations can be interpreted in terms of a negative worm-worm interaction, similar to that proposed for A. vittata.

Parastichopus californicus which is host to A. pulchra at all collecting stations was never found to harbor A. vittata. The pattern of occupancy on this host follows the same lines as A. vittata on Cryptochiton or Solaster (Table 32). In what seems to be the settling season at Friday Harbor (summer-fall), there is a unimodal distribution of the worms from very small (4mm) to moderately large (30-40mm). Later in the year the number of vacancies has increased but the modal class is not larger (Table 33). At Punta Banda there were two other hosts which provide a basis for comparison of population structure (Tables 34 and 35). The infestation rate is higher on Megathura than on Parastichopus and the average size of the worms is greater. The worms from Dermasterias are intermediate in these respects. These observations suggest a demographic parallel between the commensal populations on Diodora and Megathura on one hand, and Cryptochiton (or Solaster) and Parastichopus on the other. Both species of commensals seem to have a good host and a poor host. Members of the good host species nearly always harbor a single large commensal. Members of the poor host species only occasionally harbor a smaller large commensal. Both good and poor hosts may be multiply infested by small worms in the season of settlement. There is a further extension of this parallel in that in both cases the good host did not seem to be as abundant as the poor host. Generally Diodora and Megathura were more difficult to find and collect in numbers than Cryptochiton or Parastichopus. At Friday Harbor it is possible that Solaster is more abundant than Diodora, although they do not seem to be as abundant as Diodora at Cape Arago. Whether there is ecological significance in this observation is not certain. That both Arctonoe species compete for the good host, Megathura, at Pacific Grove could suggest that the limpets are more important to the reproductive success of the commensals than the other hosts.

Are any of the population features of *A. vittata* and *A. pulchra* common to other commensals? This aspect of the problem was probed by the examination of three other commensals, *A. fragilis*, *Podarke pugettensis* (a hesionid worm), and *Fabia faba* (pinnixid crab).

A. fragilis is quite different in appearance from either *A. vittata* or *A. pulchra*. This species was not very common at Cape Arago and was collected only occasionally. It was found on *Pisaster ochraceous*, the common purple star, and on *Evasterias troschelli*, a starfish of similar appearance. A total of 316 *Pisaster* were collected and examined, but only seven commensals were recovered. These were distributed one to a host. Eight of 27 *Evasterias* produced commensals, which, also, were distributed one to a host. It seems that one can make the beginnings of a case for the regular distribution of this commensal on the basis of these numbers.

There can be little doubt that the pinnixid crab was distributed in a regular manner. In a sample of 47 host *Schizothaerus nuttali* (*Tresus capax*?) collected from South Slough of Coos Bay, Oregon there were 46 male-female pairs, which were distributed one pair to a host, and a single female crab in one clam. When the size of the commensal (width) is plotted against that of the host (length), there is a fairly striking regression (Fig. 11). The significance of the one very deviant crab pair from the largest host is not clear, though it may suggest that the crabs grow up with the clams and that reinfestation occurs only in very old large clams. In any case, the plot of male crab size versus female crab size (Fig. 12) adds to the feeling that this is a very orderly population demographically. The

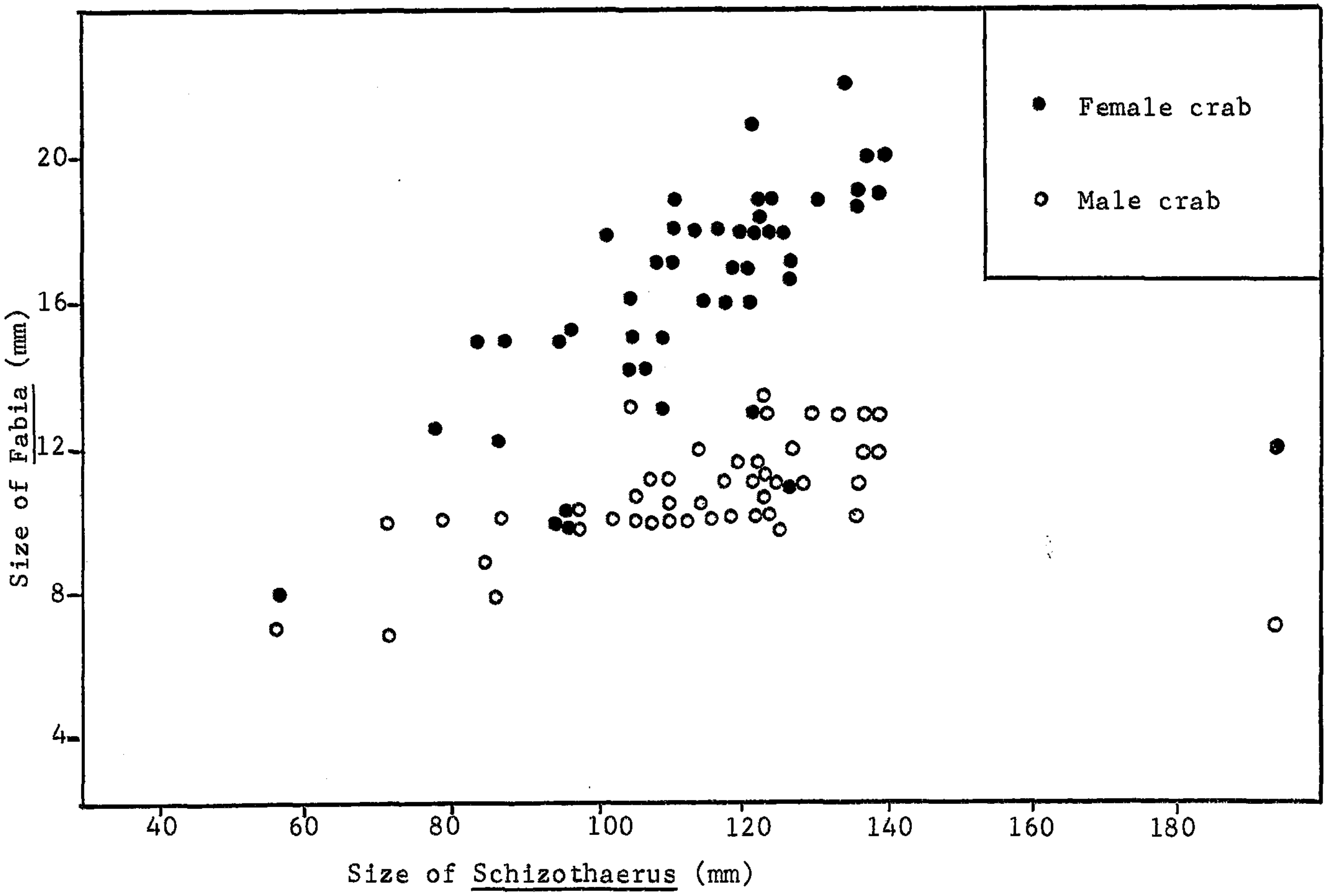


Figure 11.--Size of _Fabia faba_ and size of host _Schizothaerus_. Size of crab is width of carapace. Size of clam is length of shell. Collected from South Slough, Coos Bay, Oregon in August 1965.

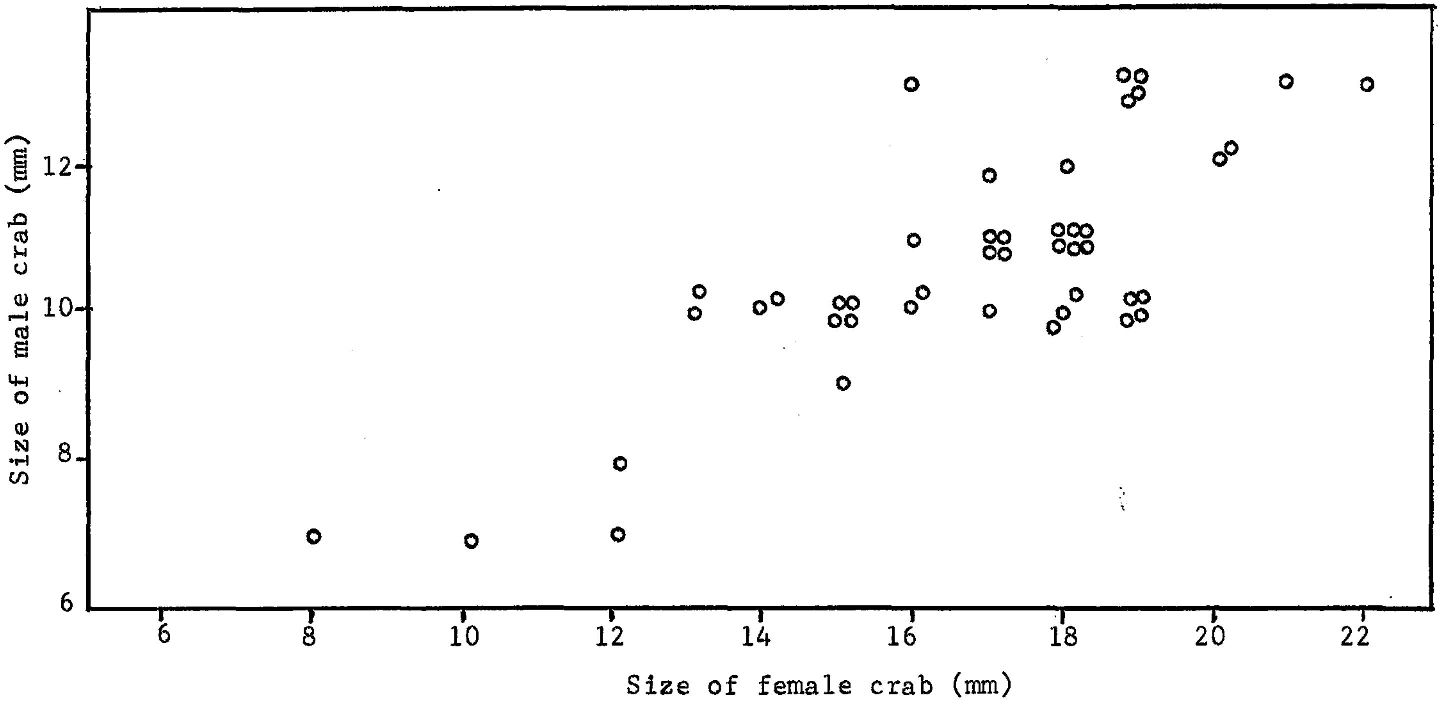


Figure 12.--Size of the male and female Fabia collected from Schizothaerus. There was a single pair in each host.

regularity of distribution and relation of commensal and host size are reminiscent of *A. vittata* on *Diodora*.

Podarke, on the other hand, is not at all like *Arctonoe* or *Fabia*. In relative size (compared to its host), it is much smaller. Several could be collected from a single host, either *Patiria miniata* or *Solaster stimpsoni*, in this study. In addition, it is known to be freeliving (Davenport, 1960). A further interesting difference is that the populations of this worm on *Solaster* at Friday Harbor seemed to be seasonal. Although they could be found in November of 1965, none could be found in April of the following year. They were observed in September, January, and March at Pacific Grove. The populations of *Arctonoe* on *Solaster* and *Parastichopus* may also decline, but they do not disappear. An analysis of a sample of *Patiria* (N = 39) is presented in Tables 36 and 37 and Figure 13. The occupancy is not regular but tends toward aggregation. This trend is accounted for mostly by the one observation of 14 worms, but this is the nature of aggregation. No relation could be found between the size of the host and any reasonable parameter of the commensal population, except possibly the number of worms per host (Fig. 13, c). However, this hypothesis should be investigated by a sampling program which deliberately includes a much larger proportion of small hosts. There seem to be no demographic parallels between this commensal and the others of the study.

Table 36.--Distribution of the number of Podarke per host Patiria collected at Pacific Grove, California in March 1967. The $S^2/\overline{X}$ statistic for these data is 1.54. The P value is between 0.01 and 0.05. The worms tend to be aggregated.

Number of worms per host	Number of hosts
0	2
1	0
2	3
3	3
4	6
5	6
6	10
7	2
8	2
9	1
10	2
11	2
12	0
13	0
14	1

Table 37.--Distribution of the size of *Podarke pugettensis* from host *Patiria* collected at Pacific Grove, California in March 1967.

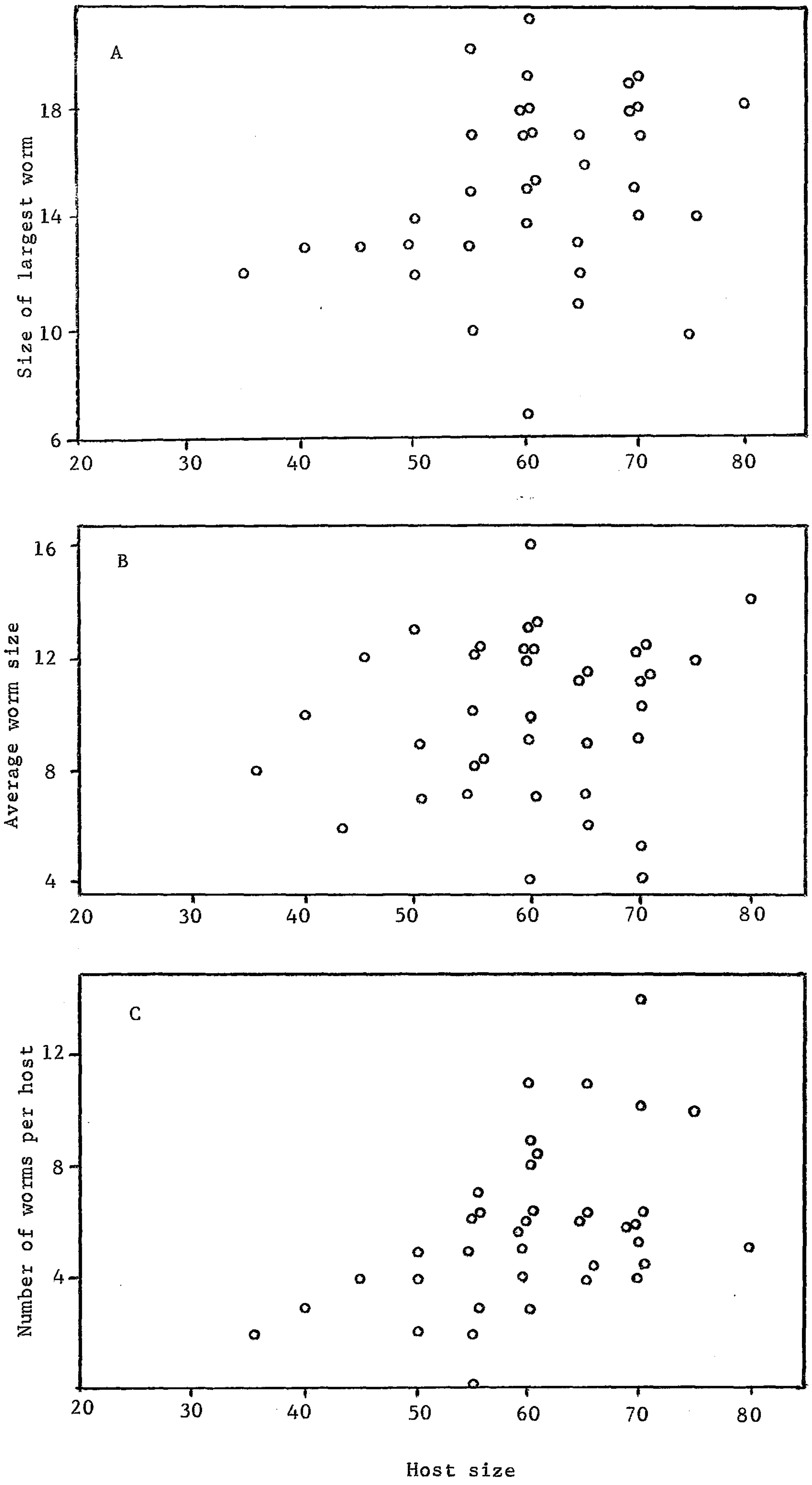
Size of worms (mm)	Number of worms
2	1
3	16
4	16
5	20
6	7
7	15
8	6
9	8
10	19
11	12
12	19
13	13
14	10
15	14
16	5
17	10
18	5
19	4
20	1
21	1

Figure 13.--Analysis of a sample of Podarke pugettensis and host Patiria miniata collected from Monterey Bay, California in March 1967. Host size is the length of the longest radius. Worm size is length of worm.

a) Host size and size of largest worm on host.

b) Average size of all worms on a host and host size.

c) Number of worms per host and host size.


A
Size of largest worm
6
10
14
18
B
Average worm size
4
8
12
16
C
Number of worms per host
4
8
12
20
30
40
50
60
70
80
Host size

SUMMARY AND DISCUSSION

The major group property examined was the static one of population distribution. The habitat of a commensal is conveniently defined (the host) and, as a consequence, it is possible to develop fairly conclusive and "natural" statements about its distribution. Although there is no necessary relationship between distribution and the dynamic attributes of natality and mortality, it must be expected that together they will fit into a consistent whole when integrated with pertinent facts of the natural history and behavior of the organism. In the present context, it was necessary to consider natality equivalent to recruitment of recently settled worms onto the hosts, since larvae were not dealt with directly. Furthermore, for *A. vittata* it seemed reasonable to speak of recruitment of the small worms (less than 20mm in length) into the population of large worms. Typically, mortality is the most difficult property of a population to deal with because it represents a summation of events (deaths) which may be difficult to attribute to any single time or cause. Mortality and longevity of the large worms were approached indirectly through turnover time of the population. As the hosts represent places in which the commensals live, certain aspects of their ecology were investigated, namely growth rate and size distribution.

The statements which describe the population ecology of commensal and hosts can be summarized: 1) The distribution of the large worms is regular. There is no more than one per host. 2) Small worms show multiple occupancy that may be random but tends toward regularity. 3) These small worms are recently settled and represent the basic recruitment into the population on the hosts. Settlement occurs in the summer and fall. 4) The infestation frequency of the large worms is higher on *Diodora* (0.75 to 1.00 worms per host) than on *Cryptochiton* (0.10 to 0.25 worms per host), and the worms are larger on the limpet host. 5) The turnover time and average age of the large worms on *Diodora* was estimated at about 4 years, and on *Cryptochiton* 1 year. 6) Mortality of the small worms is about 40 times that of the large worms on *Diodora*. The mortality of the small worms is associated with the presence of the large worm that is nearly always present on subtidal *Diodora*. The mortality of the small worms on *Cryptochiton* is about the same, but cannot be often associated with the large worms. 7) Large worms typically show host fidelity, but some vagility has been demonstrated. 8) Both hosts are more longevous than the commensal and, on a year-by-year basis, provide an essentially constant number of places in which to live.

I am confident that I will never observe two large worms on a single *Diodora*. If I do, I shall regard it either as a prank or a horrible abnormality of nature. I maintain this even though I did not set up an exact model of randomness for the worms on *Diodora*. Such a model would resemble an aggregate of binomials with n = 2, 3, 4, or 5. With infestation rates of about 0.80 worms per host, one would expect between 10 and 100 doubles in the total of *Diodora* sampled. None were observed. It is simply very difficult to believe that they were not observed merely because of sampling error. A formal test was argued for the worms on Cryptochiton, and a significant P value was extracted. However, in spite of the formal test, I do not feel that this is as convincing as the data from Diodora. One could argue against my contention that n = 5 as maximum occupancy makes good ecological sense. I maintain this only on the spatial grounds of fitting organisms (commensals) into sample space (hosts). If the formal test is rejected, the data do not speak for themselves as loudly as do the data from Diodora. The two together (data from Diodora and Cryptochiton), of course, make a very good case for the regularity in the distribution of the large worms in that the obvious complements the formal.

But how predictive is the statement about regularity in distribution? Does it apply wherever A. vittata is found? On the other hosts examined, Solaster, Dermasterias, and Megathura it seems to be true. A. pulchra, also found on the last mentioned host, appears to be distributed in isolation from its fellows. This strengthens confidence in the rule, for it may be a property of more than one species in the genus. In fact, I have not seen a single case in the literature which implied that commensal polynoids were not regularly distributed on their hosts (Davenport and Hitchcock, 1951; Davenport, 1953; MacGinitie and MacGinitie, 1949; Hornell, 1895). Such reports, though not based on extensive and careful sampling, tend to confirm the notion of regularity in distribution and lead me to assert that probably all commensal polynoids are isolated from each other on their hosts. Hornell sums up the collector's anticipation: "Each (Spatangus) we search eagerly with shrewd idea of the result. Yes, there on the under side, clinging flat and close to the test is a pretty, inch-long scale worm, Polynoe castanea...the number on each host being limited to a single individual."

The tendency toward regularity in the multiply distributed small worms is certainly not strongly established in a formal manner, yet it seems to be real. In nine samples (Table 8), differences in the distributions from a random model were not apparent at the 0.01 level. At the 0.05 level, however, four samples were significant in the direction of regularity. Such behavior is consistent with the occasional aggressive behavior of the small worms toward each other in the laboratory. The isolated habit of the large worms also strengthens the belief that this slightly expressed tendency toward isolation is real. Regularity is typically taken to imply aggressive behavior (Odum, 1959; Connell, 1963) and vice versa, although for plants this is not necessarily so (Pielou, 1960). Field data (Tables 10 and 11) show quite clearly that the large worms do interfere in some way with the size and numbers of the small worms. The possibilities are i) cannibalism, ii) exit of second worms if a large one is present, and iii) inhibition of the growth of the small by the large. The last effect has been reported in one commensal situation (Pearce, 1962). Which really does occur is not clear from the data. Given the celebrated pugnacious dispositions of scaleworms in general (Essenburg, 1917-1918; MacGinitie and MacGinitie, 1949), the most likely possibility would seem to be i, ii, or both. Only behavioral studies can really decide. Demographically, there is little doubt that the negative interaction occurs.

There is some evidence to suggest that the frequencies of large worm infestation on Diodora and Cryptochiton tend to be constant in time and space. If this is true it is another indication of the demographic stability in the rocky littoral region, and consequently of the general stability of this community as a whole (Castenholz, 1967; Frank, 1968). Tucker (1964) reports that of 237 Cryptochiton collected for physiological study between 1957 and 1959 in the Monterey region, 14% had scaleworms. These were collected from an intertidal location. This is almost the same infestation rate for large worms as in the intertidal at Cape Arago and the open Washington coast. All collections at Pacific Grove (Carmel Bay) were from subtidal stations, and the rates of large worm infestation were the same as from the subtidal at Cape Arago. Also from the Pacific Grove area, Ricketts (1962) reports that more than 25% of the Cryptochiton may have a scaleworm. He does not state how many chitons he looked at, and whether he actually observed more large worms or merely more of the smaller is not certain. His observations fall in the period between 1925 and 1945. For more than a quarter of a century, as far as can be told, the infestation rate of Cryptochiton at Pacific Grove was rather constant (14% to 25%), below the maximum level of 1 worm per host and about the same as observed at Cape Arago, Oregon.

I have found no records of infestation frequencies in the Cape Arago region. One hundred years ago the infestation rate of A. vittata on Diodora was estimated by Lord on Vancouver Island to be 4 out of 6 (see Introduction, p. 1). This was, of course, for intertidal limpets, and is well within the range of infestation frequencies observed at

Cape Arago in the intertidal. In 1962, 64 A. vittata were removed from 144 intertidal Diodora by a student at Friday Harbor Laboratories (Porcaro, 1962). In 1966, I collected 25 large worms from 37 hosts--almost the same ratio that Lord records. As far as one can be certain, the infestation frequencies of the commensal on Diodora in this region have remained about the same for a century. The rates on the limpet in the subtidal are very close to complete occupancy. It may well be worthwhile for observations of the frequency of infestation on subtidal and intertidal keyholes to be made every few years for a long period of time. I would expect that the rates in the subtidal would stay close to the maximum, while those in the intertidal would fluctuate below this level as they do in location at a given time.

The one anomaly in the constancy of infestation rates is the very low frequency of the worms on Cryptochiton in the San Juan Island region. There are no records to indicate whether this represents a stable local condition or whether it is a fluctuation in level of infestation. What is strange is that recruitment at the time of collection was fairly extensive on Solaster, whereas the chiton produced hardly any small worms, let alone large ones. Perhaps there is a behavioral preference for the starfish over the chiton. There was no indication of such a situation at Cape Arago.

When broad comparisons are made, the larger of the large worms seem associated with the higher frequency of infestation. On Diodora, the host where infestation is the highest, the average size of the worms is the greatest. This is true both of interhost comparison against Cryptochiton and of an intrahost comparison, intertidal against subtidal. A connection between the two factors may exist: Low frequency of infestation implies high mortality. This means less time on the average to grow, and therefore smaller average size. Of course, it is possible that the growth rates of the commensal are different on the two hosts between the two regions. This is not suggested by the work on growth rates, but a larger study might reveal subtle differences not detected in this work. The worms from Cryptochiton at Monterey are larger than those at Cape Arago although the infestation frequencies are the same. This could be due to differences in growth rates at the two stations.

The reliability of the estimate of turnover time depends upon the nearly complete occupancy of subtidal Diodora by large worms and complete recruitment by the small worms in every year. As has been pointed out, these conditions seem to be met in the subtidal off Cape Arago. In addition, the generality and accuracy of the growth curve for the worms must be accepted. Of the quantitative estimates in the present study, this is based on the fewest data but the most work. Four years was taken as being the best estimate of turnover time and average life span of A. vittata. This average is about in the middle of some ages for marine annelids reported in the literature. These range between 18 months and 6 years (Blevgvad, 1928; Thamdrup, 1935; Newell, 1947; Mayer, 1902; Dales, 1951). Although one cannot apply the argument to the worms on the chiton host (occupancy of the large worms is hardly complete), nearly all large worms are in the one year size class or smaller. This suggests that these worms live no longer than a year. Thus severity of the environment may be most important in determining the life span of this commensal. This situation is almost axiomatic for organisms that do not experience an abrupt senility or death at spawning.

Mortality of the small worms (those less than 20mm) was relatively high and about equal on both hosts. Yet, it is strongly suspected that the sources of mortality are different in the two cases. A second worm is never greater than 20mm and, in addition, the presence of large worms on a population of hosts may be associated with a reduction in the numbers of smaller worms. As the large worms are omnipresent on subtidal Diodora, it would seem that they are the prime cause of small worm mortality on that host. A q_x function is presented in Figure 14. The first stage of the plot represents high larval loss in the plankton (I estimate from size calculations that a female A. vittata may produce over 100,000 eggs). The broken lines of the last section reflect an ignorance of age specific mortality in the larger, older worms. A similar plot for mammals begins to rise for older animals (Caughley, 1966). I have not shown any "comfort zone" for large worms on Cryptochiton. A worm which reaches the size of 20mm on Diodora has the next few years more or less guaranteed. On Cryptochiton the same size worm may well be gone within the year even if there is no large worm present.

Vagility of the large worms has been observed to be a fact. As I am not convinced that any large population of freeliving worms exists, I believe such movement is mostly between hosts; although, since worms need not settle directly on the host, it is possible that they grow to a considerable size off any host. There is some

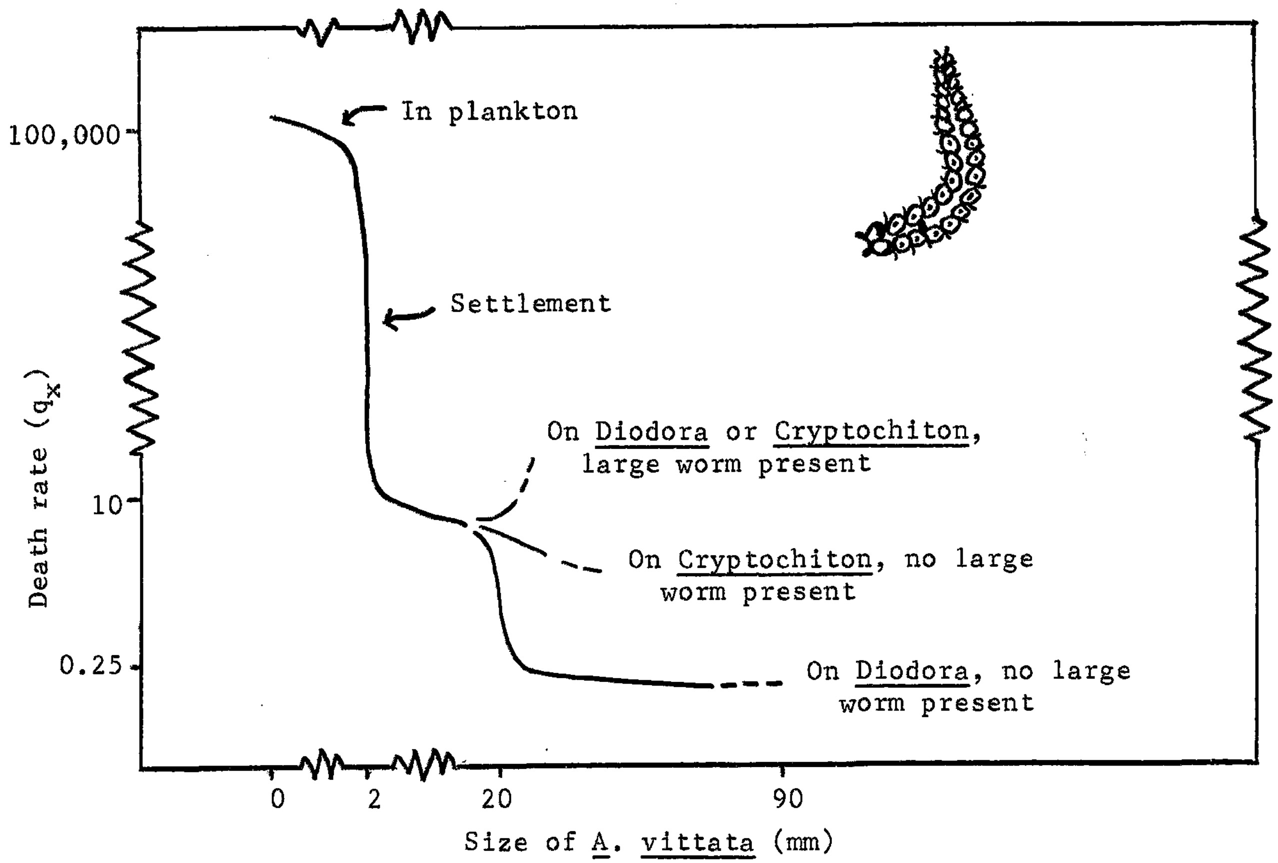


Figure 14.--Death schedule (q_x) for A. vittata on Diodora and Cryptochiton. Number of worms per host.

experimental verification of worms moving from one host to another in the field. Such behavior cannot really be regarded as classical migration, unless it occurs from one host species to another and one regards the worms on each host as separate populations. In any case, field verification of vagility involves only Diodora. From what has been said, a worm from a chiton might well welcome a place on a keyhole limpet. However, there is not very much available limpet space. The only field data which may suggest that vagility may play some observable role in the population ecology of the scaleworm is the significant correlation of worm size to Diodora size. This may only mean that a larger host can support a larger worm and so the worm may grow to this larger size. But it may be that the worms act like hermit crabs and select a larger host when the opportunity presents itself--perhaps when two hosts come into contact.

The conclusion that the hosts are longer lived than the commensals, so that the two cannot grow up together, follows from the growth curves obtained from marked hosts, the size distributions of the hosts, and the fact that recruitment to these populations seems to be very low. Without the growth curves, the claim to longevity (life span in excess of ten years) is based only on inference and the assumption that one is observing a stable population. If a stable population has little recruitment it must have little mortality, and if most of the organisms are large they must be old. But there is no way to tell without sampling over a long period of time if a population is stable. In fact, even having an estimate of individual growth will not allow one to determine, given the information available here, if the populations are stable. It is possible to say, however, that if the hosts' populations fluctuate, they do so slowly, and will, at least, exhibit short range stability. Thus, relative to the commensal life span, Diodora and Cryptochiton represent a fixed number of places in which commensals may live. All the other hosts, Solaster, Dermasterias, Megathura, and Parastichopus seem to have the same type of population structure as these two hosts. The best hypothesis, until field growth curves are developed for these creatures, is probably to regard them as longevous also.

There is some evidence now to believe that relative longevity may be rather common for many marine invertebrates (Darby, 1964; Frank, 1965b and 1967; Ebert, 1967). Two more common marine invertebrates may now be added to the list, and three others seem likely candidates. Such longevity may explain much of the apparent stability of the rocky littoral community. Of course, not all littoral populations are longevous (Frank, 1965a; Connell, 1961) or stable (Cole, 1957), yet many may turn out to be so.

The manner in which the populations of A. vittata are regulated can be put equally well in the language of Andrewartha and Birch (1954) or the density regulative school (Nicholson, 1954; Richards, 1961). Perhaps one should not try to shed light on this ancient controversy, but it does seem to account for much of the life of ecology. First, one can say that the places in which to live definitely set the limits of the population. In fact, $W = cH$, where W is the number of worms, H is the number of hosts, and c is a constant dependent on host and habitat (tidal or subtidal). This statement "explains" the worm numbers. Since occupancy is nearly complete on subtidal Diodora, the explanation of population regulation is virtually complete when one notes that interaction with other animals of the same kind sets the occupancy of the places in which to live at one large worm. For the case of the worms on Cryptochiton, it must be noted that the population level is considerably below that which the number of places in which to live would allow. Borrowing another term from the above water world of thrips, this may be explained by some (not clear) interaction of the weather and the places in which the animals live which reduces the quality of the hosts. The regularity of the distribution of the large worms on the chiton indicates that limiting interaction with animals of the same kind is still operating in this part of the habitat, but not as strongly, since each host is not occupied.

On the other hand, there is no doubt that this situation is density dependent regulation. There is a very effective feedback to the recruitment from the large worm density when that density reaches one worm per host. The sub-population on Cryptochiton seems to be subject to some legislative source of mortality which does not operate on Diodora. The relative extent to which the worms on Cryptochiton participate in reproduction is not known. It may be that they are non-reproductive individuals living on the fringes of the habitat.

As pointed out by Malthus, all organisms which reproduce by generation and are increasing, are increasing geometrically (if conditions remain unchanged). "Misery and vice" must increase proportionately to this increase. The argument is axiomatic. When a population is stationary, one must imagine that misery and vice (cannibalism?)

exactly balance some potential to increase. Some, such as Wynne-Edwards (1962) believe that symbolic misery and vice are substituted for actual. In fact, Wynne-Edwards (1967) feels that this is true "even for the marine worms at the bottom of the scale." If worms, the scale of A. vittata, merely crawl out of an occupied host, he may be right in a sense. However, if small A. vittata are eaten, battered, or come to some unpleasant end after leaving their prospective host, we might better accept the terminology of Malthus. In either case, the regulation is density dependent.

Is this density dependent view really inconsistent with the controlling four-fold division of the environment given by Andrewartha and Birch? As the example of A. vittata shows, both views can be entertained by the same data. As Nicholson (1957) points out, Andrewartha and Birch's analysis may be useful in explaining fluctuations in population numbers (and, I would add, extinctions). The Andrewartha and Birch approach is probably quite adequate for regression studies of population and chosen parameters of the environment, but not for philosophical discussion of what goes on in the semi-long run. The long run is not an equilibrium situation, as is assumed for density dependence. It is a changing evolutionary situation and beyond the pale of the present discussion.

However, one can speak of the adaptive significance of the regular distribution of the large worms. To what extent is this a common feature of commensalism? There exists apparently no review of regularity of distribution as a feature of commensalism. Emphasis is put on life history features and behavior rather than quantitative features of distribution in most works on parasitism and commensalism (Baer, 1951; Caullery, 1952; Dales, 1966; Davenport, 1966). Only Williams (1964) discusses distribution of some ectoparasites at length and reviews a fair number of cases from the literature. However, none of his examples are of regularly distributed animals. The general opinion stated in most ecological texts is that aggregation is the common mode of distribution of organisms in nature. "Contagious distributions are the rule in nature" (Allee et al, 1949); "Various degrees of clumping are characteristic of the internal structure of most populations at one time or another" (Odum, 1959); "The distribution of individuals may be more regular than random expectation, though this is very much less commonly found" (Greig-Smith, 1964). I do not wish to dispute the generality of this ecological dictum except to point out that for a number of commensals it may not be true at all. In addition to those polynoids which appear to have a regular distribution, Table 38 presents a compilation of commensals which seem to be regularly distributed. Often the distribution was of no special interest to the worker and the regularity of the distribution was only implicit in the author's discussion.

It is possible that habits which lead to regularity are of no adaptive value. Thus one might simply write off the regular distributions of commensal polynoids as a consequence of their predatory and belligerent nature. Such an explanation would not do for the pinnixid crabs, since it does not account for the reported fact that adult female crabs inhibit the development of the younger crabs so that only a single adult female is found on a host (Pearce, 1964). Of course

Table 38.--Cases of the regular distribution of commensals.

Commensal	Host	Author
Scaleworms:		
Polynoe castanea	*Statangus*	Hornell, 1895
Lepidasthenia	*Amphitrite*	Orton, 1935
Hesperonoe adventor	*Urechis*	MacGinitie and MacGinitie, 1949
H. complanata	*Callianassa*	"
Arctonoe fragilis	*Evasterias*	Davenport, 1951
Acholoe astericola	*Astropectin*	Davenport, 1953
Hesionid polychaete	Holothurian	Ganapati, 1945
Sipunculid worm and polychaete	Mitridae shells	Knudsen, 1944
Amphiprionidae	Sea anemones	Frank, 1967
Various commensal crabs		"
Pinnixid crabs	*Schizothaerus* and *Mopadina*	Hopkins and Scanlan, 1964
"	*Modiolus*	Pearce, 1966b

these are two different cases and the argument may not be transferable. But territorial-like behavior is reported for two annelids. Clark (1959) describes laboratory observations on tube defense in *Nereis pelagica*. Fighting occurred only in or over tubes, suggesting a specialized habit for home defense. Reish (1957) reports sex specific fighting (male vs. male; female vs. female) in *Neanthes caudata*. Such specialization suggests that these patterns of behavior have selective value and can occur in annelids. Certain hesionid commensals are distributed both multiply (*Podarke*, this study) and in isolation (*Ancistrosyllis*, Table 38). This case further suggests that habits leading to isolation have been selected for among annelids and are not an indirect result of some other pattern of behavior.

It seems that there are two possible arguments for the selective value of regular isolation to a commensal. Perhaps the most likely is that it allows competition for a scarce resource to be a contest instead of a scramble (Nicholson, 1954). Thus assures the supply, most likely food, for at least one worm. Pearce (1966a and 1966b) presents circumstantial evidence for believing that food is limiting for some pinnixid crabs. The amount of available food and the amount that a commensal requires could be determined. Such an investigation would be a good first step in solving this problem. It is possible, however, that in some cases where there is a single commensal or pair of commensals on a host, that several might be able to co-exist without interfering with each other. If this were shown to be the case, there might still be a good selective reason for maintaining the host as a sort of exclusive possession. Armstrong (1965) argues that bird territories may not be related to the metabolic need of the birds. They may, however, confer a reproductive advantage to their owners. A similar situation may be true for some commensals. It may pay to exclude other members of the population from breeding. This would be so if the effective breeding population was rather small and several commensals on a host would dilute each other's chances of successful spawning.

BIBLIOGRAPHY

Allee, W. C. 1931. Animal aggregations. University of Chicago Press, Chicago. 431 p.

________ et al. 1949. Principles of animal ecology. Saunders, Philadelphia. 837 p.

Andrewartha, H. G. and Birch, L. C. 1954. The distribution and abundance of animals. University of Chicago Press. 782 p.

Armstrong, J. T. 1965. Breeding and homerange in the night hawk and other birds: its evolutionary and ecological significance. Ecology. 46:619-629.

Baer, Jean G. 1951. Ecology of animal parasites. University of Illinois Press, Urbana. 224 p.

Baird, R. H. 1966. Notes on an escallop (Pecten maximum) population in Holyhead Harbour. J. Mar. Biol. Ass. U.K. 46:33-47.

Baird, W. 1863. Description of several new species of worms belonging to the Annelida Errantia and Sedentaria or Tubicola of Milne Edwards'. Proc. Zool. Soc. London. Vol. for 1863:106-110.

Berkeley, E. 1924. On a new case of commensalism between echinoderm and annelid. Canad. Field Nat. 38(10):193.

________ and C. Berkeley. 1941. On a collection of Polychaeta from southern California. Bull. So. Calif. Acad. Sci. 40(1):16-60.

Blevgvad, H. 1928. Quantitative investigations of bottom invertebrates in the Limfjord 1910-1917 with special reference to place food. Rep. Danish Biol. Stat. 34:33-52.

Brand, Theodore F. 1927. Stoffbestand und Ernährung einiger Polychaeten und anderer mariner Würmer. Zeit. vergl. Physiol. Berlin. 5:643-698.

Buchanan, J. B. 1966. The biology of Echinocardium cordatum from different habitats. J. Mar. Biol. Ass. U.K. 46:97-114.

Castenholz, R. W. 1967. Stability and stresses in intertidal populations. Pollution and Marine Ecology. Interscience Publishers, New York. 15-28 p.

Caughley, G. 1966. Mortality patterns in mammals. Ecology. 47: 906-917.

Caullery, Maurice. 1952. Parasitism and symbiosis. Sedgwick and Jackson, London. 340 p.

Chamberlin, R. V. 1920. The polychaetes collected by the Canadian Arctic Expedition, 1913-18. Report Can. Arc. Exped., 1913-18. 9(B):1-41.

Clark, R. B. 1959. The tubicolous habit and the fighting reactions of the polychaete Nereis pelagica. Animal Behavior. 7:85-90.

________. 1964. Endocrinology and the reproductive biology of polychaetes. Ocean. Mar. Biol. Annu. Rev. 3:211-255.

Codreanu, R. and Mack-Fira, V. 1961. Sur un copepode, Sunaristes paguri et un polychete, Polydora ciliata, associés au pagure Diogenes pugilator dans la Mer noire et la Mediterranée, La notion de cryptotropisme. Rapp Comm. Int. Mer Medit. 16: 471-494.

Coe, W. R. 1957. Fluctuations in littoral populations. Geol. Soc. Am. Memoir. 67(1):935-939.

Connell, J. H. 1963. Territorial behavior and dispersion in some marine invertebrates. Res. Popul. Ecol. 5:87-101.

Dales, R. P. 1951. An annual history of a population of Nereis diversicolor. Biol. Bull. 101:131-137.

________. 1957. Interrelations of organisms: A, Commensalism. In Treatise on marine ecology and paleoecology, vol. 1: Ecology, ed. by J. W. Hedgpeth. Memoir 67. Geol. Soc. of Amer. 1296 p.

________. 1963. Annelids. Hutchinson University Library. London. 200 p.

________. 1966. Symbiosis in marine organisms. In Symbiosis I, ed. by S. Mark Henry. Academic Press, New York. p. 299-326.

Darby, R. L. 1964. On growth and longevity in Tegula funebralis. Veliger. 6(Supplement):6-8.

Davenport, D. 1950. Studies in the physiology of commensals in the polynoid genus Arctonoe. Biol. Bull. Woods Hole. 98:81-93.

________. 1953. Studies in the physiology of commensalism III, the polynoid genera Acholoe, Gattyana, and Lepidasthenia. J. Mar. Biol. Ass. U.K. 32:161-173.

________. 1954. Notes on the early stages of the commensal polynoid Acholoe astericola (Delle Chiaje). J. Mar. Biol. Ass. U.K. 33:123-127.

________. 1955. Specificity and behavior in symbiosis. Quart. Rev. Biol. 30(1):29-46.

________. 1966. The experimental analysis of behavior in symbioses. In Symbiosis I, ed. by S. Mark Henry. Academic Press, New York. p. 381-429.

________ and Hickock, J. E. 1951. Studies in the physiology of commensalism 2. The polynoid genera Arctonoe and Halosydna. Biol. Bull. 100(2):71-83.

Ebert, T. A. 1965. A technique for the individual marking of sea urchins. Ecology. 46:193-194.

________. 1966. Growth of sea urchins at Sunset Bay. Ph.D. Thesis. University of Oregon. 133 p.

Essenberg, C. E. 1917-1919. The factors controlling the distribution of the Polynoidae of the Pacific Coast of North America. Univ. of Calif. Pub. in Zoology. 18:171-283.

Frank, P. W. 1965a. Growth of three species of Acmaea. Veliger. 7:201-203.

________. 1965b. Shell growth in a natural population of the turban snail, Tegula funebralis. Growth. 29:395-403.

________. 1967. Personal communication.

________. 1968. Longevity and community stability. Ecology (in press).

Ganapati, P. N. and Radhakvishna, Y. 1945. Inquilinism between a new hesionid polychaete and a holothurian, Molpadia sp. Current Sci. 31:382-383.

Greig-Smith, P. 1964. Quantitative plant ecology. 2nd ed. Washington, Butterworth. 251 p.

Haecker, Valentin. 1894. Die Spätere Entwickelung der Polynoe Larve. Zool. Jahrb. Anat. Jena. 8:245-288.

Harrington, N. R. 1897. On nereids commensal with hermit crabs. N. Y. Acad. Sci. Trans. 16:214-221.

Hartman, O. 1936. Nomenclatorial changes involving California polychaete worms. J. Wash. Acad. Sci. 26(1):31-32.

________. 1938. The types of the polychaete worms of the families Polynoidae and Polyodontidae in the U. S. National Museum and the description of a new genus. Proc. U.S. Nat. Mus. 86: 107-134.

________. 1939. Polychaetous annelids. Pt. 1: Aphroditidae to Pisionidae. Allan Hancock Pac. Exped. 7(1):1-156.

________. 1944. Polychaetous annelids from California including the descriptions of two new genera and nine new species. Allan Hancock Pac. Exped. 10:239-290.

________. 1948. The polychaetous annelids of Alaska. Pac. Sci. 2(1):3-58.

________ and P. J. Reish. 1950. The marine annelids of Oregon. Ore. State Monographs, Studies in Zool. 6:1-64.

Hopkins, T. S. and Scanland, T. B. 1964. The host relations of a pinnotherid crab, Opisthopus transversus Rathburn. Bull. So. Calif. Acad. Sci. 63(4):175-180.

Hornell, J. 1895. Notes on the marine worms of the Channel Islands: Instances of commensalism. Guernsey Soc. Nat. Rep.:33-78.

Johnson, H. P. 1901. The Polychaeta of the Puget Sound region. Proc. Boston Soc. Nat. Hist. 29(18):381-437.

Knudsen, J. 1944. A gephyrean, a polychaete and a bivalve living together in the Indo-Malayan seas. Dansk Naturhistorisk Forening Copenhagen Videnskabelige Meddelelser. 108:15-24.

MacGinitie, G. E. and N. MacGinitie. 1949. Natural history of marine animals. McGraw-Hill, New York. 282 p.

Margolin, A. S. 1964. The mantle response of Diodora aspera. Animal Behavior. 12:187-194.

Mayer, A. G. 1902. The Atlantic palolo (Eunice fucata). Sci. Bull. Brooklyn Mus. 1(3):93-103.

Moore, J. P. 1908. Some polychaetous annelids of northern Pacific coast of North America. Proc. Acad. Nat. Sci. Phil. 60:321-364.

________. 1909. Polychaetous annelids from Monterey Bay and San Diego, California. Proc. Acad. Nat. Sci. Phil. 61:235-295.

________. 1910. The polychaetous annelids dredged by the U.S.S. "Albatross" off the coast of southern California in 1904. II. Polynoidae, Aphroditidae and Sigalionidae. Proc. Acad. Sci. Phil. 62:328-402.

Newell, G. E. 1947. Life history of Arenicola. Mar. Bio. Ass. Jour. 27:554-580.

Nicholson, A. J. 1954. An outline of the dynamics of animal populations. Australian J. Zool. 2:9-65.

________. 1958. Dynamics of insect populations. Ann. Rev. Ent. 3:107-135.

Nordisches plankton. 1901+. K. Brandt and C. Apstein, editors. Kiel, Lipsius, und Tischer, Amsterdam.

Odum, Eugene P. 1959. Fundamentals of ecology. 2ns ed. Saunders, Philadelphia. 546 p.

Okuda, S. 1936. Japanese commensal polynoids. Annot. Zool. Japan. 15:561-571.

________. 1950. Notes on some commensal polychaetes from Japan. Annot. Zool. Japan. 24:49-53.

Orton, J. H. 1935. Experiments with Amphitrite and commensals. Ann. Mag. Nat. History, London. ser. 10. vol. 16:644-645.

Paris, J. 1956. Commensalisme et parasitisme chez les annelide polychetes. Vie et Milieu. 6:525-536.

Pearce, J. B. 1962. Adaptation in symbiotic crabs of the family Pinnotheridae. The Biologist. 45:11-15.

________. 1964. On reproduction in Pinnotheres maculatus. Biol. Bull. 127:384.

________. 1966a. The biology of the mussel crab, Fabia subquadrata, from the waters of the San Juan Archipelago, Washington. Pacific Sci. 20:3-35.

________. 1966b. On Pinnixa faba and Pinnixa littoralis symbiotic with the clam Tresus capax. In Some Contemporary Studies in Marine Science, ed. by H. Barnes. p. 565-589.

Pettibone, Marian H. 1953. Some scale bearing polychaetes of Puget Sound and adjacent waters. University of Washington Press, Seattle. 90 p.

Pielou, E. C. 1960. A single mechanism to account for regular, random, and aggregated populations. J. Ecol. 48:575-584.

Porcaro, C. A. 1962. Some aspects of the Arctonoe vittata - Diodora relationship. University of Washington Zoology 533 Report.

Reish, D. J. 1957. The life history of the polychaetous annelid Neanthes caudata (Delle Chiaje) including a summary of development in the family Nereidae. Pacific Science. 11:216-288.

Richards, O. W. 1961. Theoretical and practical study of natural insect populations. Ann. Rev. Ent. 6:147-162.

Ricketts, E. F. and J. Calvin. 1962. Between Pacific tides. 3rd ed. Stanford University Press, Stanford, California. 499 p.

Seidler, H. J. 1924. Beiträge zur Kenntnis der Polynoiden I. Arch. Nat. Wieg. 89 (Abt. A, Heft 2):1-217.

Skogsberg, T. 1942. Redescription of three species of the polychaetous family Polynoidae from California. Proc. Calif. Acad. Sci. 23:481-502.

St. John, Dennis. 1966. Oregon State Marine Science Laboratory Invertebrate Zoology Class Report.

Thamdrup, H. M. 1935. Beiträge zur Oekologie der Wattenfauna auf experimenteller Grundlage. Medd. Komm. Danmarks Fishog Havunders, Ser Fiskeri. 10:1-125.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. C. A. Reitzels, Copenhagen. 523 p.

Treadwell, A. L. 1926. Polychaetous annelids collected by Captain R. A. Bartlett in Alaska in 1924, with descriptions of new species. Am. Mus. Nov. 223:1-8.

________. 1937. The Templeton Crocker Expedition VIII: Polychaetous annelids from the west coast of Lower California and Clarion Island. Zoologica. 22:139-160.

Tucker, J. S. 1964. Personal communication.

Tucker, J. S. and A. C. Giese. 1962. Reproductive cycle of *Cryptochiton stelleri* (Middendorff). J. Ex. Zool. *150*:33-43.

Wikswo, Muriel A. 1965. A study of the commensalism of the polynoid worm *Arctonoe vittata*. University of Oregon Zoology 460, 461 Report. 12 p.

Williams, C. B. 1964. Patterns in the balance of nature. Academic Press, New York. 320 p.

Wilson, D. P. 1958. Some problems in larval ecology related to the localized distribution of bottom animals. In *Perspectives in Marine Ecology*, ed. by A. A. Buzzati-Traverso. University of California, Berkeley. p. 87-103.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behavior. Oliver and Boyd, London. 630 p.

________. 1967. Birth control among the birds and the bees. Realities. May 1967.

APPENDIX 1

Success of Tagging Methods for Cryptochiton and Diodora

The method used for marking Cryptochiton is an adaptation of the method of Ebert (1966). The details have been described (p. 10). The history of the chitons marked in this study is set out and analyzed in Tables 1 and 2. It can be seen that Cryptochiton tags can be expected to endure more than five months. The recapture of intertidal Cryptochiton is rather good, with an average of about 50% success. The number of times that a cohort of marked animals is exposed to collection does not, at first sight (Table 1, column B/A), seem to have a great effect on the success of recovery. A reasonable explanation can be offered. In the winter, between September and March, recovery success was very high. This may be explained by the absence of most large algae during this time, exposing the chitons to ready discovery. Throughout the rest of the year the growth of laminarians was much more extensive, and the chitons were difficult to locate. The high return of the August 8, 1965 cohort may be explained by the shorter than usual period to the first recovery and the fact that these were concentrated in an unusually small return area.

The ratio C/B was expected to be larger than B/A. In other words, there would be a high initial tag loss from mortality of the newly marked chitons. A number of dead Cryptochiton had been observed in the release area, and none of the first 17 marked in June, 1964 were ever recovered. Since animals once recaptured do not, as a rule,

Table 1, Appendix 1.--Return data for all marked Cryptochiton released at the Cape Arago Lighthouse, a protected rocky intertidal area.

Date cohort released	Number of times cohort exposed to collection	Total number marked (A)	Total number recaptured at least once (B)	Total number recaptured more than once (C)	$^B/_A$	$^C/_B$
July 8to28, 1964	13	94	51	22	0.54	0.43
Aug. 9, 1964	12	13	13	8	1.00	0.63
Nov. 20, 1964	11	20	11	4	0.55	0.36
Dec. 18, 1964	10	8	7	3	0.88	0.43
Jan. 16, 1965	9	30	23	13	0.77	0.57
Feb. 14, 1965	8	4	3	1	0.75	0.33
March 14, 1965	7	3	3	2	1.00	0.66
April 17, 1965	6	24	11	6	0.46	0.55
May 15, 1965	5	43	18	11	0.42	0.61
June 14, 1965	4	14	6	2	0.43	0.33
July 14, 1965	3	28	6	3	0.21	0.50
Aug. 8, 1965	3	21	12	5	0.57	0.42
Aug. 27, 1965	2	27	7	1	0.26	0.41

Table 2, Appendix 1.--Duration of tag life for marked <u>Cryptochiton</u>. Entries are numbers of hosts. Original number marked and the number of times the hosts were exposed to recapture may be determined from Table 1.

Date cohort released	Period between tagging and final recapture of host (months)			
	0 to 4	5 to 8	9 to 12	12+
July 8to28, 1964	10	9	23	9
Aug. 9, 1964	1	3	7	2
Nov. 20, 1964	2	8	0	1
Dec. 18, 1964	2	4	1	0
Jan. 16, 1965	8	10	5	0
Feb. 14, 1965	2	0	1	0
March 14, 1965	2	1	0	0
April 17, 1965	8	2	0	0
May 15, 1965	9	8	1	0
June 14, 1965	4	2	0	0
July 14, 1965	4	2	0	0
Aug. 8, 1965	10	2	0	0
Aug. 27, 1965	6	1	0	0

seem to be more prone to further recapture, it seems likely that tag loss does become important in a matter of months.

It was not practical to carry out a sustained program of monthly collections with Diodora, as was done with Cryptochiton at the Lighthouse Channel (LHC, Fig. 1). It is, therefore, more difficult to express the success of marking quantitatively. Animals with good tags were often moved from one study area to another, so the success of cohorts is difficult to evaluate. Overall, 665 Diodora were marked and 227 were recaptured at least once. This seems to be a bit less successful than the recapture work with Cryptochiton, but certain cohorts of well-tagged limpets showed recovery at least as good as recovery of marked Cryptochitons. Some examples follow: On August 6, 1964, 50 Diodora were marked and returned to CAI. Eight months later, under adverse conditions, 30 of these were collected by free diving. Of 24 marked and returned to an intertidal station, 12 were subsequently recovered, 10 in the first collection of the station after 2 months. Of these 12, 6 were later recaptured a second time. After 1 month at this same station, 17 of 25 marked limpets were recovered. One can expect, with good choice of return area and secure tags, returns of better than 50% for periods of a few months. A good return area may be identified by a density of native Diodora greater than 3 per square meter on sloping or vertical rock face. The tags on Diodora may be expected to last longer than those on Cryptochiton if the tag is properly made and the limpet is not exposed to abrasion. A number of tags have lasted 2 years. The method of Frank (1965) has met with even greater success with other gastropods.

APPENDIX 2

Host Factor Responses of *A. vittata*

Davenport (1950), who studied the chemoresponses of various commensals found *A. vittata* too sluggish to work with. However, if some material such as nylon bolting cloth is introduced into the Y-tube or experimental vessel for traction, the worms will show chemoresponses which can be studied. Wikswo (1965) showed that *A. vittata* does respond to a host factor from *Diodora*. Her work also suggested that worms removed from a given host species might respond more strongly to that host than an alternative one. The same apparatus and criteria for response used by Wikswo were used again. A given worm was exposed twice to a blank, once to *Cryptochiton* factor and once to *Diodora* factor in a randomly selected order, then squashed. The first run with 8 worms from *Diodora* confirmed Wikswo's results. The next 3 runs with 22 worms from *Diodora* clearly denied the former experience. A further run with 8 worms from *Cryptochiton* confirmed the denial. All this is depicted in the accompanying table.

Table 1, Appendix 2.--Response of *A. vittata* to host factor from *Diodora* and *Cryptochiton*. A worm was tested 4 times to a mixed sequence of 2 blanks, 1 *Diodora* factor, and 1 *Cryptochiton* factor. The worm either did not respond (0) or responded to the stimulus (+) with a characteristic jerk of the anterior body region usually followed by up-current movement. A single run lasted 30 seconds. There were 5 to 15 minute rests between runs. Entries are the number of runs in each stimulus-response category. Below the observed number of runs the expectation is given for the case in which worms respond to either host without preference.

	Stimulus-response category						
	Diodora factor		Blank		*Cryptochiton* factor		Remarks
	0	+	0	+	0	+	
Observed	0	8	15	1	8	0	First trial: 8 worms from *Diodora*.
Expected	0	8	16	0	0	8	
Observed	3	19	38	6	2	20	Second trial: 22 worms from *Diodora*. Results conflict with previous trial.
Expected	0	22	44	0	0	22	
Observed	0	8	12	4	3	5	Third trial: 8 worms from *Cryptochiton*. Results seem to confirm those of second trial.
Expected	0	8	16	0	0	8	

APPENDIX 3

Part 1.--Recapture record of marked *Cryptochiton* at the Cape Arago Lighthouse from August 1964 to December 1965. Each entry has three portions presented as a solumn. The bottom entry is the number of chitons recaptured. The top entry is the number of small worms (less than 20mm long) and the middle the number of large worms recovered from these chitons.

Month of recapture	Month of release of marked host *Cryptochiton*					
	Aug. 1964	Oct. 1964	Nov. 1964	Dec. 1964	Jan. 1965	Feb. 1965
Oct. 1964	10 0 9					
Nov. 1964	6 3 14	-				
Dec. 1964	2 1 15	-	0 0 1			
Jan. 1965	0 0 1	-	0 0 4	0 0 2		
Feb. 1965	0 0 4	-	0 0 3	0 0 6	0 0 6	
March 1965	0 1 3	0 0 3	-	0 0 4	0 0 1	0 0 8
April 1965	0 3 9	-	0 0 8	0 0 4	0 0 10	0 0 2
May 1965	0 0 7	-	0 0 6	0 0 3	0 2 6	0 0 2
June 1965	0 0 1	-	0 0 1	-	0 0 2	0 0 3
July 1965	0 1 2	-	-	0 0 1	0 0 2	0 0 1
Aug. 1965	-	-	0 0 1	1 0 2	0 0 1	-
Oct. 1965	1 0 1	-	-	-	-	-

Part 2, Appendix 3.--Continuation and conclusion. Entries as in Part 1.

Month of recapture	Month of release of marked host *Cryptochiton*						
	March 1965	April 1965	May 1965	June 1965	July 1965	Aug. 1965	Oct. 1965
April 1965	0 0 9						
May 1965	0 0 5	0 0 23					
June 1965	-	0 0 7	0 0 18				
July 1965	-	1 1 6	0 0 20	0 0 20			
Aug. 1965	0 0 1	1 0 1	1 0 2	2 0 2	1 0 6		
Oct. 1965	-	-	7 1	-	-	17 5	
Dec. 1965	-	-	3 1 13	-	-	1 0 4	0 0 7

APPENDIX 4

Part 1.--Recapture record of marked *Diodora* from the Cape Arago region during summer 1963 to early summer 1966. Entries are as in Appendix 3.

Period of recapture	Period of release of marked host *Diodora*		
	Summer 1963	Summer-fall 1964	Winter 1964-65
Summer-fall 1964	0	12	
	3	0	
	9	10	
Winter 1964-65			0
	-	-	0
			4
Spring-early summer 1965	0	3	0
	1	23	1
	1	33	4
Spring-early summer 1966		0	
	-	7	-
		9	

Part 2.--Continuation and conclusion. Entries as in Part 1.

Period of recapture	Period of release of marked host *Diodora*			
	Spring-early summer 1965	Summer-fall 1965	Winter 1965-66	Spring-early summer 1966
Spring-early summer 1965	0			
	2			
	74			
Summer-fall 1965	9	21		
	8	6		
	22	19		
Winter 1965-66	1	2	0	
	3	6	0	
	7	18	7	
Spring-early summer 1966	0	2		6
	3	0	-	0
	5	1		26

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