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DASCYLLUS ALBISELLA GILL, A
POMACENTRID REEF FISH.

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LIFE HISTORY AND BEHAVIOR OF DASCYLLUS ALBISELLA GILL,
A POMACENTRID REEF FISH

by
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of Hawaii in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

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SECTION I

INTRODUCTION

Fishes of the family Pomacentridae are most abundant in calm tropical or subtropical waters where they are associated with various kinds of shelter. Most species inhabit crevices or holes in the bottom but some form commensal relationships. Amphiprion sp. are well known because they associate with large sea anemones, and Dascyllus sp. are known as coral fishes because they associate with various species of corals.

Dascyllus albisella Gill is a reef fish endemic to Hawaii. It is a small, deep-bodied fish reaching a maximum length of about 5 inches. Juveniles are usually black with a white spot on each side and a turquoise spot on the head. Adults are either pale or dark, the white spots fading with age.

Adults and juveniles occur both on inshore and offshore reefs in aggregations of a few to over 100 individuals. They are usually associated with coral heads into which they retreat when alarmed. Adults spawn on the bottom and care for the eggs until they hatch. Like many Hawaiian fish species, the larvae are pelagic and the juveniles return to the bottom at an early age.

Preliminary observations showed that juveniles were

closely associated with ramose coral heads located on particular parts of reefs. On the other hand, adults were most often associated with glomerate coral heads either on in-shore or offshore reefs, and did not seem as dependent on shelter as juveniles. However, the environmental conditions associated with their distribution as well as most essential details of the life history remained unknown.

The objectives of this investigation were twofold. The first objective was to investigate the life history and habits of the species, including reproduction, growth and food. The second objective was to associate distribution with physical and biological influences in the environment, including temperature, salinity, water movement and predation. It was hoped that this study would not only provide details of the life history of the fish, but would also show the interaction between environmental factors that determine the distribution of the fish.

SECTION II

LIFE HISTORY

2.1 DISTRIBUTION

Dascyllus albisella Gill, a species of coral reef fish, occurs throughout the main Hawaiian Islands and possibly exists in the other islands of the chain extending to the northwest. Its closest relative, Dascyllus trimaculatus (Rüppell), is widely distributed throughout the Indo-Pacific region and may approach Hawaii at Johnston Island, some 660 miles to the southwest.

The fish, common around the island of Oahu, is found both in shallow bays and off exposed shores as well as in sheltered reef areas. It is particularly abundant in Kaneohe Bay on the windward shore of Oahu, where it occurs along the sloping sides of the shallow reef platforms and around the masses of living coral found in deeper areas in portions of the bay. Although the adults are free-living, they are found mainly in the vicinity of coral of the genus Porites. They usually do not develop an association with a particular coral head, but roam freely over the surface of beds of coral, in which they take shelter when sufficiently disturbed. Apparently, they also live in exposed waters outside of Kaneohe Bay, but their distribution in this habitat has not been studied.

Adults are very common in the exposed waters beyond the surf zone off the Waikiki Beach and Ala Moana areas on the leeward side of the island, where they form aggregations numbering from a few to several hundred fish. The aggregations are associated mostly with patches of Porites coral, varying in size from a few square feet to an acre or larger. They occur at depths ranging from 20 to at least 180 feet, but are most numerous at depths of 50 to 80 feet. The limit of the distribution of fish in a seaward direction is determined most likely by the distribution of coral, and in a shoreward direction, by the increasing force of the surges found there.

Juveniles and adults are found in both shallow and deep water. However, since the young are more closely associated with ramose coral heads, their distribution depends in large part on the distribution of the coral. In addition to occupying the deeper waters where adults are found, juveniles are also abundant on shallow reef flats where they are most numerous in spring and early summer. Like adults, they are also occasionally found around piles of rocks, wharf pilings and in other sheltered locations.

2.2 REPRODUCTION

2.2.1 Materials and Methods

Fish were collected during 1959 and 1960 by spearing,

trapping and poisoning, and their gonads were examined to learn more about the reproductive habits of the species. Entire ovaries, or portions of ovaries, were weighed on a chainomatic balance to thousandths of a gram after excess moisture had been removed. When egg counts were made, portions of the ovaries were weighed and the number of eggs they contained were counted. The weight of the remainder of the ovaries was then determined and the total number of eggs was calculated by dividing the weight of the aliquot into the total weight and multiplying by the number of eggs.

The sizes of eggs in various stages of maturity were measured to hundredths of a millimeter by using a microscope equipped with an ocular micrometer. Aliquots from different areas of the ovaries were mixed together to minimize possible differences in the ratio of various egg size groups. Numbers of spawnable eggs in the ovaries were calculated by multiplying the number of mature eggs in an aliquot by the number of aliquots in the pair of ovaries (based on weight as expressed in the preceding paragraph.)

2.2.2 Time and Duration of Spawning

Information on the spawning cycle may be gained from a study of seasonal variation in mean gonad weight (Tester, 1951). The relatively rapid development of gonads during the onset of the breeding season leads to a relative increase

of gonad weight in relation to body weight of the fish. When eggs are spawned, the ratio decreases. Thus a peak in the mean ratio can be expected to coincide with the mid-part of the spawning season.

Figure 1 shows the monthly average ratio of gonad weight to body weight based on a total of 254 adult Dascyllus albisella captured during 1959. The ratio increased slightly between January and February, and then rose more rapidly to a peak in June. The ratio decreased slightly during July and August, and then declined rapidly. The figure indicates that a spawning peak took place during June or July with a period of maximum spawning from May to August. A low value of the ratio during other months of the year does not necessarily preclude the possibility of a small amount of spawning. That spawning did take place during the winter months is indicated by the presence of small numbers of fish with ovaries containing ripe eggs, and by the presence of very small juveniles collected at Coconut Island during January of 1961 (see Figure 20).

Helfrich (1958) conducted a similar analysis on gonads of the maomao, Abudefduf abdominalis (Quoy and Gaimard). His results show a peak of spawning activity that coincides with that for Dascyllus albisella, but the peak falls off more rapidly during the months of July and August. There was a similar reduced activity during the winter, although

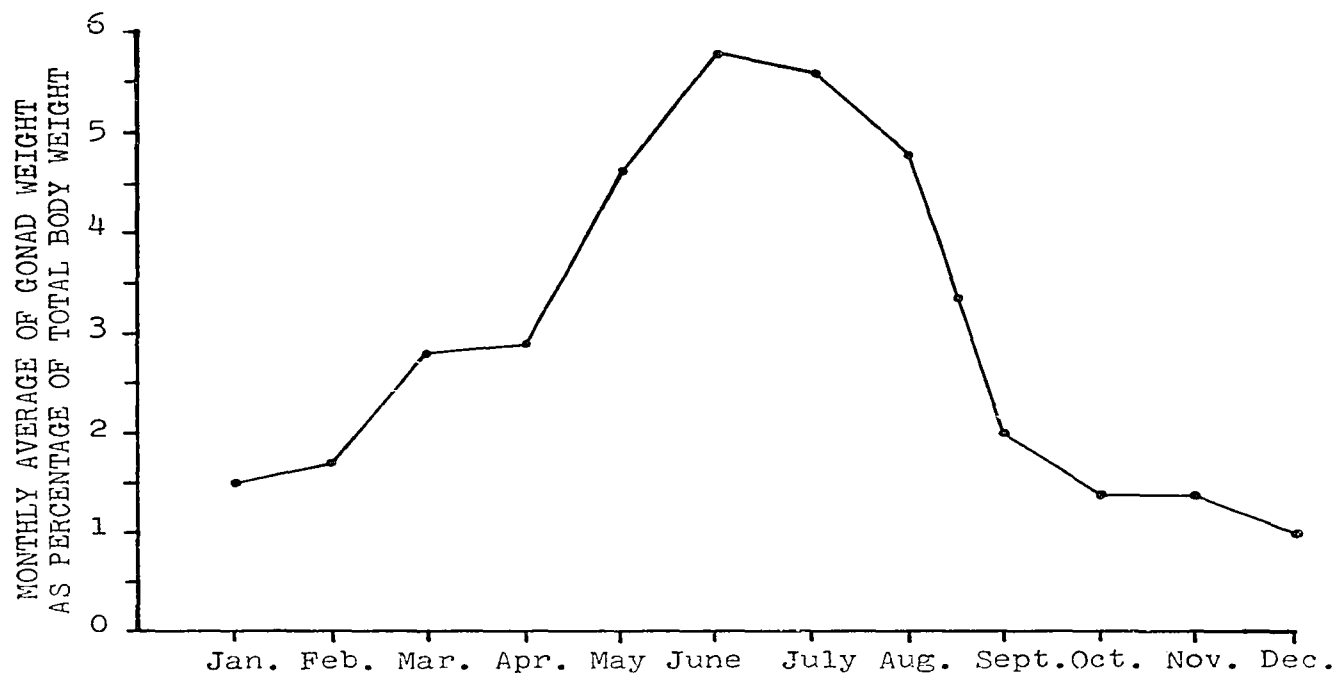


Figure 1. Ovary weight expressed as a percentage of total body weight of 254 female Dascyllus collected during 1959.

the ratio in A. abdominalis reached the lowest point in November, while that for D. albisella occurred in December.

Garnaud (1957) has shown that a pair of fish of the closely related species, Dascyllus trimaculatus, spawned three times each month during a four month period in an aquarium at the Musée Oceanographique de Monaco. Although his observations were interrupted for several months, they were sufficient to show a reduced period of egg laying during the autumn. He stated, furthermore, that most pomacentrids spawn frequently and lay numerous eggs.

Verwey (1930) reported that another pomacentrid, Amphiprion percula (Lacepede), spawned 14 times between April and November in the Onrust Aquarium, Batavia. He observed the greatest spawning activity during June through August.

The observations on these other species conform with a conclusion that Dascyllus albisella may spawn throughout the year but has a period of maximum spawning during the summer months.

During the course of gonad analyses, it became apparent that none of the fish examined from Kaneohe Bay had mature ovaries, although all of the fish were captured in traps during the height of the spawning season. This seemed unusual, because the physical and biological factors

initiating spawning should be as applicable in Kaneohe Bay as elsewhere. An explanation emerges from an examination of length frequency distributions of fish from Kaneohe Bay and from Waikiki.

The length frequency distributions shown in Figure 2 result from grouping fish lengths in 5 mm. intervals. The fish captured at Waikiki were significantly larger ($P < 0.01$) than the fish from Kaneohe Bay, and the distribution was more symmetrical. The fish from the latter area were much more variable in size, ranging from 75 to 120 mm. in fork length, and the major portion of the size distribution (72%) was below the mode of 105 mm.

In the Waikiki collections, very few of the fish smaller than 110 mm. had mature gonads. It seems likely that Dascyllus albisella reaches sexual maturity at approximately this size, although the estimate is not exact because of the small numbers of fish available for study. Thus the majority of the fish caught in Kaneohe Bay were probably too small to have attained sexual maturity.

The reason for the differences in size between fish from the two areas is not known. Since food is plentiful in Kaneohe Bay, fish should grow to sizes comparable to those at Waikiki. It is possible that traps are in some way selective and that sexually mature fish are not caught

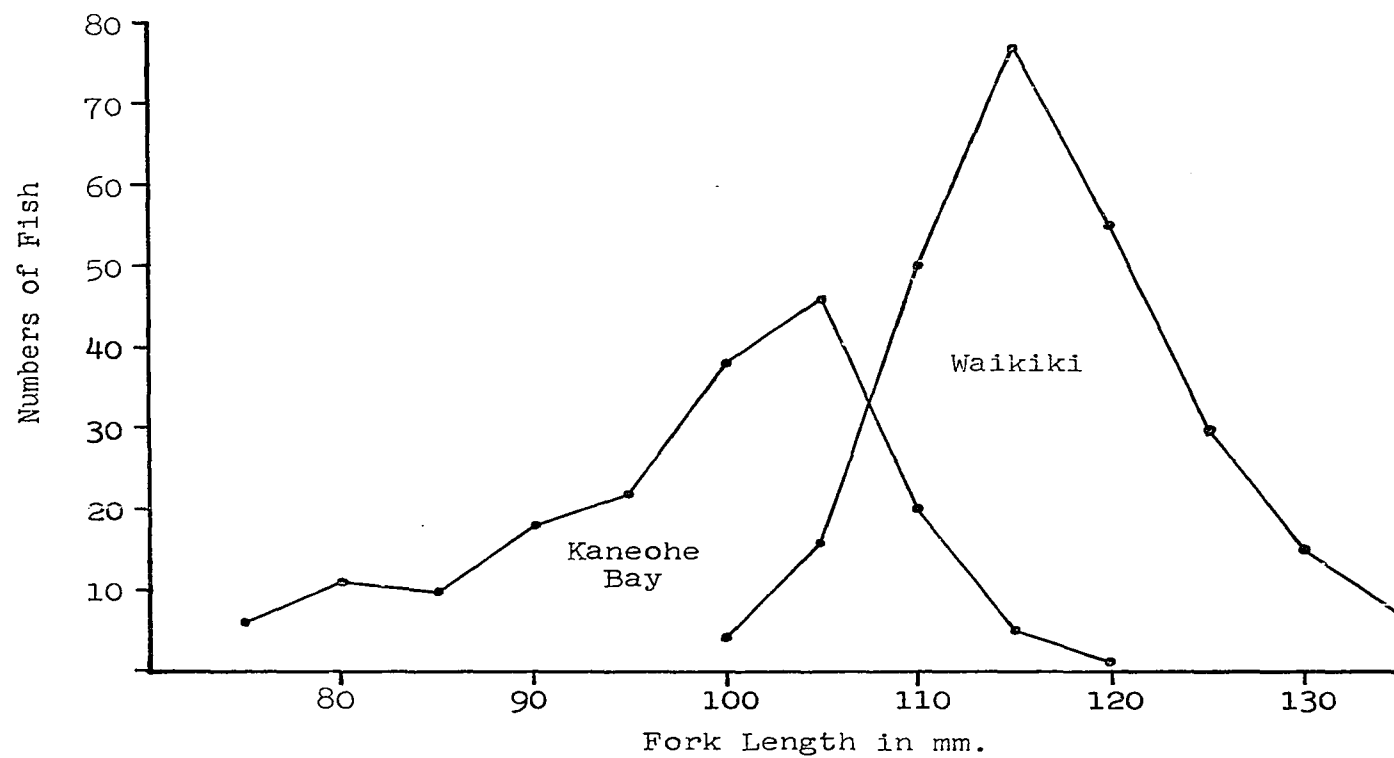


Figure 2. Length frequency of female *Dascyllus albisella* captured at Waikiki and Kaneohe Bay during 1959 and 1960.

because some behavioral activity of the fish in relation to nesting might prevent them from entering. However, many other species of fish in the gravid condition are commonly taken in traps in the same areas. Since spawning activity was never seen in Kaneohe Bay, despite many hours of searching, it is possible that the fish spawn only in parts of the bay which were not covered by observation or trapping, or in the deeper waters outside the bay. It is possible that depth might be a factor, since adult Dascyllus albisella off Waikiki were not seen to spawn to any great extent at depths shallower than 40 feet.

2.2.3 Fecundity

It is difficult to determine the total annual egg production of a female because an individual probably spawns more than once during the year. The presence of fishes in various stages of ovarian development throughout the year makes it difficult to trace a progressive increase in egg diameters because of small numbers of fish available for this study. The mature ovary of this species (Figure 3) contains two distinct modal groups of developing eggs resembling those of the maomao, Abudefduf abdominalis, (Helfrich, 1958), and the aholehole, Kuhlia sandvicensis, (Tester and Takata, 1953). However, spent ovaries with residual eggs in a particular stage of development that allowed the latter authors to "suggest that one aholehole

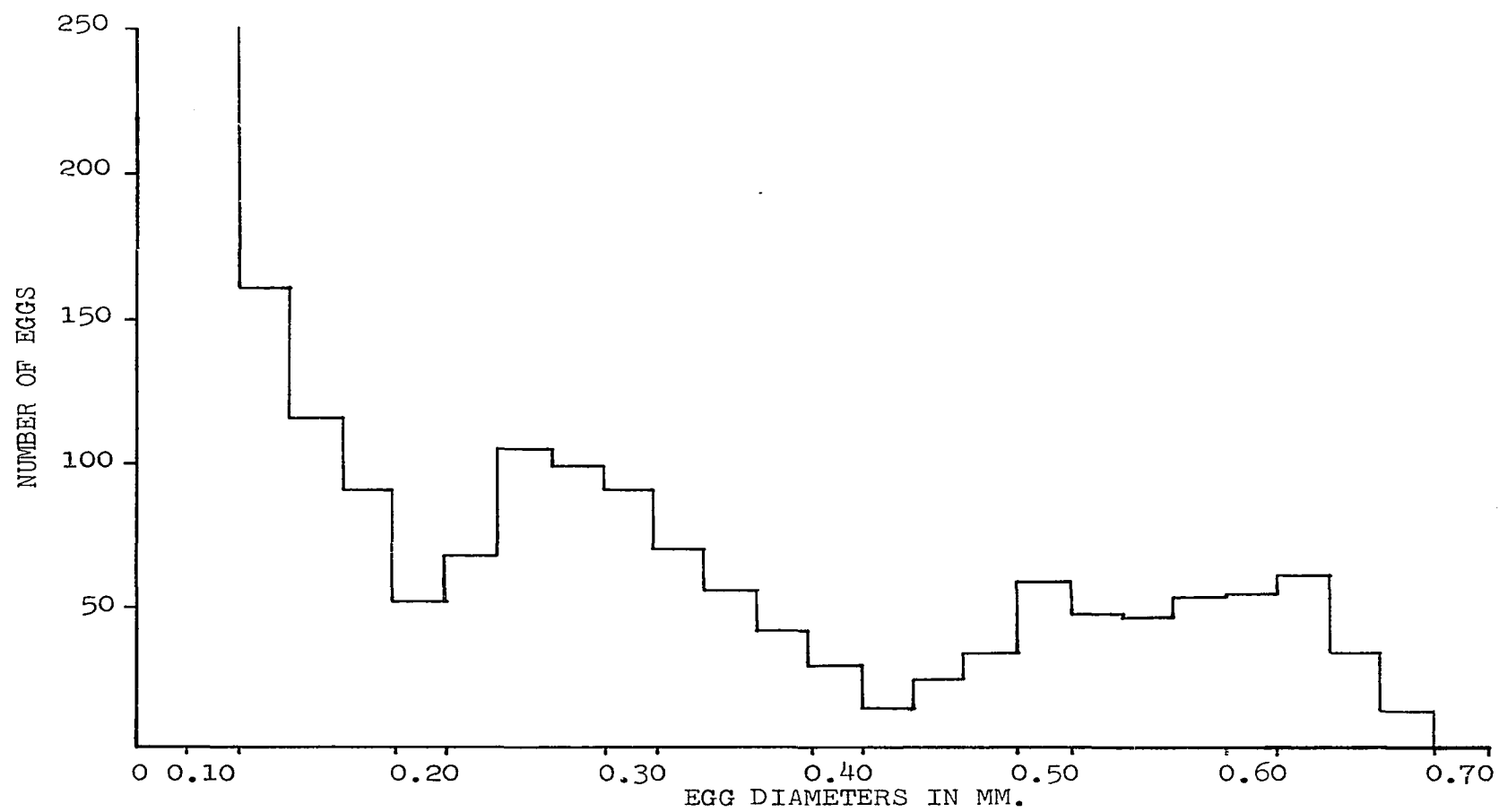


Figure 3. Frequency distribution of egg diameters for a typical ripe ovary.

may ripen and spawn two or more batches of eggs during the course of the year" were not found in Dascyllus albisella.

Although it is not possible to determine total egg production during the year, it is possible to determine the number of eggs that females can spawn at any one time. This was accomplished by counting the numbers of ripe or nearly ripe eggs in portions of the ovaries of gravid female fish. Such eggs are easily distinguished from others in the ovary because of their large size (0.8 - 1.0 mm.), translucent whiteness, the presence of conspicuous oil globules and the fact that they are free in the lumen of the ovary.

Table 1 summarizes the results of this work and shows the increase in numbers of ripe eggs in the ovaries of progressively larger fish, a phenomenon that is widespread among fishes. Estimates from the counted aliquots give an average of 25,000 eggs per fish. A regression of numbers of eggs on size of fish was made by transposing the data into logarithms. The width of the 95% confidence belt shows that the mean egg count of the population at a given length may vary by about 6,000 eggs (Figure 4).

Garnaud (1957) determined the number of eggs in a nest of Dascyllus trimaculatus and stated that the number for the species varied between 20,000 and 25,000. He observed 17 spawnings by a single pair of these fish over a

TABLE 1. INCREASE IN NUMBERS OF RIPE OVARIAN
EGGS WITH INCREASING LENGTH OF FISH.

<u>Fork Length (mm.)</u>	<u>Estimated No. Eggs (thousands)</u>
104	12.7
106	14.9
110	15.8
112	19.1
117	25.2
117	27.0
120	29.1
122	38.0
125	43.7

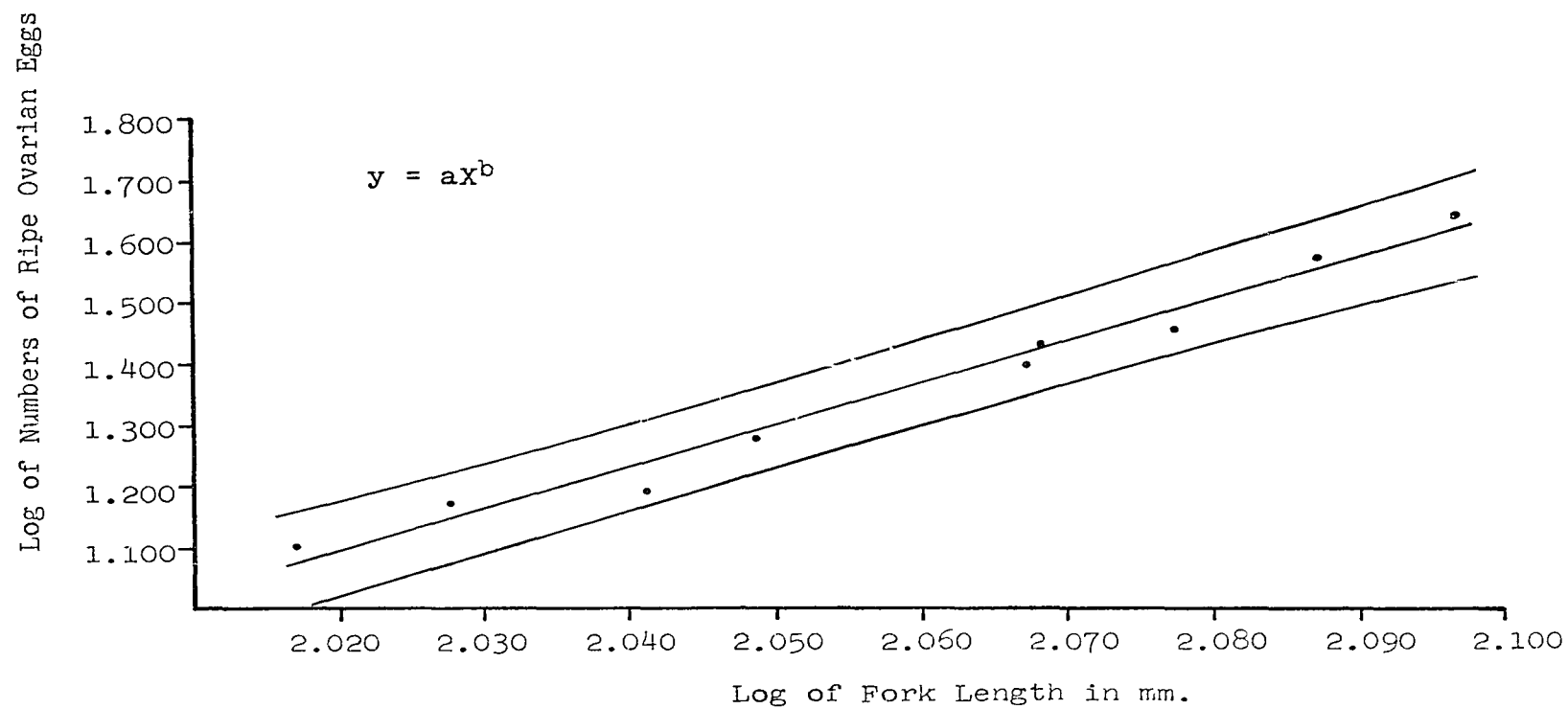


FIGURE 4. LOGARITHM OF NUMBERS OF MATURE
OVARIAN EGGS ON FISH LENGTH.

7 month period, placing the fecundity of the pair at about 350,000 to 400,000 eggs for a period of less than one year. Helfrich calculated an average of 21,000 spawnable eggs in the ovaries of the maomao, Abudefduf abdominalis, from a range of 9,400 to 41,000 eggs; however, he made no estimate of the number of spawnings made by single fish during one year.

If individual Dascyllus albisella spawn as frequently as Dascyllus trimaculatus, then these two species are probably among the most fecund in the family. Other pomacentrids, though spawning frequently, lay much smaller numbers of eggs. Garnaud (1951) observed an average of 880 eggs laid by two female Amphiprion percula (Lacepede), although numbers varied considerably. The fish spawned at least 10 times in one season, laying a total of about 8,800 eggs. Verwey (1930) determined that this species spawned only 200 - 300 eggs at one time and placed the yearly fecundity at about 5,000 eggs. He also observed broods of eggs spawned by Amphiprion ephippium (Bloch) to be about the same size as those of Amphiprion percula. Breder (1932) and Breder and Coates (1933) reported that the beau gregory, Pomacentrus leucoris Gilbert, deposited 400 - 500 eggs per spawning in the New York Aquarium.

The large numbers of eggs laid by Dascyllus albisella and Dascyllus trimaculatus may be related to their habit of

making nests on open patches of bottom where they might be more vulnerable to predation. It is generally accepted that fish exhibiting parental care spawn fewer eggs than pelagic spawners that leave their eggs unattended (Hoar, 1957).

Many of the pomacentrids including Amphiprion percula, Pomacentrus leucostictus Müller and Troschel, and Dascyllus reticulatus (Richardson) lay eggs in more sheltered locations. The smaller numbers of eggs produced by these species in relation to those produced by Dascyllus trimaculatus might be an example of the general tendency as it occurs within a single family.

2.2.4 Sex Ratio

The sex ratio for this species was determined by examining the gonads of a total of 723 fish that had been caught by trap, spear, and poison during 1959 and 1960. The majority of fish (456) were caught on the leeward side of Oahu and the remaining 267 came from traps set in the vicinity of the Coconut Island Marine Laboratory in Kaneohe Bay on the windward side during 1960.

The collections from the leeward side contained 44% males and 56% females (Table 2). Similarly, in Kaneohe Bay, females (67%) greatly outnumbered males (33%). Using the pooled data, it was found that the ratio differed significantly from a 50:50 ratio. A test of heterogeneity showed

TABLE 2. SEX RATIO OF DASYLLUS ALBISSELLA

CAPTURED BY TRAP, SPEAR AND POISON

AT WAIKIKI AND KANEOHE BAY DURING 1959 AND 1960.

<u>Waikiki</u>				
<u>Month</u>	<u>Total No. Sampled</u>	<u>Number Males</u>	<u>Number Females</u>	<u>Percent Females</u>
<u>1959</u>				
May	57	26	31	54
June	38	15	23	61
July	45	24	21	47
August	36	12	24	67
September	40	16	24	60
October	18	11	7	39
November	20	14	6	30
December	32	10	22	69
<u>1960</u>				
January	39	18	21	54
February	22	13	9	41
March	49	21	28	57
April	<u>60</u>	<u>22</u>	<u>38</u>	<u>63</u>
Total	456	202	254	
Percent males = 44				
Percent females = 56				

<u>Kaneohe Bay</u>				
<u>1960</u>				
April	48	21	27	56
May	110	28	82	74
June	75	31	44	59
July	34	10	24	71
Total	267	90	177	
Percent males = 33				
Percent females = 67				

a consistency within samples.

More data are needed before it can be definitely asserted whether or not an excess of females is present in the populations as a whole. The ratio might vary from place to place, although the reasons for such variation would be difficult to explain. Tester and Takata (1953) found a significantly greater number of male Kuhlia sandvicensis at Diamond Head, but also found a significantly greater number of females at Hauula Park on the opposite side of the island of Oahu. Helfrich (1958) found a greater number of male than female Abudefduf abdominalis, but he attributed the difference to selective sampling by traps employed in the capture of the fish. Randall (1955) found a greater number of males in trap-caught Acanthurus sandvicensis than in those captured by poison and spear.

2.3 NESTING

2.3.1 Study Areas

Studies on nesting Dascyllus albisella were carried out in waters extending in a seaward direction from the surge zone off Waikiki and Ala Moana Beach off the leeward side of Oahu. It was necessary to use a boat and diving apparatus because the study areas were located in water that ranged in depth from 45 - 70 feet.

Studies were carried out in two sections of this area (A and C, Figure 5). Section A was located about $3/4$ mile offshore from the Ala Moana Yacht Harbor in water about 70 feet deep (see 3.2.4 for a description of the bottom). Three rectangular plots were marked off by placing bent iron bars at the corners to indicate the confines of the plots. Each plot was located on flat bottom with one of the two longest sides adjacent to a large mass of glomerate coral. Each plot measured about 30 x 15 feet, and enclosed an area of about 450 square feet.

Section C was located about $1/2$ mile in a seaward direction from the Royal Hawaiian Hotel where the water was about 45 feet deep. The section consisted of a low ridge of flat rock bottom covered by patches of the glomerate coral, Porites lobata. The ridge ran in a northeast-southwest direction and sloped gently into a sandy bottom on the east side. On the west side, the slope leveled off as a hard bottom with a few dead glomerate, or massive, coral heads lying about. Three plots larger than those at section A (20 x 40 feet = 800 square feet) were marked off along the sides of the ridge where spawning seemed to be heaviest.

The plots at section C were marked off on June 10, 1959, and those at section A on July 10, 1959. During each observation, nests were found by first locating a male fish guarding the nest, and then searching for the nest itself.

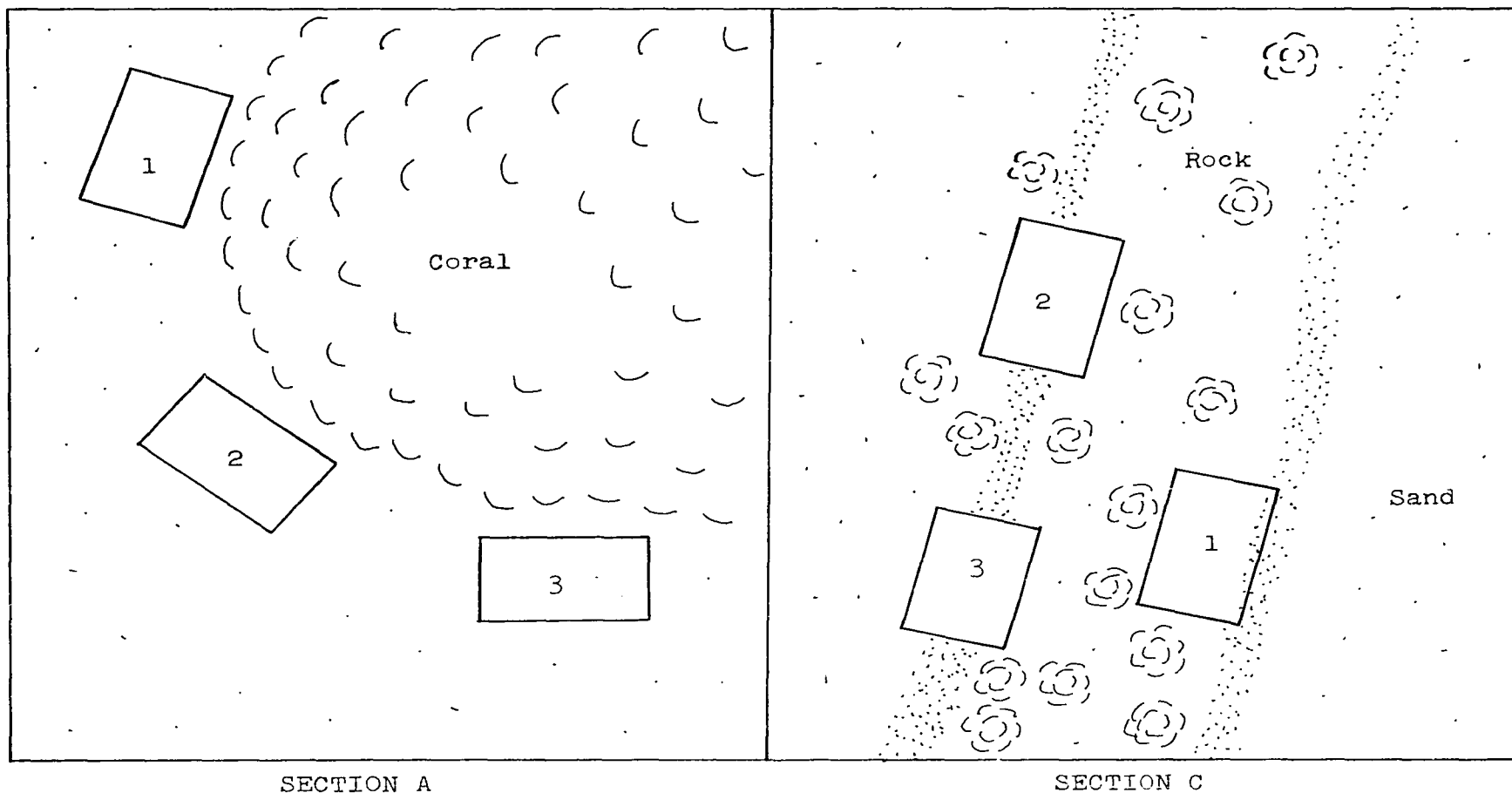


Figure 5. Positions of experimental plots in which numbers of nests were observed at Waikiki during 1959 and 1960.

An attempt was made to count the number of nests in the plots twice each month, but difficulties involved in reaching the study area made it impossible to maintain a regular schedule of observation. However, two observations were made during most months of the year.

2.3.2 Description of Nests and Eggs

The nests of this species are difficult to distinguish from their surroundings. They are usually found on flat rock bottom but occasionally may cover an entire rock or a portion of one. They are generally rectangular in shape and are occasionally broken up into patches or strips if the bottom happens to be irregular. When first made, they are relatively conspicuous because of their greenish color in contrast to the dull whitish color of the bottom. The greenish color results from the removal of sediment from the nest by the male fish. The contrast is reduced and the nest becomes less conspicuous when filled with eggs.

The eggs average 0.85 mm. in length and 0.4 mm. in width. They are "typical" pomacentrid eggs, elliptical in shape, and are anchored to the substrate by a group of adhesive strands attached to one end. They are hyaline with very pale straw-colored yolks and are almost invisible on the bottom. They are distributed in the nests in dense patches of varied size. The patches may comprise only a few eggs and cover only a fraction of an inch, or they may

comprise many eggs and cover several square inches. The patches as well as the individual eggs are often very close to each other, giving the nest a uniform appearance upon cursory examination.

No nests of this species were found in Kaneohe Bay, and the question arises whether or not fish actually spawn there. Much of the bottom is mud and would be unsuitable for spawning. The sloping sides of the reef flats are usually overgrown with algae and other sessile forms of marine life and likewise would not be suitable. Some areas of rock bottom with relatively few encrusting organisms were observed, but nests were not seen in these apparently suitable locations. In addition, the reproductive behavior associated with spawning activity was not seen. It appears that spawning either does not occur in the bay, or that it occurs in some locality that has not been seen.

It is likely that spawning occurs outside the bay in the deeper water. Since most spawning at Waikiki occurs at depths between 40 and 70 feet, it is possible that depth of water might influence this activity. Photographs taken by people diving for black coral in the deep waters off the windward side of Oahu show groups of large adult Dascyllus albisella as well as suitable kinds of bottom. The presence of nests on that side of the island would also explain the presence of juvenile Dascyllus albisella that occur on the reefs in the area. The presence of juveniles is an indication

that nests are probably present in the vicinity. This problem can probably be settled by more field observation in both Kaneohe Bay and in offshore waters.

2.3.3 Frequency of Nesting

Observations of numbers of nests in the study plots were made over a period of one year beginning on June 10, 1959, and ending on May 23, 1960. Since it was recognized that fish spawned in nests that were located mostly on flat rock bottom, plots were set up in such locations in section C. Similar plots were set up in section A although a number of coral heads were present within their borders. Since old nests became inconspicuous within a day or two after being abandoned, it is obvious that all of the nests observed were recently made.

The number of nests counted in the two sections during 1959 and 1960 are summarized in Table 3 and the total numbers for each month are plotted in Figure 6. The data show a peak of nest building activity in June that declined slightly during July and declined rapidly during August. A rather definite increase that occurred in October was followed a month later by a decline until no activity was noted in January. Activity slowly increased during February and March and then rose quickly during May.

The data show a picture of spawning activity that is very similar to that shown by the ovary weight-body weight

		1959												1960									
S E C T I O N	Plot No.	June		July		Aug.		Sept.	Oct.			Nov.		Dec.	Jan.	Feb.	Mar.		Apr.		May		Total
		10	26	10	24	7	13	11	2	16	30	8	20	2	9	3	4	20	13	21	8	23	
A	1			6	5	3	3	2	3	1	0	2	3	0	0	1	2	3	1	3	4	6	48
	2			7	4	4	3	5	0	0	0	1	3	0	0	0	0	1	1	2	5	3	39
	3			4	6	5	2	2	2	2	0	0	1	0	0	0	1	2	1	2	6	5	<u>41</u>
	Total																						127
C	1	9	9	8	5	3	2	4	2	3	0	0	0	0	0	1	2	0	3	2	7	5	65
	2	6	7	4	5	3	4	2	2	5	0	2	0	0	0	1	3	0	1	3	6	8	63
	3	8	7	10	10	4	3	1	4	3	0	0	3	3	0	0	0	0	2	4	4	6	<u>72</u>
	Total																						200

TABLE 3. NUMBERS OF DASCYLLUS ALBISELLA NESTS OBSERVED
IN SECTIONS A AND C AT WAIKIKI DURING 1959 AND 1960.

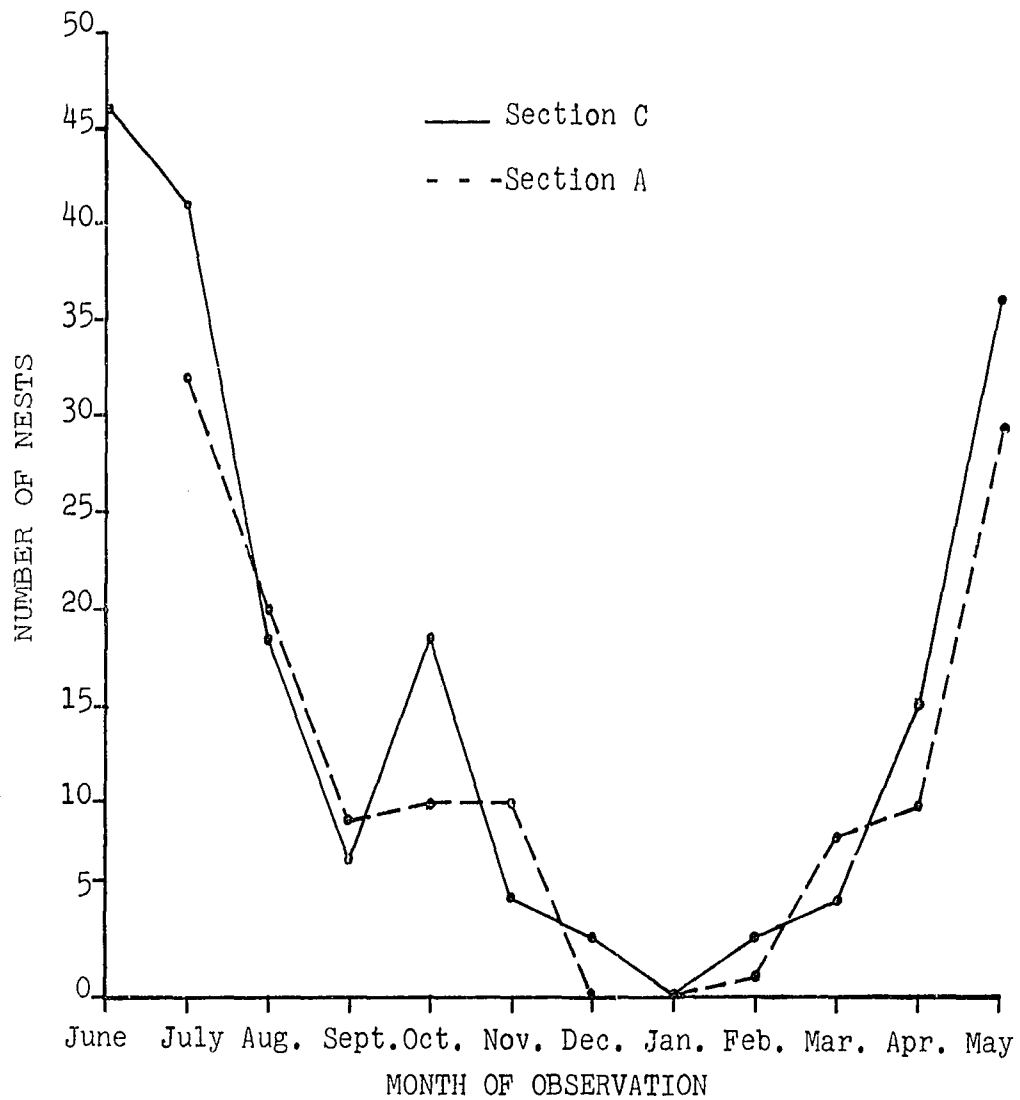


Figure 6. Seasonal fluctuations in numbers of nests observed at Waikiki during 1959 and 1960.

ratios of Figure 1. The peaks of reproductive activity both occur in June although the data on nesting show a more rapid decline of activity in August than do the ovary data.

Nest building activity showed a slower build-up during February, March and April than the ovary data do; the difference however may have been due to the fact that the data were taken in different years.

2.3.4 Incubation Period

An unusual opportunity was presented for studying the nesting cycle in detail. On August 16, 1960, 11 nests without eggs were observed at section C, and 5 were observed at section A. Four nests at section A were selected for detailed study and 7 others were spot-checked to determine how long the eggs remained. Observations were made daily for the next six days during the late afternoon. Temperatures were recorded during each of the observations.

On October 17, the outlines of the four nests were traced on a piece of plastic so that any future change in size could be noted. Two of the nests were full of eggs completely covering the surfaces within their borders. One had been abandoned and was already almost completely covered by silt. The fourth nest contained eggs which were still being guarded by the male fish. A spot-check of the other nests revealed that 5 had been abandoned and the other 2 contained eggs.

On October 18, the nests had not enlarged in size and did not appear to contain any additional numbers of eggs. However, the nest that was empty the previous day contained eggs. The nests were again measured, but proved to have the same dimensions as the previous day.

On October 19, no change was noted in the areas of the nests, and the number of eggs was apparently the same. One of the nests had a small patch of opaque eggs that were presumed to be dead.

The patch of opaque eggs was not seen on October 20 and a bare patch was apparent in the nest where they had been. One of the nests had been enlarged by about 30 square inches, but the new section had not been thoroughly cleaned and contained no eggs.

On October 21, the 2 nests that had first contained eggs were empty and the guarding males had left them; the same was true for the other 2 nests that had been spot-checked. The nest that had received eggs on October 18 still contained them and the male was present. This nest was vacant the next day on October 22 when the final check was made. The period of time from the initial observation of the eggs until they hatched extended over a 4 day period.

It is difficult to compare the incubation period of Dascyllus albisella with that of other pomacentrids since

most of the information on the latter is based on laboratory studies. The incubation period for Abudefduf abdominalis was 6 days at 24.5° C. (Helfrich, 1958), which corresponded with that of its close relative Abudefduf saxatilis (Shaw, 1955). Brinley (1939) reported that the eggs of Pomacentrus leucostictus hatched in five days at temperatures between 28° and 31° C. The shorter incubation time is similar to that of Dascyllus albisella which occurred at temperatures ranging from 26.2° to 27.5° C. The temperatures during the early fall are usually about 2 degrees higher than in early summer which might shorten the incubation period. However, Garnaud (1957) stated that eggs of Dascyllus trimaculatus required 4 days to incubate in aquaria at temperatures of about 24° C., a figure he mentioned as being optimum for retaining the fish. He further stated that hatching began in the morning and lasted at least throughout the day.

It has been shown in other pomacentrids that more than one female fish may contribute eggs to a single nest (Brinley, 1939; Helfrich, 1958). To study this possibility in Dascyllus albisella, ten nests were chosen at random in section A at Waikiki. The contours of the nests were drawn in the field by tracing them on a sheet of plastic held close over the surface of the nests and the number of square inches within the nest was calculated. Four 1-inch square

areas within each nest were scraped and the number of eggs was counted. This number of eggs, when multiplied by the total area of the nest, gave an estimate of the total number of eggs they contained, and the 95% confidence interval for each of the nests (Table 4). The average of 25,000 eggs per fish calculated from ovary data in Table 1 may be applied to the estimated numbers of eggs in nests to give an approximate estimate of the possible number of fish that might have contributed.

Table 4 summarizes the results of this investigation and shows that numbers of eggs contained in the nests are sufficiently large in comparison with numbers of ripe eggs found in ovaries to show that more than one fish probably laid in some of the nests. The actual number contributing to a single nest, however, is uncertain because the size of the fish contributing was unknown.

2.4 REPRODUCTIVE BEHAVIOR

2.4.1 Nuptial Coloration

At the time when male fish have established a nest site and are engaged in courtship activity, their coloration becomes brighter than usual. The entire body of the fish is white and only the caudal, anal and pelvic fins retain the black coloration. The dorsal fin, which is usually black, also becomes white except for a black strip along

<u>Nest Measure in Inches</u>	<u>Area in Sq. In.</u>	<u>Est. No. Eggs in Thousands</u>	<u>Confidence Interval 0.05</u>
12.0 x 10.0	120.0	125.6	103.0-148.0
10.5 x 8.5	89.3	82.6	73.1- 92.1
9.6 x 6.1	58.6	55.3	47.7- 62.9
8.3 x 6.5	53.9	43.6	38.2- 49.2
9.0 x 5.5	49.5	46.7	40.3- 53.2
12.0 x 4.0	48.0	47.9	41.7- 54.0
12.0 x 4.0	48.0	45.1	37.3- 52.9
10.0 x 4.3	43.0	36.5	31.5- 41.4
7.5 x 5.5	41.3	33.7	26.3- 40.9
7.1 x 5.6	39.8	35.9	32.6- 39.2

Avg. nest = 52.4 sq. in. (excluding the data for the largest nest.)
 Avg. no. spawnable eggs / fish = 25,000

TABLE 4. ESTIMATED NUMBERS OF EGGS IN NESTS OF VARIOUS SIZES.

its free edge. At times the fins have an amber tint that may be seen when the fish turn in various directions. This fin color, however, is occasionally seen in feeding fish and may seem to be more pronounced in breeding males only because of their greater activity during courtship.

As in many fishes, characteristic color changes occur in male pomacentrids during the reproductive season. Longley and Hildebrand (1941) briefly describe the breeding coloration of Pomacentrus leucostictus, which changes from a bluish-black to a uniform dusky yellow-olive or may assume a yellow color over only the dorsal surface. They also state that Chromis insolatus (Cuvier and Valenciennes) displays spawning coloration. Helfrich (1958) observed that the normal black stripes of male Abudefduf abdominalis, when, breeding, became a pale gray and were often invisible whereas the normal brassy green to yellow base color was transformed into a pale blue. Part of the color manifestation of at least some pomacentrids occurs as an enhancement of already existing colors such as was seen in the brighter white appearance of Dascyllus albisella and in the yellow tail of Stegastes chrysurus (Cuvier and Valenciennes) described by Longley and Hildebrand (op. cit.) as being bright yellow in a fish that was guarding a nest.

2.4.2 Courtship

Male fish normally hover several feet over the nest

site, moving closer when other fish intrude into their established territories. While hovering, they feed on planktonic organisms which drift past the nest. Apart from defending the territory against intruders, they occasionally fan the eggs, or engage in the nuptial display which serves to attract females to the nest. The display becomes most intense when other Dascyllus albisella approach the territory, but is also carried out when fish are not in the immediate area.

At the beginning of a display, the male swims upward at a steep angle using only its pectoral fins for locomotion. Quite suddenly, it turns on its side and darts toward the bottom in a curving half loop, at the bottom of which it turns upright and sometimes immediately repeats the performance. The curving loop is accomplished by an exaggerated anguilliform motion which, along with their white color, makes them very conspicuous to an observer and presumably also to other fish of the same species. If the performance is repeated continuously, the exaggerated swimming motion is also used for the upward phase of the display and the fish accomplishes a complete loop. A series of loops may be performed in rapid sequence but the fish usually rights itself after each loop.

The display is apparently directed toward a particular fish as activity often increases or decreases with the

approach or withdrawal of a particular individual. If the "courted" fish swims in the general direction of the nest, the male discontinues his display and swims in front of her, and leads her to the nest site. If the female begins to swim away from the nest, the male resumes his display until she either turns again toward the nest or withdraws completely. The fact that some Dascyllus albisella are chased from a territory while others are "courted" indicates that the displaying male can distinguish between sexes or perhaps between gravid and non-gravid females.

At the approach of a feeding aggregation of fish (Section 2.7), a displaying male may leave its nest and swim ten or twelve feet up from the bottom to join them and to perform his display. Here he sometimes encounters competition from other displaying males that have temporarily joined the aggregation from nearby territories. Three or four males may sometimes be seen displaying within a single feeding aggregation. However, not all displaying males in such aggregations are territory holders. Those with territories return to them, sometimes accompanied by a female, whereas the others remain with the aggregation as it moves along. The fact that some fish carry out this activity while not occupying a territory indicates a high level of motivation for the display which probably takes place in response to the stimulation from a nearby female or from a

displaying male, although an external "sign" stimulus may not be necessary (Tinbergen, 1951).

When the male and female arrive at the nest, the two fish may begin to spawn immediately. In most cases they tilt sideways with their abdomens close or touching in a V-shaped arrangement. In this position, they circle slowly almost touching the surface of the nest, the female laying eggs and the male fertilizing them while shivering noticeably at times. This activity may cease for short periods during which the fish engage in chasing each other over the surface of the nest. Later during spawning, the female may continue to lay eggs in one portion of the nest while the male continues to fertilize in another.

Spawning ceases when the female swims away from the nest. The male neither pursues her nor continues the nuptial dance, but continues to spend some minutes fertilizing the eggs, picking at the nest with its mouth, or dashing around over the surface. It gradually ceases this activity, again taking up a station close to the nest where it spends its time driving away intruders or fanning the eggs. After the nest is full of eggs the male becomes more aggressive and persistent in its attacks on other fish as well as on an observer. Approaching fish are intercepted farther from the nest than previously and the dashes of the male are sometimes accompanied by audible grunting noises.

The male spends a considerable amount of time fanning the eggs and picking at the nest, apparently removing dead eggs and perhaps debris not removed by fanning. When engaged in this activity the fish swims on its side, but with the longitudinal axis of the body tilted slightly upward. From this position, a vigorous swimming motion of the body coupled with a vigorous backing motion by the pectoral fins produces a strong current of water that washes over the nest removing debris and aerating the eggs. The fish moves slowly across the nest while performing this activity, occasionally dashing quickly to another part of the nest where the activity is resumed. Occasionally, several fish on adjacent nests have been seen fanning the eggs simultaneously, indicating mutual visual stimulation. A group effort such as this might conceivably result in more frequent fanning which would lead to better aeration and removal of foreign material and thus increase the possibility of survival of the eggs.

The nesting activity of Dascyllus albisella follows a similar pattern to that shown by other pomacentrids. Whereas other species may prepare the nest over a period of several days (Garnaud, 1957), Dascyllus albisella like Dascyllus trimaculatus takes only a short time. However, Dascyllus albisella spends considerable time fanning loose materials from the nesting site before eggs are deposited, whereas Dascyllus trimaculatus does not (Garnaud, op. cit.).

The body of the former species becomes bright white; and the latter species turns pale, assuming a bluish or greenish tinge. The nuptial dance of the two species appears to be the same and in both, the male performs in front of the female and leads her to the nest.

The nuptial dance of Dascyllus albisella is similar to that of other species in the genus that were observed by the author at Eniwetok Atoll. The similarity with Dascyllus trimaculatus has already been noted. Dascyllus reticulatus (Ruppell) and Dascyllus aruanus (Linnaeus) both displayed essentially the same type of activity, although in both cases the looping motion was less vigorous. In making the downward half of the loop, Dascyllus aruanus appeared to turn on its side at a less steep angle than the three other species. In all species, the accentuated swimming motion by which the fish carried out the characteristic maneuver was evident.

The display exhibited by Dascyllus albisella appeared to be much the same as that which Abel (1961) described for Chromis chromis Linnaeus and called the "signalsprung" or signal jump. The fish performed a similar looping motion at the nest site apparently in response to the presence of other fish of the same species that swam above the nest site. Like Dascyllus albisella, the females occasionally deserted this aggregation and moved to the bottom to spawn

in the nests. In chromis chromis, the nests were jointly defended by the males rather than individually defended as in Dascyllus albisella. The males of both Dascyllus albisella and Chromis chromis no longer engaged in nuptial display after the females had left the nesting area.

The nuptial dance of Abudefduf abdominalis (Helfrich, 1958) is somewhat different from that of Dascyllus albisella. Although Abudefduf abdominalis performs a barrel-roll type of activity like that of the species discussed above, it appears to incorporate other maneuvers such as "zigzag swimming", as well as assuming a vertical position in which it more or less stands on its head. Longley and Hildebrand (1941) gave a brief description of the nuptial dance of Pomacentrus leucostictus that is similar to that of Abudefduf abdominalis.

In all pomacentrids that have been studied, the nests are guarded aggressively. In most species the male fish apparently guards and fans the eggs after they are deposited in the nest. Breder and Coates (1933), however, noted that both male and female Pomacentrus leucoris attended the eggs that were laid in the New York Aquarium. Gohar (1948) observed that only one Amphiprion bicinctus ["]Ruppell attended a clutch of eggs laid at the aquarium in the marine biological station at Ghardaqa on the Red Sea. The situation in the field, however, is obscure since Amphiprion sp. lay

their eggs close to anemones, and it is uncertain whether they are defending the nest or the anemone.

2.5 OBSERVATIONS ON LARVAE

Dascyllus albisella eggs are easily hatched in the laboratory at room temperature and with good aeration. A number of hatchings were made in order to compare the larvae with those of Abudefduf abdominalis (Helfrich, 1958). It is hoped that the comparison might be an aid to others in distinguishing between the larval forms of the species.

Newly hatched larvae of Dascyllus albisella are about 2.5 mm. in length and have a filiform appearance and a prominent yolk sac. The yolk sac is oval-shaped instead of triangular as in Abudefduf abdominalis. At the time of hatching, they have a series of yellow patches which may merge into a yellow line, running the length of the trunk on both the dorsal and the ventral sides. It is believed that this consists of accumulated fatty material since it disappears within a day or two after hatching. This material may be characteristic of the species for it was seen in three different broods of newly hatched larvae and it has not been reported for Abudefduf abdominalis.

At the time of hatching, the eye of Dascyllus albisella is almost completely unpigmented except for a very fine

accumulation of dark particles on the ventral side. The pupil is at first colorless, but appears black on the second day. This change is associated with the further development of pigmentation within the eyeball, which also becomes black. Apparently the eye of Abudefduf abdominalis is in a later stage of development at hatching, as the pupil appears black at that time.

The behavior of the larvae undergoes a rapid change within the first few days after hatching. At hatching, they are quite helpless and float passively in the water. Such movements as occur do not produce oriented motion. At this time they may easily be caught by scooping them into a beaker or cup. By the end of the first day, oriented movement occurs over a distance of two or more inches. In consequence, they are much harder to catch as they will dart away from the beaker or cup.

During the second day, they appear to dart at particular objects in the water and also at each other. Larvae that are approached by others dart away as if in fright. It appears that these actions are the first manifestations of responses associated with feeding and escape from enemies. On the third day, the larvae strike at minute objects on the bottom and lower sides of the containers. This behavior is accompanied by jaw movements, which suggest that the fish are trying to ingest objects. However, attempts at

feeding them failed.

Soon after hatching, the larvae collect at the surface or in the upper half of the water column. It is not certain whether they arrive there as a result of their own activity or as a result of positive buoyancy. After a day or so when they become better oriented, they dart toward the surface of the water and remain at or near the surface while it is illuminated by overhead lights. Garnaud (1957) observed similar activity in Dascyllus trimaculatus larvae and concluded that the larvae were pelagic, a conclusion that also seem justified for Dascyllus albisella.

2.6 GROWTH RATE

The difficulties in obtaining juvenile Dascyllus albisella in quantity have been dealt with under the section on length frequency of juveniles (Section 3.3). Determining growth rates under natural conditions by tracing the progression of modal groups in length frequency distributions in time series was not possible with this species. Therefore, a number of attempts were made to determine the growth rate in other ways.

Four cages measuring 4 x 4 feet square were constructed from galvanized wire with 1 inch mesh size. They were placed in an old excavation in the fringing reef about six

feet deep located on the east side of Coconut Island at the end near the entrance to the channel leading into the lagoon. One living coral head was placed in each of the cages on a platform raised off the bottom, and 10 juvenile Dascyllus albisella were introduced into each. It was thought that the fish would remain close to the protection of the coral head and that the presence of the cage around them would act as a further stimulus causing them to remain associated with the coral. However, within two days all but two of the fish had disappeared. Both of the fish had developed a very pale coloration and a translucent snout. Both disappeared within a few days.

The cages were restocked with more fish, but some of these disappeared the next day and all but three had left by the end of one week. The three remaining fish had developed the same appearance as those in the previous attempt. Four of the fish, recognizable because of the translucent snout, were found with a group of wild fish in a large coral head located about six feet from one of the cages. Both the wire in the cages and the coral heads had become silted. The method was abandoned in view of these difficulties.

An attempt was made to establish measured juveniles in coral heads that were placed in more or less natural positions in characteristic habitats. On November 10, 1959,

5 live coral heads were transported from Coconut Island to the south side of Kewalo Easin on the leeward side of Oahu where they were placed on the bottom in the dock area, and five juveniles were introduced into each. By the time that all of the fish had been released, a check of the results showed that most of the fish in two of the heads had already been eaten by trumpet fish (Aulostomidae), which were abundant in the vicinity. The predators were hovering around the coral heads in their attempts to capture the remainder of the fish. After two days, one coral head still contained five fish, three heads were empty, and one had apparently been removed by someone.

On November 26, 4 fish that remained in one of the coral heads were captured and their fork lengths were measured. An attempt was made again to catch them on December 10, but the fish deserted the coral head and hid among the rocks beneath it. Surprisingly, they remained within the head on December 15 when they were again captured and measured. After this, attempts to capture them by raising the coral head failed as did an attempt to poison them. The experiment was abandoned.

Table 5 shows the lengths of the fish over the 35 day observation period during which they increased in mean length from 18.9 to 23.9 mm. This corresponds to a mean growth rate of 0.14 mm. per day.

TABLE 5
 MEASUREMENTS OF THE FORK LENGTHS OF
 JUVENILE DASCYLLUS ALBISELLA IN ONE
 EXPERIMENTAL CORAL HEAD AT KEWALO BASIN
 DURING NOVEMBER AND DECEMBER, 1959.

	<u>Fork Length in mm.</u>		
	<u>Nov. 10</u>	<u>Nov. 26</u>	<u>Dec. 15</u>
	15.2	16.2	18.0
	16.7	20.9	23.0
	19.0	23.8	26.7
	20.0	25.5	27.0
	<u>24.0</u>	<u> </u>	<u> </u>
Mean Length	18.9	21.4	23.9

A similar experiment was started at Coconut Island on November 14. Three living coral heads were mounted on wooden platforms and placed on stakes driven into the bottom of the lagoon in front of the laboratory. One was placed close to the bank near the southeast boat landing and the other two were close to the bank on the opposite side of the lagoon, one being near the entrance channel and the other near a mangrove patch farther inside the lagoon. Six measured fish were introduced into each of the coral heads which were removable so that fish could be shaken out and periodically remeasured.

At the end of the first two-week period, the fish had all disappeared from the coral head near the entrance to the lagoon, and four remained in each of the other two heads. Because of this initial loss, the measurements recorded on November 29 were used as the first recorded lengths of the remaining fish.

Growth was followed for a 14 week period, after which the study was terminated because of a three month absence of the investigator. The average lengths of the four fish in each of the two coral heads are given in Table 6 and plotted in Figure 7. Growth followed a linear pattern with no significant curvilinear component. The increase in length during the 14 week period was 16.8 mm. with an average increase of 1.2 mm. per week or 0.17 mm. per day (the latter

TABLE 6. GROWTH RATE OF DASCYLLUS ALBISELLA
 IN LAGOON AT COCONUT ISLAND MARINE LABORATORY
 DURING 1959 AND 1960.

<u>Date of Observation</u>	<u>Coral Head #1</u>	<u>Coral Head #2</u>	<u>Number Fish in Each Coral Head</u>
1959 Nov. 29	13.3 mm.	14.2 mm.	4
Dec. 13	16.4	17.8	4
Dec. 27	19.4	19.9	4
1960 Jan. 10	21.4	22.1	4
Jan. 24	23.6	24.5	4
Feb. 7	25.6	26.3	4
Feb. 21	27.5	28.4	4
March 6	30.0	31.1	4

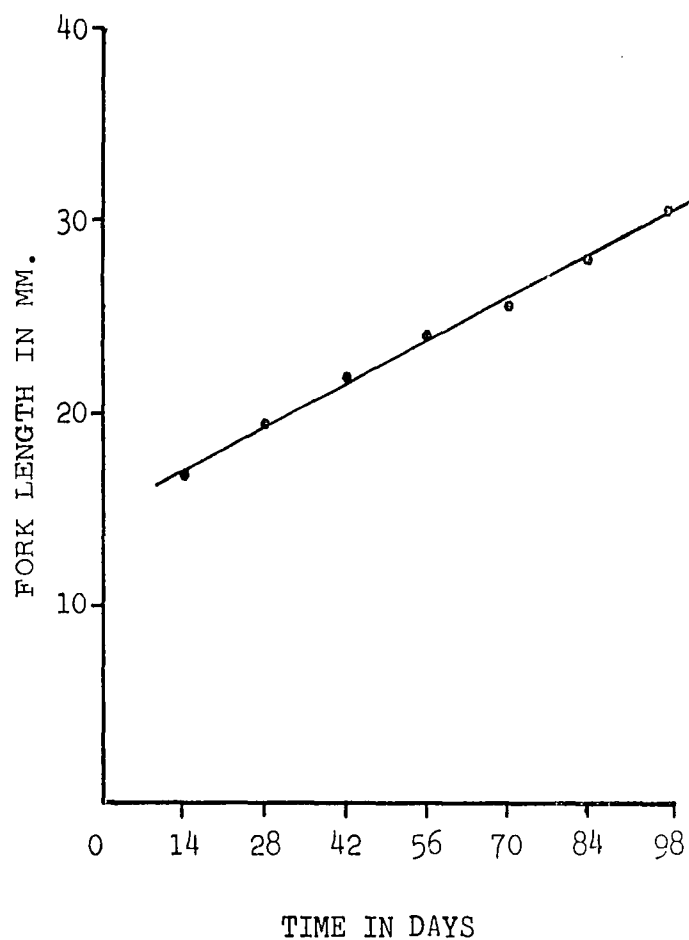


Figure 7. Average growth rate of juvenile *Dascyllus albisella* from November 1959 to March 1960 in the lagoon at the Coconut Island Marine Laboratory.

figure is a daily average and is not based on the slope of the line).

One additional observation of growth rate under natural conditions is available. A large number of juvenile fish appeared in experimental coral heads at Waikiki on or about June 22, 1961 (Section 3.12.1). This group of fish together with those that appeared late were captured on July 30. The length frequency distributions (Figure 35) show two distinct modal groups, one constituting recently arrived fish and the other, those which had grown in size since their arrival on or about June 22. If the average size of juveniles (14.7 mm.) at the time they first enter coral heads is used as the initial size of the latter group (17.1 mm.), it may be calculated that the fish have grown 2.4 mm. over a period of 38 days. The average growth per day, 0.06 mm., is considerably less than that of 0.18 mm. for the experimental fish in the lagoon at Coconut Island. One might expect the growth rate of the Waikiki fish to be greater rather than less than that of the Kaneohe Bay fish for the observations were made in the summer in the former and in the winter for the latter, and there is about a 5 degree difference in temperature that could be expected to influence growth. The discrepancy may be due to the rough nature of the Waikiki data. Another very likely explanation is that growth rate was depressed at the Waikiki

coral heads because of intense competition for food. The coral head was populated by a very large aggregation of fish.

The information concerning the growth rate of juvenile Dascyllus albisella may be compared with observations made by Helfrich (1958) on the growth of Abudefduf abdominalis. In comparing the progression of length frequency modes with time, he found that in February and March of 1957, fish grew an average of 0.13 mm. per day in comparison to an average of 0.17 mm. per day for juvenile Dascyllus albisella that were slightly larger in size. Thus, the growth rate of juveniles is similar in order of magnitude, but may be slightly higher in Dascyllus albisella. If the two species also grow at similar rates during the summer when presumably the rate is comparable, then it is possible that juvenile Dascyllus albisella could reach sexual maturity in about one year.

The sampling data are inadequate for drawing broad conclusions on the growth rate of Dascyllus albisella. It is apparent from its behavior that growth rate could vary widely depending on the location of the habitat. Observations of the feeding behavior of fish in the lagoon at Coconut Island, where water flow is slight, show that they feed much less actively than in Kaneohe Bay where a much greater water flow is encountered. This suggests that food

is less available in the former locality and that the growth rate should be slower. Again, as indicated by the Waikiki data, the intense competition for food in overpopulated coral heads may produce a slow rate of growth, thus further complicating the problem of evaluating the growth of fish that remain in a very restricted location. Since temperature was not studied in detail, its effects on growth cannot be evaluated.

2.7 FOOD AND FEEDING

2.7.1 Feeding Behavior

Dascyllus albisella feeds almost exclusively on planktonic organisms. Juveniles remain very close to coral heads on the bottom, and feed exclusively on plankters that drift past them, thus depending on water movements for their food. Adults are not as intimately associated with coral and move around within a restricted area which might be extensive if the bottom offers sufficient cover.

Adult fish off Waikiki differ in feeding behavior from those in Kaneohe Bay. In the former area, fish form feeding aggregations of from a few to hundreds of individuals, which are separated from each other by several feet or more, and which move independently in various directions while feeding. Individuals move rather slowly and deliberately as they feed, picking small organisms from the water;

They do not exhibit the quick darting motions of the juveniles. Although the organization of the school is loose, an integrity exists and fish move slowly along as a unit. The individuals of an aggregation congregate in a stratum of water that may vary in thickness from 10 to 20 or more feet.

Because of turbidity, it was difficult to make observations on feeding in Kaneohe Bay. The few groups of adults that have been seen did not ascend more than a few feet off the bottom in their feeding activity. The aggregations maintained a much closer relationship with the bottom than those at Waikiki and the former were much wilder. The readiness with which they took flight suggests that they were in a more excited state. Fish in such a state of agitation might not have spent much time feeding as those that inhabited clear water off Waikiki. In addition, their behavior in staying close to the bottom probably restricted the amount of water available to them from which to catch plankters.

Feeding aggregations such as those seen in adult Dascyllus albisella are characteristic of other pomacentrids. In Hawaii, Chromis ovalis and Abudefduf abdominalis fed in this manner and Chromis verator, Chromis vanderbilti and Chromis leucoris Gilbert did so to a lesser extent. Limbaugh (ms.) observed that off the coast of California,

Chromis punctipennis (Cooper) gathered in large aggregations while feeding on plankton that drifted in on the currents. Abel (1961) observed that Chromis chromis Linnaeus gathered in swarms over the nesting area where there can be little doubt that the fish fed on the plankton when not engaged in egg laying and related activities.

This type of feeding behavior appeared to a lesser degree in the behavior of Dascyllus trimaculatus and Dascyllus reticulatus at Eniwetok Atoll. There the fish did not wander over relatively large areas, but were restricted to a particular coral head or knoll. Although Dascyllus trimaculatus fed up to 15 or 20 feet from shelter, they always returned to a certain area when pursued. Dascyllus reticulatus fed only up to about 10 feet from shelter and Dascyllus aruanus rarely departed more than one or two feet from a coral head. It is probable that the abundance of large predatory species at Eniwetok Atoll kept the fish more closely confined to shelter. On two occasions, the appearance of carrangid fishes resulted in immediate withdrawal of aggregations of Dascyllus reticulatus into their coral heads.

2.7.2 Food

The food of Dascyllus albisella is much like that of other plankton feeding species and is comprised of many different kinds of planktonic organisms. The stomach

contents of 90 fish caught at different times and places were identified and measured for volume in a graduated cylinder. The results were summarized by calculating the percentage of various organisms contained in the stomachs of fishes that were arranged into three size groups (Table 7).

Copepods were the most abundant organisms found in stomachs and fragments of polychaete worms, larvaceans, miscellaneous crustacea and adult shrimp-like crustaceans were also well represented. Copepods also formed the greatest volume in stomach contents of the smaller fish, whereas larvaceans and shrimp-like crustaceans formed the greatest volume in the larger fish. A discussion of relationships between organisms found in the stomachs of juveniles and selectivity in feeding appears in Section 3.8.

2.8 MIGRATION

Large concentrations of adult Dascyllus albisella live in the immediate vicinity of patches of glomerate corals in the waters of Waikiki on the leeward side of Oahu. The coral beds serve as cover for the fish, and range in area from a few square feet to an acre or more. The patches of coral occur on very flat rock bottom and may be either far from other similar patches, adjacent to them or separated by varying distances. Figure 8 is a photograph taken at a depth of 70 feet off Waikiki showing a fairly large

Item	Number of Fish Containing the Item			Percentage of Stomachs Containing Item	Average Percent Composition by Vol- ume (as Percentage of Total Volume)		
	Fork Length (mm.)			All Fish	Fork Length (mm.)		
	10-30	30-90	90-130		10-30	30-90	90-130
Copepods	30	26	24	89	84	30	23
Larvacea	11	14	14	43	13	61	66
Larval crab stages		3	10	14		5	14
Shrimp-like crustaceans	2	11	17	33	11	43	60
Amphipods	1	3	6	11	2	3	1
Polychaet worm fragments	12	13	19	49	18	22	13
Eggs	1	1	16	20	1	1	20
Algae	4	2	8	15	4	6	2
Salps			4	4			1
Siphonophores			2	2			1
Misc. small crustaceans	2	13	16	34	8	2	3
Fish larvae		8	12	22		2	1
Foraminifera	3	1	3	8	1	1	1
Veligers or post-veligers		2	6	9		1	1
Chaetognaths			7	8			4
Unidentified remains	<u>3</u>	<u>15</u>	<u>18</u>	40	2	12	5
TOTAL	69	112	182				

TABLE 7. STOMACH CONTENTS OF 90 DASCYLLUS ALBISSELLA
CAPTURED IN DIFFERENT LOCATIONS AROUND THE ISLAND OF OAHU.



Figure 8. Habitat of adult *Dascyllus albisella* showing *Porites lobata* coral head cover and flat bottom where nesting occurs.

glomerate head of Porites lobata with two adult Dascyllus albisella hovering over it. To the right of the patch can be seen a typical section of flat rock bottom on which fish make their nests and lay their eggs.

In many cases two patches of coral that are relatively close to each other have aggregations of fish that appear to be associated with only one or the other of the patches. When feeding, an aggregation travels over the bed of coral, which may be fairly extensive, and does not appear to depart more than 20 or 30 feet beyond the periphery.

A situation was encountered at section A off Waikiki in which three patches of coral were located at varying distances from each other (Figure 9). The two large patches (I and III), had aggregations of fish estimated at between 300 - 400 individuals, which were never seen to stray more than about 20 feet in any direction beyond the coral. The smaller patch (II) had only about 40 fish which appeared to remain in the one spot. An attempt was made to obtain information on possible movements of fish between these three locations.

Since Dascyllus albisella do not readily enter commercial traps off the Waikiki area, a special trap was designed to catch the fish. The trap was 3 feet square with the four vertical edges made from 1/2 inch pipe. The top and bottom were made of transparent sheet plastic, but the

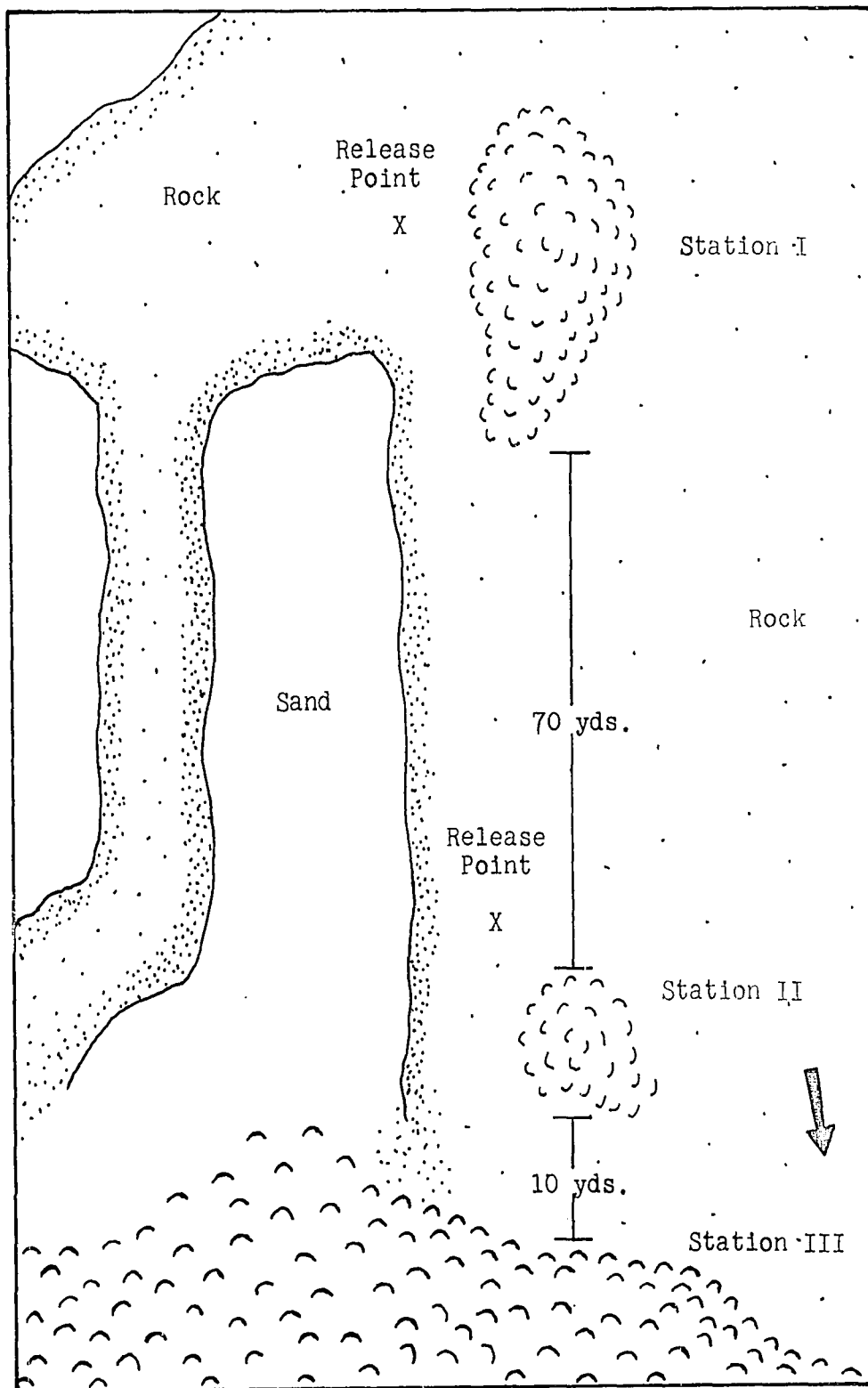


Figure 9. Position of stations and release points used in studies on migration of adult Dascyllus albisella.

sides were open. A square metal frame with an attached net was designed to fold down flush with the bottom. Lengths of rubber tubing were attached to each of the four corners of the frame and to the tops of the pipe stanchions above them. Pulling the frame and net down to the bottom of the trap opened the sides of the trap and put a strain on the four lengths of tubing. When a trigger was released, the net was pulled upward by the stretched tubing thus closing the sides of the trap. Adult fish quickly gathered in the open trap when sea urchins were crushed or when hamburger was released. When a sufficient number had entered, the trap was sprung and they were caught.

The trap was fairly efficient, but was difficult to use from a small boat and required the efforts of at least two people. Difficulty was experienced in getting it out of the water, particularly when the surface was choppy or a slight current was running. Even under ideal conditions, only two sets could be made during one day. Trapped fish had to be raised slowly to the surface to allow them to decompress; this process required more than an hour of work. After tagging, fish were taken immediately to the bottom and released. In spite of the difficulties, a number of successful catches and taggings were made.

Since observations of tagged fish were to be made visually underwater, a type of tag was employed that

streamed back over the dorsal side of the fish for greater visibility. This consisted of a 6 inch piece of yellow spaghetti nylon tubing inserted through the back of the fish below the soft dorsal fin. The ends were brought around to form a loop and were clipped together. The tag was treated with bacitracin ointment in an attempt to reduce infection of the wound.

About four days after release many tagged fish had developed raw areas about $\frac{1}{2}$ inch in diameter around the tag wound and the holes through which the tags were inserted had increased to about twice their original size, thus loosening the tags. After about a week, the tags on a few fish had worked through the enlarged area of deteriorating flesh and were lost. Some fish which had shed their tags survived and the wounds healed within five weeks after release, leaving a longitudinal scar along the postero-dorsal side.

The behavior of tagged fish after release may be of interest to others who may use this method with other species. Upon release, a tagged fish would swim away in an unsteady fashion and would sometimes swim a straight course that seemed to be independent of the presence of other fish. After traveling 50 or 60 feet, it would turn and then join other fish in the vicinity, which showed no noticeable reaction toward it. The locomotory behavior was altered.

A tagged fish swam with greater effort than an untagged fish and used its trunk musculature as well as its pectoral fins.

The tagged fish tended to remain together immediately upon release and thereafter for a period up to one week after release. At times as many as 5 tagged fish were seen together in the feeding aggregation and all were behaving normally. The knowledge that some tagged fish remained closer to each other than to other fish in the feeding aggregation is important to programs designed to sample the Dascyllus albisella stock by utilizing this method of tagging. It is apparent that the failure of tagged fish to disperse randomly throughout the stock might lead to erroneous conclusions concerning the population.

Tagged as well as untagged fish were also seen among the coral on the bottom. However, it was apparent that there were proportionally more tagged than untagged fish in such places. This tendency of tagged fish to remain close to the bottom rather than in the feeding aggregation might also lead to non-random sampling.

Three groups totaling 38 fish were caught and tagged over a period of 10 days (Table 8). It had originally been decided to tag separate batches of fish with different colored tubing, but since the catches were small, the same yellow color was used and the three groups were considered

TABLE 8. NUMBERS OF TAGGED FISH REMAINING AT VARIOUS
STATIONS OFF WAIKIKI DURING 1959 AND 1960.

	<u>Number Tagged Fish Observed</u>			<u>Percent Tagged Fish Observed</u>
	Station			
	<u>I</u>	<u>II</u>	<u>III</u>	
Nov. 15, 1959	12	5	0	45
Nov. 22, 1959	16	8	1	66
Dec. 6, 1959	10	8	1	50
Dec. 20, 1959	8	8	1	45
Jan. 10, 1960	8	7	no obs.	39
Jan. 31, 1960	3	2	1	17
Feb. 14, 1960	0	0	1	3

<u>Date of Tagging</u>	<u>Number of Fish Tagged</u>
Nov. 1, 1959	7
Nov. 7, 1959	14
Nov. 11, 1959	<u>17</u>
TOTAL	38

as one release, and thus could not be distinguished. Other releases with different colored tags were not made because of the difficulties of catching and tagging the fish.

All of the fish were captured at station I and were tagged between November 1 and 11, 1959. It was planned to release the fish at station I, but due to the turbid condition of the water and the fact that the boat drifted, 7 fish were accidentally released at station II. The error was not discovered until the next observation was made and the presence of the fish was noted at station II along with certain landmarks seen at the time the release was made. Thirty-one fish were tagged and released at station I as planned.

The number and percentage of tagged fish observed between November 15 and February 14 is shown in Table 8. A relatively large percentage of tagged fish (45 - 60%) were observed during the first five weeks after tagging. Fewer tagged fish were observed after this period, probably because the tags dropped off and the fish became relatively inconspicuous. Occasionally, fish were seen that had scars resulting from tag wounds. Such fish were recorded along with those that still retained tags.

It is apparent that some movement of fish occurred since the number of fish at station II increased from 5 to 8. However, since 7 tagged fish were released at station

II, it is certain that only 1 fish moved there from station I. One other fish moved to station III from either station II or station I. Apparently, movement was not extensive at any time and particularly after November 22.

Little information is available concerning the movements of coral reef fishes. After a number of tagging experiments, Randall (1955) concluded that extensive migrations of the surgeon fish, Acanthurus triostegus sandvicensis, do not take place, and Helfrich (1958) noted that Abudefduf abdominalis tagged along the south edge of Coconut Island remained in the vicinity for a period of about four weeks after which they lost their tags or migrated to other areas. Bardach (1958) tagged a number of reef fishes in Bermuda and observed that two out of five specimens of the pomacentrid fish, Abudefduf saxatilis (Linnaeus) remained at the same small reef on which they were tagged for 30 and 50 days, while Pomacentrus fuscus and Pomacentrus leucostictus were observed in the same locality for over 40 days.

2.9 COLORATION

Because of their more accessible location in shallow water, juveniles are more often seen than adults. In such locations, they are usually well pigmented and show a maximum of contrast between the dark and light areas of the

body. They also have a conspicuous spot that may be either white or turquoise. However, under certain conditions, juveniles become very pale in appearance although not to the same extent as the adult.

The coloration of adults ranges from an almost pure white (except for caudal, anal and ventral fins) to an almost pure black condition with intermediate shades of gray. The particular coloration of an individual is closely related to its behavior and therefore, is discussed as a function of that behavior. Three types of coloration are recognized in relation to the state of activity of the fish -- nuptial, feeding and excitation. The first has already been discussed (Section 2.4.1) but will be compared with the other two in the following sections.

2.9.1 Feeding Coloration

Adult as well as juvenile Dascyllus albisella spend almost all of their time feeding. The only time when fish do not feed is when they are engaged in reproductive activity and when they are within the coral head. Since most of the time is spent feeding, the general coloration of the fish is called "feeding coloration" in this work. Although fish in Kaneohe Bay spend most of their time feeding, their behavior is such that the general coloration might result from the influence of other stimuli in the environment (Section 2.7.1).

The colors of feeding fish vary from jet black to almost pure white depending on the age of the fish, the composition of the bottom over which they are feeding, and their state of excitation. Juveniles living under identical conditions, except for the type of bottom around the coral head, are darker in color over rock bottom than over sand bottom. Figures 10 and 11 (taken at a depth of 70 feet off Waikiki) show two aggregations of juveniles on the same day under conditions as described above. The darker fish over the rock bottom (Figure 10) show only a suggestion of gray surrounding the white spot on the body and on the snout. The fish over the sand (Figure 11) are very pale except for two vertical gray-black stripes.

It is suspected that the reflection of light from the bottom is not the only factor influencing the coloration. Juvenile fish over rocky bottom behave differently from those over sandy bottom. The former stay much closer to the coral head and only make occasional short dashes outward after food. The latter, however, extend much farther out and do not dash back into the head as readily as the former, although they may return part way when frightened. It is quite apparent that the fish over the rock bottom are more active than those over sand. As will be seen shortly, adult fish show a darker coloration under the influence of increased activity. The basis for the increased activity

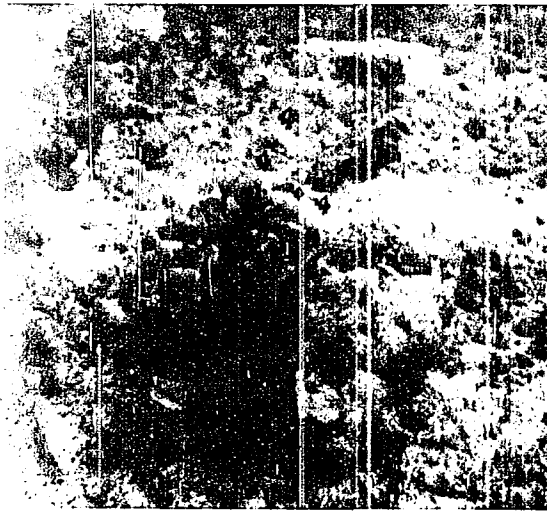


Figure 10. Dark feeding colors of juvenile Dascyllus albisella associated with an experimental Pocillopora meandrina coral head located on rock bottom off Waikiki Beach.

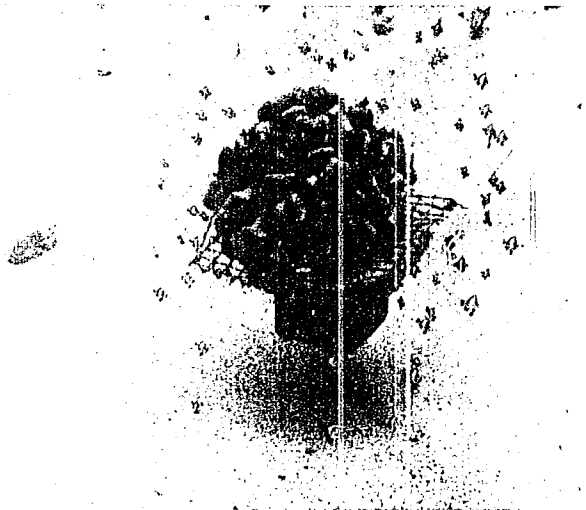


Figure 11. Light feeding colors of juvenile Dascyllus albisella associated with an experimental Pocillopora meandrina coral head located on sand bottom off Waikiki Beach.

of fish over hard bottom is believed to be an interaction between factors such as water movement (in some areas), the presence of other fish (including predators) and possibly sign stimuli presented by surrounding physical features.

The coloration of adult Dascyllus albisella in Kaneohe Bay is different from that of adults found off Waikiki. In the former area, the fish are black with the white body spot showing very distinctly. However, off Waikiki, the fish are almost entirely white, except for caudal, anal and pelvic fins. The whiteness, however, is slightly dulled by a faint pigmentation on the borders of the scales. This coloration is almost identical to the nuptial coloration of reproducing fish and appears to differ only in the presence of the pigmentation on the borders on the scales and possibly in the lack of an orange tint in the caudal fin. It must be emphasized, however, that these differences are subjective impressions, and no difference actually may exist. The only sure way to differentiate between a fish in nuptial colors and a feeding fish is to study its behavior and its location in respect to the bottom. Figure 12, which shows a guarding male Dascyllus albisella in nuptial colors, may be compared with Figure 13 which shows the feeding colors of an aggregation of adult Dascyllus albisella.

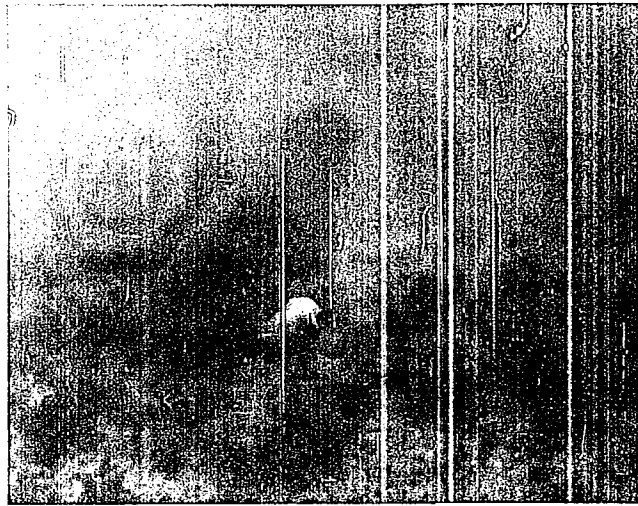


Figure 12. Male Dascyllus albisella in nuptial colors over nest site.

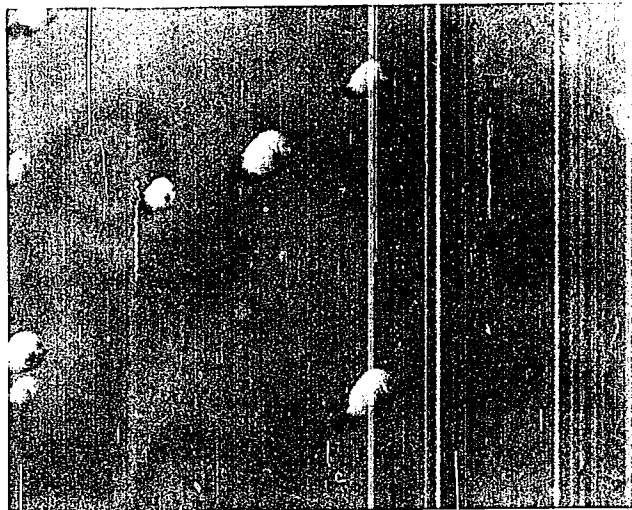


Figure 13. Part of an aggregation of adult Dascyllus albisella showing feeding coloration.

2.9.2 Excitation Coloration

Fish that are in a state of agitation or excitation show a different coloration from those already mentioned. The head and anterior part of the body posterior to the pectoral fin turn a dark gray-black as does the dorsal fin, and the caudal peduncle. The remainder of the body becomes a light shade of gray and the white spot high on the body is often conspicuous. Figure 14, taken at a depth of 70 feet off Waikiki, shows this type of coloration which here is displayed in the presence of the diver, who has stirred up the bottom.

This coloration becomes prominent within a matter of minutes when fish become excited. Male fish that are engaged in nesting change from the white to the dark condition if they are continually disturbed. The intensity of the contrast depends on the duration of disturbance. If sea urchins are crushed near the fish, or a disturbance is made on the bottom which they come to investigate, they also make the transition from the white to the dark coloration.

The fish become quite active before the actual color change occurs. Nesting fish often grunt loudly and dart quickly around a human observer disturbing the nest site. Fish that gather at some disturbance on the bottom mill around excitedly and make short dashes at particles that



Figure 14. Adult Dascyllus albisella showing excitation colors in response to the activity of the diver.

are stirred up. After the cessation of such activity, the color gradually fades and the fish "settle down" and move quite slowly again.

It is thought that the reason for the dark coloration of the fish in Kaneohe Bay is related to their more active state. They appear to be relatively timid and cannot be approached closely by an observer. They spend their time close to the coral and make more darting movements than Waikiki fish. They approach a stationary observer with the greatest caution and with many quick advancing and fleeing motions. They show a high state of activity similar to that of juveniles that are associated with coral heads.

The similarity in color between the feeding fish at Waikiki and those on the nesting site is believed to result, partly at least, from a relative state of inactivity. The fish guarding the nests spend most of the time hovering quietly in the water. Attacks upon other fish are rather infrequent and are of very short duration. They engage in the nuptial display only infrequently. However, as the nest becomes older, the guarding male becomes darker. This can be related to the extent of excitation for the fish spends more time fanning the eggs and chasing away other fish with more prolonged attacks.

Feeding adult fish, in contrast to juveniles, move

very slowly. They maintain their positions in the water by using the pectoral fins only. The trunk musculature is apparently used for other activities, such as reproduction and rapid movement in escaping from enemies. The general appearance of a feeding aggregation is one of unhurried activity in which fish seem to be suspended in the water and pick out the plankters that drift past. The energy expenditure of the fish is obviously not great.

The significance of color and color changes in fishes has received wide attention in the literature. In many teleosts, the color changes so as to blend with that of the background. Variation in this phenomenon ranges from species like Carassius and Pomacanthus, which show no grossly evident response to the background (Breder, 1959), to species of flounders which may change the pattern as well as the color to match the surroundings (Mast, 1916). Within the flatfish family Pleuronectidae, the color may vary from extremes of gray and black to shades of blue, green, orange, pink or brown. Coloration and color changes in cyclostome, elasmobranch and teleost fishes as well as a discussion of the role of chromatophores has been the subject of an extensive review by Parker (1948).

The basic color assumed by fishes in relation to their background is strongly influenced by particular drives. Breder (1959) pointed out that "colors in response to an

emotional state act more or less independently of and may interfere with the full expression of colors that match the background and in some cases may fully suppress them." Such phenomena have been most often studied in relation to courtship coloration where male fish often assume vivid hues that make the fish contrast more or less strongly with the background rather than blending with it. This type of adornment is particularly marked in male fish of species that show territoriality and guard the eggs (Noble, 1938). Earlier opinions as to the attractiveness of such colors to females of the species, were confirmed and some of the properties of the particular colors and behavior involved in the response were elaborated by Pelkewijk and Tinbergen (1937) in their classical experiments with models of the three-spined stickleback, Gasterosteus aculeatus Linnaeus. Their findings revealed that to evoke courtship in a female, the model must have a red patch on the underside, a greenish-blue upper side and a blue eye. On the other hand, courting by the male occurred in the presence of a model which was silvery colored and had a swollen abdomen. Baerends and Baerends-van Roon (1950) showed that in some species of cichlid fishes (e.g., Hemichromis bimaculatus Gill), the young followed the parents in response to a combination of typical movements and color. The same authors also present an analysis of changes in the chromatophore systems that produce color changes in the cichlid fishes.

The high state of excitement shown by fish during reproductive activity as well as fighting is accompanied by brighter hues. The basis for such a correlation no doubt lies in the interaction of nervous and hormonal elements that generally combine to produce color changes (Parker, 1948; Baerends and Baerends-van Roon, 1950; Breder, 1959). Like male Dascyllus albisella, which becomes darker when fertilizing eggs, the color of Abudefduf abdominalis rapidly intensifies during certain maneuvers associated with reproductive activity (Helfrich, 1958); similarly, Dascyllus trimaculatus briefly changes to a pale blue color (Garnaud, 1957). It is not unreasonable to expect that a generally higher level of activity in Dascyllus albisella in relation to stimuli other than that produced by reproductive activity would result in fish assuming (darker) coloration. It is likely that coloration changes resulting from fright and curiosity also occur in other fishes, although such changes could be expected to be specific to different species.

The author has observed that Dascyllus albisella and also Dascyllus trimaculatus assume a light coloration when they are inactive in aquaria at night. This is probably typical of pomacentrids as it has also been observed by Breder (1949) in Pomacentrus leucostictus and Abudefduf saxatilis, and by Franzisket (1959) in Dascyllus aruanus. These observations are in accord with the hypothesis that

in Dascyllus albisella lighter color is associated with lesser activity and vice versa, although the intensity of light itself is doubtless involved.

Coloration of fishes in relation to background has been given considerable attention by Breder (1948, 1949, 1959), who points out that one of the most obvious and widespread reactions of fishes is their tendency to match the tone and often the color of the background against which they are seen. However, fish usually keep dark colors unless the bottom within the visible range is light sand. He also stated that changes in locomotion, color and pattern, which are both hormonally and nervously controlled, are generally the first responses of a teleost to a given stimulus. The behavior of at least some fishes appears to be related in some way to changes in background coloration since Breder (1959) showed that lighter colored clupeoids would only swim over a matching background and avoided darker backgrounds that contrasted with their coloration. The author has also seen pale goatfishes avoid darker patches of reef even when pursued vigorously.

In contrast to the above observations, some fishes assume a maximum contrast rather than a blending with the background. This was the case with juvenile Chaetodipterus fabre (Breder and Rasquin, 1955), which assume a dark coloration, thus resembling conspicuous particles of

inanimate objects over sandy bottoms. Randall (1960), in a study of mimicry and protective resemblances in marine fishes, pointed out a number of species of different families that contrast with the general background while matching such floating materials as sticks, leaves, and algae. The great diversity in coloration of fishes in relation to background points out the complex nature of the nervous-endocrine mechanisms involved.

SECTION III

ECOLOGY OF JUVENILES

Ecological studies of the interrelationships between coral reef fish and the physical and biological factors in their environment are relatively few in number. Most of the literature deals with a few specialized ecological aspects involving such conditions as commensal relationships between fish and anemones as reported by Garnaud (1951), Gohar (1934), Gudger (1929), and Verwey (1930). The increased interest in the productivity of marine environments in recent years has given considerable impetus to ecological studies, but the invertebrate organisms and primary producers have received the bulk of the attention (Odum and Odum, 1955). Predator-prey relationships among marine animals remain obscure particularly from the point of view of field observations. Most field work that deals with the interactions between populations of animals has been carried out by observing insects (Brian, 1952; De Bach, 1949; Elton, 1949). Information concerning the coral reef fishes and their environment is widely scattered throughout the literature and usually exists as brief notes concerning some occurrence that has not been integrated with other pertinent facts in the animal's ecology.

However, a few works dealing with the biotic and physical interactions between species of coral reef fishes

are available. Among these are the works of Helfrich (1958) and Randall (1955), which dealt with the life histories of Abudefduf abdominalis and Acanthurus triostegus sandvicensis respectively. Among other things, these works deal with the early life histories of juveniles in their most characteristic habitat, the tide pool. The effects of surge, temperature and predation were considered in these habitats, but little attention was given to these factors in the areas where juveniles were not present. As a result, it is not possible to make a comparison between habitats that might indicate which factors are influential in determining distribution. Hiatt and Strasburg (1960) gave what is probably the most comprehensive account available of the ecological relationships between fauna on coral reefs. They dealt mainly with food and feeding interrelationships as well as with the general aspects of distribution in relation to substrate and hydrographic features. Gosline and Brock (1960) gave a brief account of the types of fishes found on coral reefs under varying conditions of water movement and types of shelter.

The present study was suggested by a number of questions that arose from observations on the habitat of juvenile Dascyllus albisella. The tendency for juveniles of this species to congregate around living coral of the genus Pocillopora is widely recognized throughout the islands.

However, they are also fairly often found in sizable numbers around pilings, sea walls, and other species of coral as well as in less numbers around sponges, poisonous sea urchins and large sea anemones. Therefore, it was apparent that a study of the fish in relation to such seemingly diverse habitats was essential to a life history study.

The scarcity of young Dascyllus albisella in the presence of surge led to the suspicion that this environmental factor was very important in determining their distribution. Gosline and Brock (1960) as well as Hiatt and Strasburg (1960) also recognized the possibility that this factor was important to the distribution of different coral reef fishes. Therefore, the investigation of this specific component of the environment was singled out for particular emphasis in this study.

In addition to providing details of the life history of one of the little known coral fishes, the present study was envisioned as having more far-reaching application. Any knowledge that can be gained in connection with the ecology of marine fishes is much needed as a basis for future studies of both the ecological interrelationships of marine animals and their behavior. According to Andrewartha (1961) ". . . we must first discover the laws governing the distribution and abundance of animals before we can advance very far in our understanding of the relationships

between the populations that make up a community."

The study embraced portions of two of the "three levels of complexity" in the laws of ecology referred to by Andrewartha (1961). The first of these, and apparently the least complex, are the "laws governing the physiology and behavior of individuals in relation to their environments." The second are the "laws governing the numbers of animals in relation to the areas that they inhabit: this is sometimes called population ecology." The third level of complexity, "the laws governing communities, which may be thought of as groups of interacting populations", is dealt with only lightly. The study was also expected to contribute toward an understanding of the dynamics of the ecosystem as a whole, which Clarke (1954) referred to as "the operation of the community and its environment as a functional unit." However, the present work does not deal with the complete ecosystem since certain biotic factors, e.g., surgeon fishes and wrasse fishes, were not studied because they were not considered important to the survival of juvenile Dascyllus albisella.

The basic criterion involved in much of this study was the distribution of young Dascyllus albisella in relation to their abundance. The commonness or rareness of the fish was a relative, rather than an absolute consideration. For example, it became clear that the fish were relatively

scarce in the presence of strong surge and large numbers of predators, and they were relatively abundant in calm water where predators were lacking and in coral heads of a particular type. The investigation probably most closely approaches that which Macfadyen (1957) would call a "field level" of investigation, which in this case also included experiments in the field. Attempts to carry out studies in the laboratory at the "experimental level" of investigation were largely unsuccessful.

It is very difficult to present simply the results of an analysis of various environmental factors as they occur in the field. Since the factors influence each other in various known and unknown ways, it is almost impossible to refer to one without considering its relationship to the others. For this reason it has been necessary to make cross references when discussing a particular environmental factor. In this dissertation, the factors are dealt with as separate units but are discussed in relation to each other and to the areas and sections in which they occur.

3.1 FEATURES OF STUDY AREAS

Four areas were selected for the study of the fish in relation to their environment. The Waimanalo, Kaneohe Bay and Kualua areas were selected because they contained the largest populations of juvenile fish that were found (see

Figure 15). The Waikiki area was selected because it offered an area of quiet water that presumably should be, but actually was not, inhabited by very large numbers of juvenile fish. All the areas, except Kaneohe Bay, had sections in which fish were concentrated alongside of sections in which fish were scarce. Different hydrographic and geographic conditions occurred in the areas with and without fish, thus affording a possible basis for the differences in numbers of fish.

3.1.1 Waimanalo Area

The area is located about three miles southeast of the town of Waimanalo (see Figure 15). The portion of reef studied was divided into four sections in such a way as to take the fullest advantage of natural geographic features as boundaries.

3.1.1.1 Section A

This section is a shallow flat ranging in depth from about three to five feet. The bottom is composed of basalt rock encrusted with various marine animals and algae, and from which isolated coral heads jut to heights of from six to twelve inches from the bottom. A few crevices of not more than a foot in depth and a few low mounds produce a slightly uneven bottom. The southern boundary is clearly defined by a sharp upward slope about 100 feet from shore. The slope is the outer boundary of a shallow flat adjacent



Figure 15. Map of Oahu showing study areas.

to the shore, which is exposed at low tide. The western boundary, due to the lack of natural geographic features, is an imaginary line fixed by range markers located on the shore. The eastern boundary is also a range line since the bottom continues in that direction where it terminates at the edge of section D. The northern boundary terminates at the edge of section C, which is a well defined channel with steeply sloping sides. The total area encompassed by section A is about 10,000 square feet.

3.1.1.2 Section B

This section is much like section A except that the depth is shallower, ranging from about 2 to 4 feet in the central, northern and western portions. The southern portion is a gradual slope from the shallower central portion down to the edge of section C, where the depth is about 8 feet. The northern boundary is marked by a fairly abrupt slope which drops down to another channel, the bottom of which lies about 5 feet below the surface. The eastern and western boundaries, as in section A, are bounded by imaginary lines that are accurately located by ranges. Coral heads are somewhat more scarce than in section A and the relative numbers of the two dominant species is slightly different (see Table 9). The area encompassed is smaller than section A, being about 7500 square feet.

<u>WAIMANALO</u>	<u>TOTAL NUMBER HEADS</u>	<u>PERCENT P. MEANDRINA</u>	<u>PERCENT P. MEANDRINA INHABITED</u>	<u>PERCENT P. LIGULATA</u>	<u>PERCENT P. LIGULATA INHABITED</u>
Section A	32	22	8	78	92
Section B	43	32	21	68	79
Section C	-	0	0	100	100
Section D	-	0	0	100	100
Kaneohe Bay	30	37	50	63	50

TABLE 9. COMPARISON BETWEEN NUMBERS OF CORAL HEADS OBSERVED
IN THE FOUR SECTIONS COMPRISING
THE WAIMANALO STUDY AREA.

3.1.1.3 Section C

This section is a channel extending in a northeast-southwest direction at a fairly uniform depth of 8 feet, the sides sloping rather abruptly up to section A and much more gradually up to section B. Interspersed sparsely throughout the sandy bottom are boulder-sized glomerate coral heads of the species Porites pukoensis. A few isolated coral heads of the coral Pocillopora ligulata are irregularly distributed throughout the area. An island in the sand, which is populated by a few coral heads, was chosen as the northeastern boundary and the southwestern boundary terminates at a large head of Porites pukoensis. The length of the channel is about 75 feet and the average width about 10 feet enclosing an area of about 750 square feet.

3.1.1.4 Section D

This section is also a channel lying about 100 feet south of section A and running in an almost north-south direction. At the shallower inshore end marked by an island in the sand, the channel is about 50 feet across. It gradually narrows in a seaward direction and then opens out again to a width of about 40 feet. The seaward terminus was taken as a fairly large island that rises some 6 or 7 feet from the bottom. Except for the narrowest portion, the western edge slopes gradually back toward sections A

and B, while the eastern edge is composed of a nearly vertical rock outcropping that rises some 10 to 12 feet from the bottom. As in section C, there are large glomerate coral heads and small ramose types scattered throughout the sandy bottom, which varies in depth from about 10 to 15 feet. The length of the ditch is about 130 feet and the average width is about 20 feet enclosing an area of about 2600 square feet.

3.1.2 Kaneohe Bay Area

The Kaneohe Bay study area presents a different type of habitat than the Waimanalo area. The bottom is flat and is located alongside the western edge of the sampan channel at a depth of about 10 to 12 feet. For the most part, the bottom consists of areas of barren coral rock from which juts an occasional coral head, usually of the species Pocillopora ligulata and Pocillopora meandrina. Lying between the areas of flat, encrusted rock are areas of sand that range in size from small pockets to areas of 100 or more square feet. In the center of the study area, which measures about half an acre, is an oval-shaped plot of the low growing alga, Dictyosphaeria sp. The plot measures about 50 feet in length and contains a number of coral heads of the species Pocillopora ligulata that protrude above the surrounding algae. This particular area had a large population of Dascyllus albisella, measuring from

about 30 to 80 mm. in length. No juveniles were associated with the coral heads that were interspersed among the algae. The area is more uniform than the Waimanalo area, which is broken up by a few channels and smaller crevices.

3.1.3 Kualua Area

This area consists of the general reef area between shore and the surf zone off the Kamehameha Highway about one mile northwest from Mokuiki (Chinaman's Hat Island). The reef at that point is about one-half mile wide from the shore to the surf zone, which closely approaches the shore about one-half mile north of the general area of observation, but holds well offshore in a southeasterly direction.

The reef itself is shallow ranging in depth from about 2 to 4 feet in the central portions. The bottom is mostly flat with occasional very shallow depressions running through it. The shallower portions lie nearer the shore, the bottom sloping very gently toward the surge zone, where it again rises within about 2 or 3 feet of the surface. Coral heads mostly of the species Pocillopora ligulata protrude noticeably above the bottom all through the area, but tend to be more abundant toward the middle of the flat. They also extend along the sloping inner edge of the reef behind the area where the ocean waves strike the reef.

3.1.3.1 Section A

This section is located approximately in the middle of the area where the water is about 3 - 4 feet in depth. The bottom is composed of a mixture of sand and chunks of worn coral as well as outcroppings of flat encrusted rock that has been worn smooth by the action of flowing water. Large patches of algae (Acanthophora sp. and Sargassum sp.) as well as extensive bare areas are present with juvenile Dascyllus albisella being found in the latter areas. Most of the coral heads extend in a "belt" that runs parallel to the shore for an undetermined distance.

3.1.3.2 Section B

This section is a flat rock outcrop that runs parallel to the surge zone, thus acting as a barrier to the waves coming from the open ocean. It is heavily indented by crevices and channels that mostly run in a seaward direction. Coral heads of the species Pocillopora ligulata and Pocillopora meandrina are present in the area, the former species being located farther back on the outcrop away from the more immediate influence of the breaking waves. There is very little algal growth as in the more inshore section, and as would be expected, the water movement in the section is much stronger than in the inshore section.

3.1.4 Waikiki Area

The Waikiki area (Figure 15) is located in the waters

off Ala Moana Yacht Harbor and extends southeastward to a position off the Royal Hawaiian Hotel. Three sections within this general area were selected for further study.

3.1.4.1 Section A

This section lies approximately $3/4$ mile offshore from the Ala Moana Yacht Harbor at a depth of 70 feet. The bottom is very flat rock and is broken by very few cracks or gullies. Interspersed here and there in the bottom are patches of sand that range in size from several feet in diameter to many acres. Patches of glomerate corals (Porites lobata) lie in scattered locations and provide cover for large aggregations of adult Dascyllus albisella. Ramose coral heads such as Pocillopora sp. are rare and with one exception (Section 3.2.4) were never observed to harbor juvenile Dascyllus albisella. Long-spined sea urchins (Echinothrix diadema) are common in the area and were seen to accommodate considerable numbers of juvenile Dascyllus albisella during certain times of the year (Section 3.13). Otherwise, juveniles were very scarce in the section, being found mostly as single individuals that hid from view in holes in coral rocks.

3.1.4.2 Section B

This section is located on a sloping bottom at a depth of about 15 to 18 feet. The bottom is level with a few Pocillopora meandrina and Porites sp. coral heads protruding above it and is indented by numerous cracks, often one foot

or more in depth. There is little sediment in the section due to the scouring action of the waves and sand-filled pockets are scarce. The section lies in the surge zone, although it is located some 200 yards seaward of the actual breaker zone. The surges are generated by unbroken ocean waves in contrast to the surge zone at Kualua where the surges are generated by waves on the landward side of the breaker zone. Juvenile Dascyllus albisella have never been seen in the section although apparently suitable coral heads are present. In this respect, the section is similar to section B at Kualua.

3.1.4.3 Section C

This section consists mostly of heads of glomerate coral of the genus Porites but was apparently almost devoid of juvenile Dascyllus albisella. Since studies on nesting behavior were carried out here, a fuller description is given under that topic (Section 2.3).

3.2 AGGREGATIONS OBSERVED IN THE FIELD

Juveniles were observed in the field under natural conditions by swimming with face mask and snorkle or with the aid of underwater diving apparatus (SCUBA). Frosted plastic sheets were used for recording underwater observations. Thermometers, salinity bottles, nets and tools were carried in a weighted bag which could be left on the bottom

when not needed.

In making observations in shallow water it was usually possible to remain on the surface of the water and count the fish. However, in the channels it was necessary to dive to the areas of the coral heads and to hold on to the bottom while the observation was being made. Fish could usually be approached to within about three feet before they would seek cover in the coral head. At this distance, the fish associated with the coral head could be seen and counted before they retreated.

One formidable problem arose in connection with counting the numbers of fish in the coral heads. It was extremely difficult to judge the size of the fish, particularly because of the continual motion of both fish and the observer. During the first few observations, an attempt was made to judge the length frequencies of the fish. However, the tendency of the fish to constantly change their positions and to intermingle with each other created a problem.

An attempt was made to identify the fish in a given head as "new fish" or "old fish" in relation to their period of residence in the coral head. The criterion for such judgements was based on the tendency for the caudal fin of very young fish to show a hyaline condition when they

initially colonize a coral head. However, aquarium observations showed that the tendency for the progressive spread of pigmentation over the caudal fin was variable with the size of the fish. The potential method of determining numbers of "new fish" in a head was not reliable because some larger fish retained the hyaline condition while some of the smaller ones rapidly lost it.

The best that was accomplished in respect to identifying size changes of fish in the heads was to note that the great majority of fish associated with them were seen to increase progressively in size during the period of months when they were under observation. The increase in size of fish in both individual coral heads as well as in an area as a whole is unmistakable and has been referred to by a number of different collectors that were interviewed.

In 1961, coral heads in sections A and B at Waimanalo (Figure 16) were identified by the same numbers as in 1960. In other words, coral heads having a certain number in 1961 represent the same heads that were known by that number in 1960, except that a new population of fish was present. The head lettered "a" in section A and those lettered "a, b, c, d and e" in section B represent heads that were populated in 1961, but not in 1960. The heads lettered "s, t, u and v" in section B and "w, x, y and z" in section D are experimental heads and will be dealt with under Section 3.12.2.

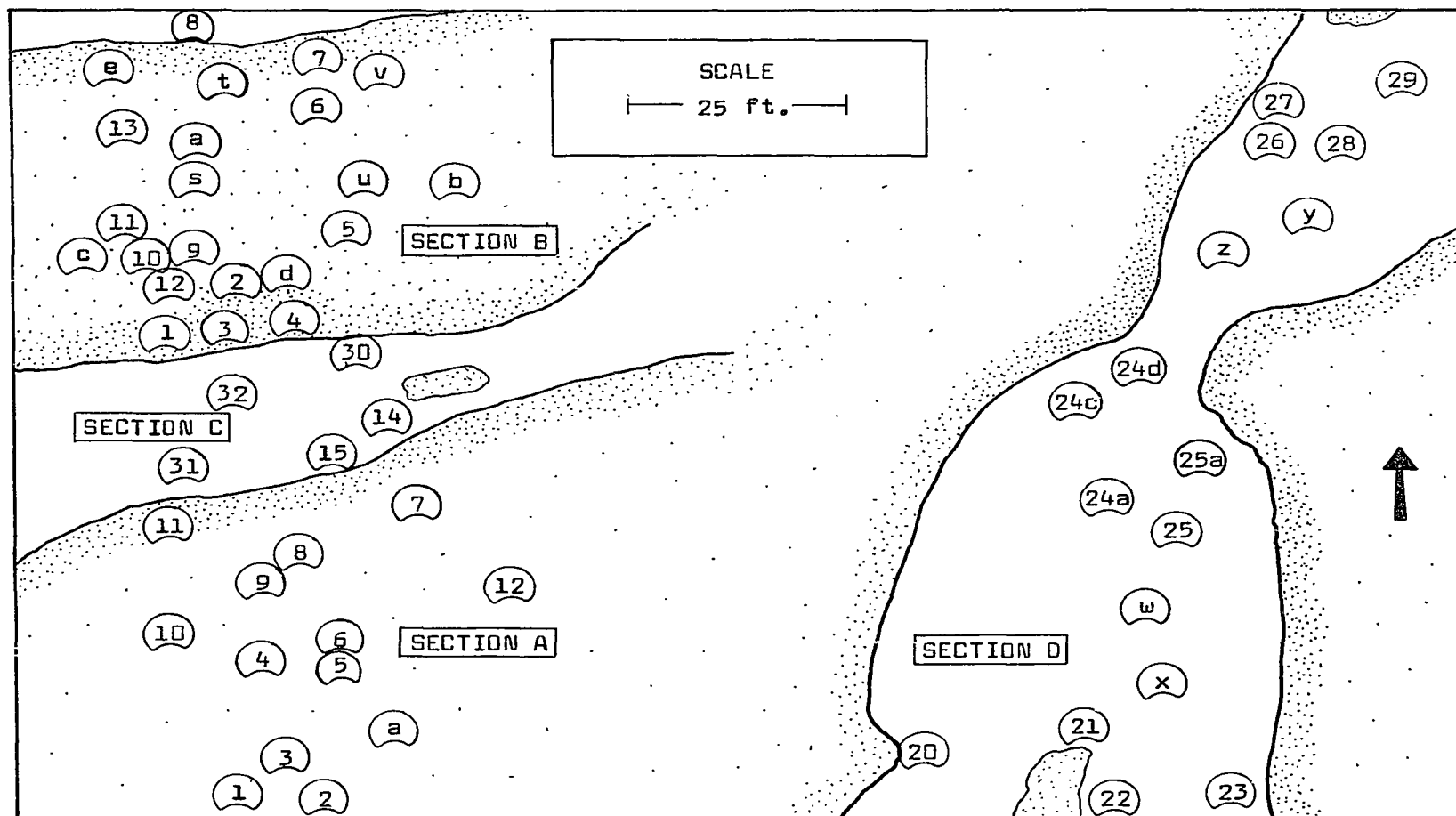


Figure 16. Map of the Waimanalo study area showing sections studied and locations of coral heads.

Coral heads were numbered as they were found and since all heads were not found at the same time, the numbering does not follow a regular pattern. The two heads known from section D in 1960 were given the numbers 22 and 23 during both 1960 and 1961 to indicate that they were the same heads that were populated part of the time during those years. Other than these two heads, all the heads with Dascyllus albisella that were found in 1961 in section D were not observed the year before.

3.2.1 Waimanalo Area

The results of the observations of numbers of fish seen at Waimanalo in 1960 and 1961 are summarized in Figures 17 and 18. In 1960 in section A, there were five coral heads (1, 2, 3, 4 and 10) that were populated by relatively large numbers of juvenile Dascyllus albisella. In contrast, section B had only three aggregations (1, 4, and 8) in which numbers of fish tended to approach those of section A. These three heads were located in deeper parts of section B that offered a habitat more like sections C and D that were a more optimal habitat judging from the numbers of fish found there. Aggregations of relatively few fish were found in the shallower central portions of section B, which in respect to surge, is a more turbulent environment. The remainder of the aggregations found in section A, which appeared to be rather homogeneous in respect to surge,

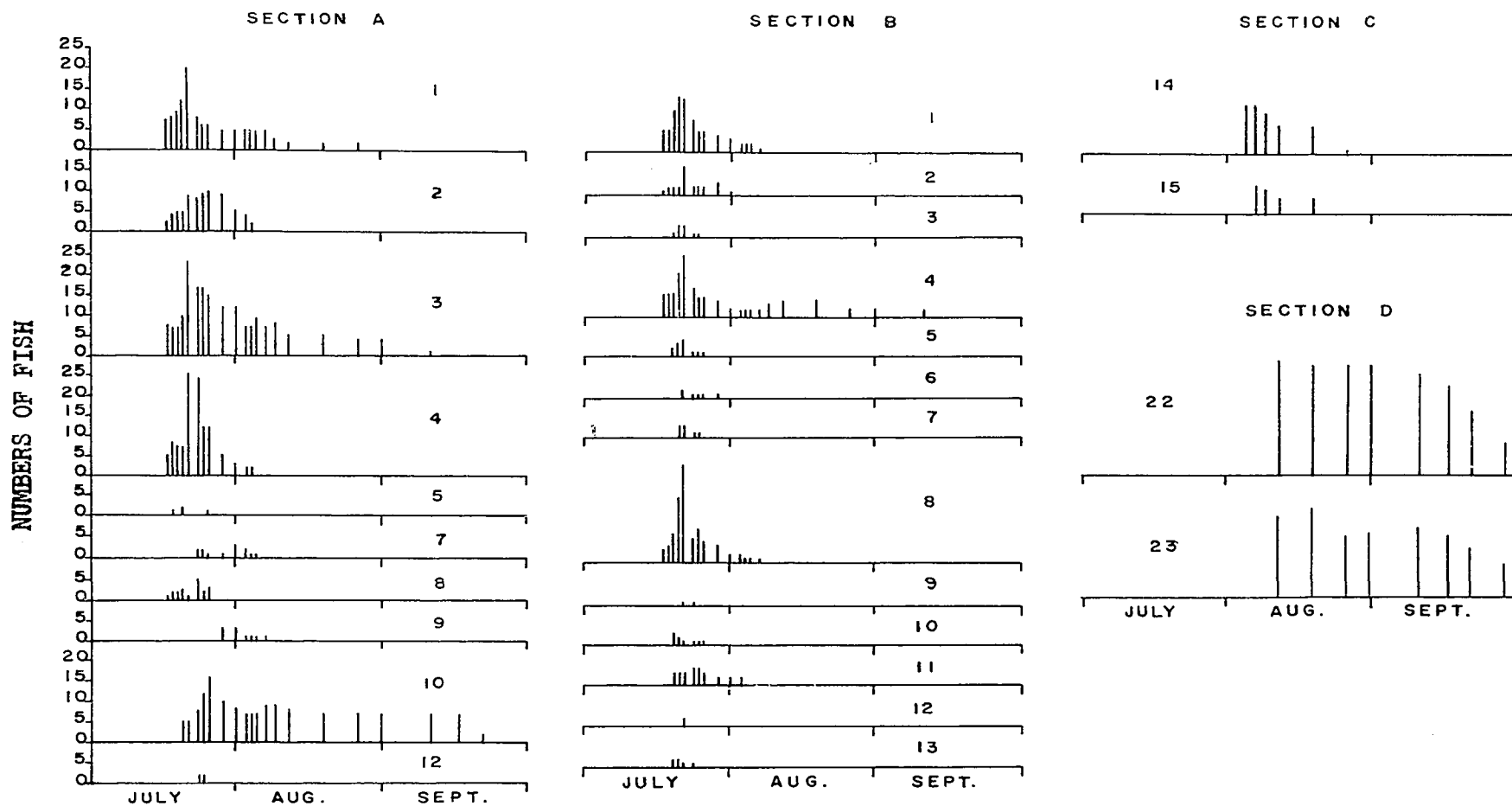


Figure 17. Numbers of juvenile *Dascyllus albisella* observed in the field at the Waimanalo study area during the summer and fall of 1960.

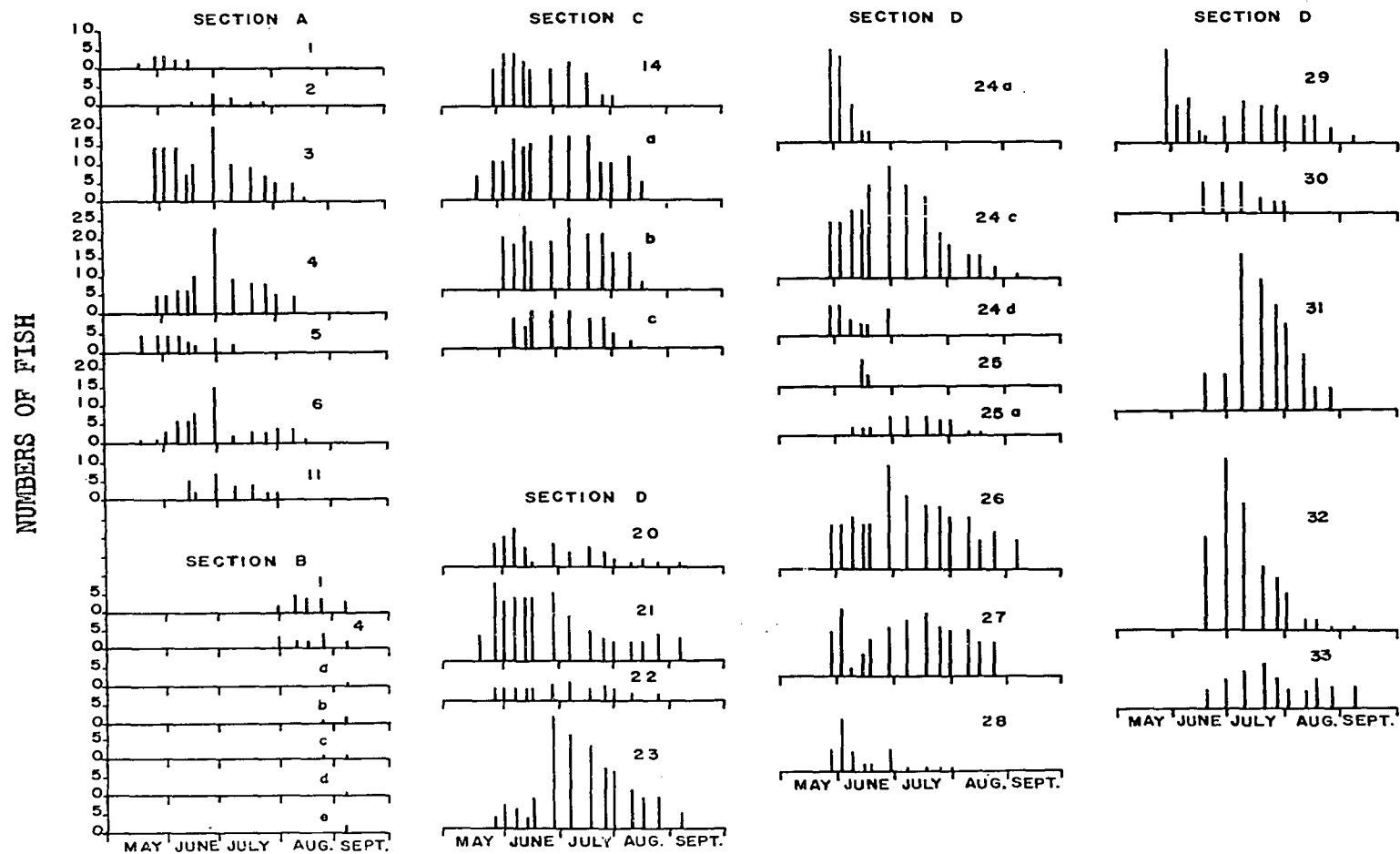


Figure 18. Numbers of juvenile *Dascyllus albisella* observed in the field at the Waimanalo study area during the summer and fall of 1961.

consisted of relatively few fish.

In 1960, a population peak occurred around July 20 after which there appeared to be little recruitment of juveniles. If recruitment occurred after this time, it was small since numbers of fish progressively decreased and the size of most of those fish present was noticeably larger. Numbers of fish continued to decrease through September and coral heads were almost completely devoid of fish by early October. At that time, a few free-living juveniles were seen roaming around over the bottom (Section 3.7).

It should be noted in Figure 17 that except for a 48 hour interval between July 20 and 22, daily observations were made between July 16 and 24. Therefore, the fluctuations observed are the daily increases and decreases in numbers of fish in specific coral heads. An examination of the histograms in this light shows that fish arrived at these heads daily and after a peak, the numbers in general dropped sharply. The lack of an observation on July 21 is unfortunate because of the 48 hour gap in time during which a great decline in numbers occurred. The reason for the sharp decline is not known and since there was no noticeable change in the weather during this period, it is suspected that the cause is associated with some other factor.

In 1961, another peak in numbers of fish occurred. As in 1960, aggregations seemed to decrease after one particularly large influx of fish. However, it is possible that in both years, there may have been another large influx of juveniles earlier than the time during which the first observations were made. Section 3.13 (association with sea urchins) shows three influxes of juveniles in 1961 that could possibly be related to those at Waimanalo, although the dates involved are not exact enough to pin-point the time of arrival. In any event, these sudden increases in numbers of juvenile fish may indicate the presence of some sort of cyclic phenomenon such as lunar periodicity as reported for Abudefduf abdominalis (Helfrich, 1958), Acanthurus triostegus sandvicensis (Randall, 1955), and Kuhlia sandvicensis (Tester and Takata, 1953). However, the irregularity of observations prevented the acquisition of data that might have related such fluctuations in numbers with lunar periodicity.

As stated previously, the sharp decline in numbers of fish soon after a peak was reached is not thought to be related to weather conditions. The fact that the same phenomenon appeared in both sections A and D where surge conditions are quite different (Section 3.9) indicates that some biological factor may be responsible. It is possible that the crowded conditions that occur at night

when fish retreat into the coral head may lead to excessive fighting which results in the smaller fish being driven away from the head (Section 3.2) where they would be vulnerable to predation. Small juveniles might be prone to readily leave a coral head since they are at a stage in which they are probably returning from a planktonic existence and are still disposed toward moving around.

Figure 18 shows a population situation similar to that of 1960 (Figure 17). Section A again had aggregations with larger numbers of fish and had the same number of heads populated as section B. However, most of the heads in section B had only one or two fish, and the majority of heads occupied were different from those occupied in 1960. The two heads that had the most fish in section B were the same heads as those that had the most fish in 1960.

A situation was noticed in sections C and D that was not seen in other areas of the environment. Numbers 24a, 24c, 24d, 25, 28 and 30 (Figure 18) represent coral heads of the species Porites pukoensis that usually do not have associated aggregations of juvenile Dascyllus albisella. Three of these heads contained fish for a considerable length of time and 24c had a very sizable aggregation of fish. Since Porites of this species is also found in areas of greater surge, it would seem possible that the milder conditions presented by the deeper channel in some way

enable fish to survive in the latter areas where they are associated with a species of coral that elsewhere may provide suboptimal shelter.

3.2.2 Kaneohe Bay Area

Since this area was not studied with an effort comparable to that focused in the Waimanalo area, there are relatively few data available in connection with aggregations of fish. Although observations in the area were relatively few, the length frequency distributions in Figure 19 show that coral heads there built up large aggregations of fish. Five of the eight collections made on October 1, 1960, had numbers of fish that were comparable with those found in aggregations in sheltered areas such as sections C and D at Waimanalo and section B at Waikiki.

The area is known among collectors as a place that abounds in juvenile Dascyllus albisella. Mr. Lester Zukeran has reported that on many occasions he has captured up to 50 or more juveniles from a single coral head. In the early days of the investigation, the author himself has seen large aggregations of fish that were not seen again due to failure to properly locate the coral heads.

3.2.3 Kualua Area

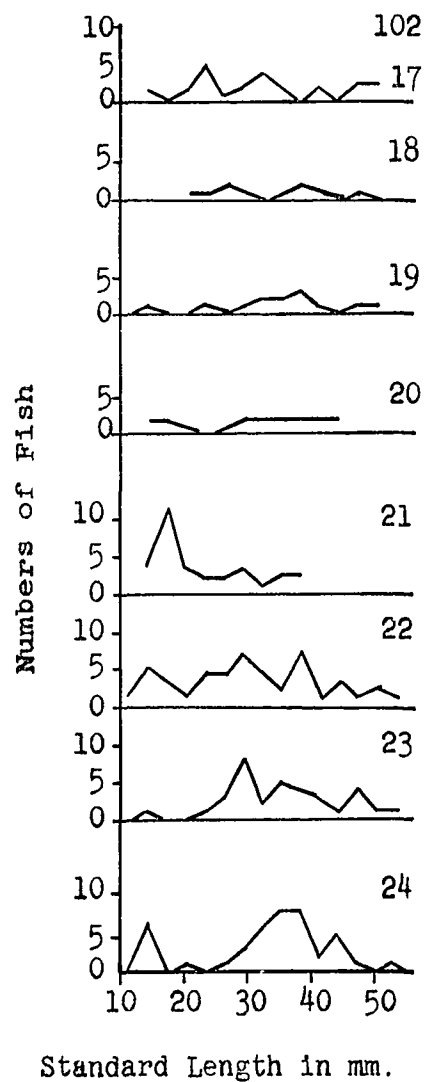
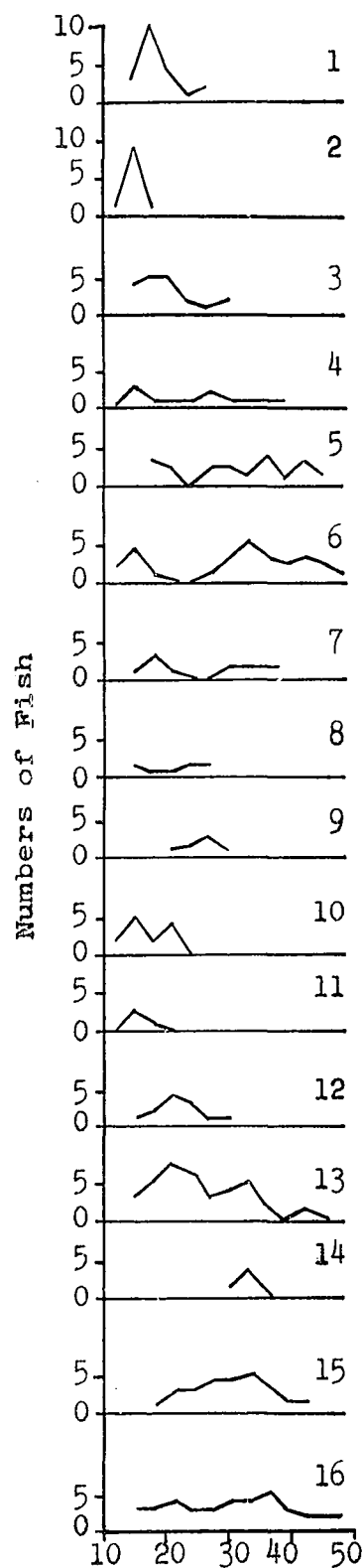
A total of four collections of fish were made at Kualua (Figure 20) from section A where the water was less



COLLECTION AREAS OF FISH

RECORDED IN FIGURE 19.

1. Pier 7, Honolulu Harbor, February 2
2. " " " " February 20
3. Coconut Island, March 16
4. " " May 1
5. " " May 1
6. " " June 15
7. " " June 20
8. Waimanalo, June 27
9. Coconut Island, July 10
10. " " July 16
11. Ala Wai Harbor, July 24
12. Waimanalo, August 6
13. " August 6
14. Ala Wai Harbor, August 6
15. Coconut Island, September 10
16. " " September 10
17. Kaneohe Bay, October 1
18. " " October 1
19. " " October 1
20. " " October 1
21. " " October 1
22. " " October 1
23. " " October 1
24. " " October 1



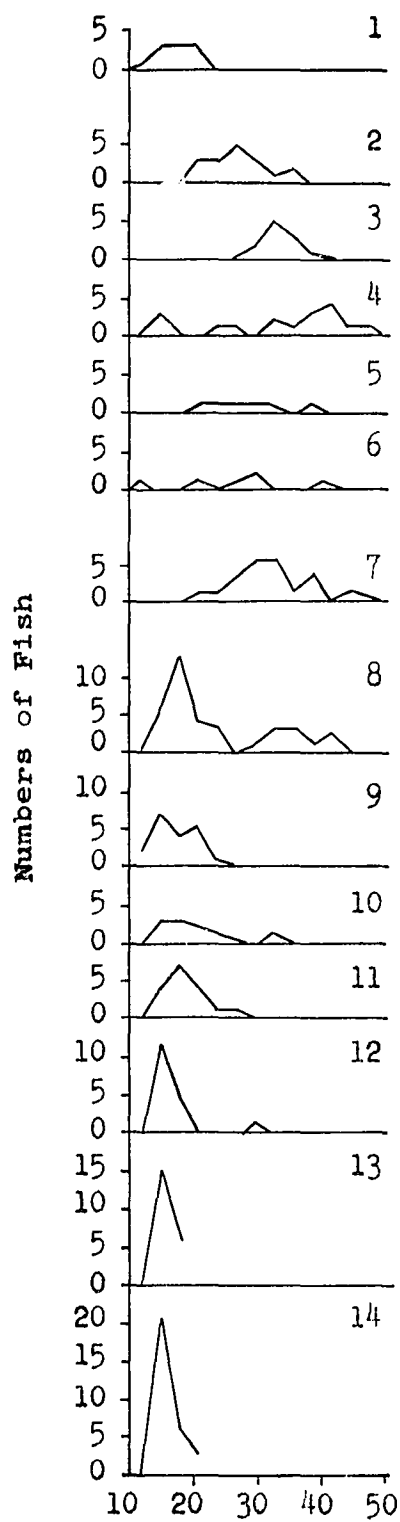
Standard length in mm.

Figure 19. Length frequency distributions of fish captured during 1960. Area and date of capture are located on the facing page.

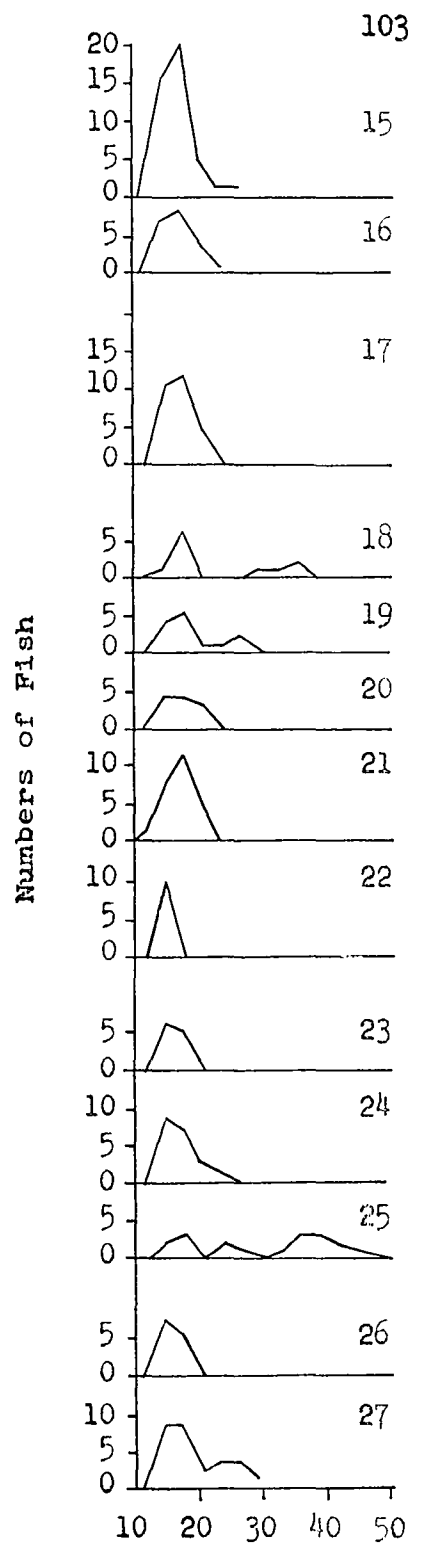
COLLECTION AREAS OF FISH

RECORDED IN FIGURE 20.

1. Coconut Island, January 6
2. " " January 7
3. " " January 7
4. " " January 11
5. " " January 18
6. " " January 18
7. " " January 18
8. Kaneohe Bay, March 11
9. Waimanalo, May 20
10. " June 14
11. " June 14
12. " June 20
13. Waikiki, June 23
14. Waimanalo, July 1 (no. 1)
15. " July 1
16. " July 1
17. " July 9
18. " July 9
19. " July 9
20. " July 9
21. " July 12
22. " July 14
23. Kualua, July 16
24. " July 16
25. " July 16
26. Waimanalo, July 20
27. Kualua, July 27



Standard Length in mm.



Standard length in mm.

Figure 20. Length frequency distributions of fish captured during 1961. Area and date of capture are located on the facing page.

turbulent. Two searches were made in this section with a total of 33 occupied heads being found. Numbers of fish per coral head ranged from 2 to 23 with an average of 12 fish per head. The "fish zone" comprised a belt extending parallel to the surge zone about 300 yards farther to seaward. In numbers of fish and behavior of the aggregations, section A appeared similar to section A at Waimanalo, which appears to be an intermediate type of habitat between surge zones and areas of calm water.

The coral heads in section B were also observed during the time of the above surveys. With two exceptions, they were found to be devoid of fish. In one case, a single fish was observed associated with a Pocillopora ligulata coral head while three others were seen in another head of the same species. An estimated 50 coral heads were examined in an area about 300 yards in length and about 150 feet in width, which comprised a larger area than the inshore section, but contained fewer heads than were examined in the inshore section.

Few fish were seen during observations in section B where surge was strong. A number of other incidental observations have been made in this and similar areas, but juvenile Dascyllus albisella have always been scarce or non-existent.

3.2.4 Waikiki Area

The calm, deep offshore waters of section A are populated by relatively few juvenile Dascyllus albisella. Most of the fish in this section have been found at certain times associated with poisonous sea urchins. As many as 81 fish have been observed at one time with 23 urchins. Other juveniles in the section live in holes that perforate many of the dead glomerate coral heads found there. However, very few fish were found in the latter habitat probably because they were scarce there or because they were difficult to find in such locations. Very few of the larger sized juveniles were seen and it was assumed that few fish had originally been present or that a high degree of predation occurred on the young that had been present.

An almost complete absence of ramose coral heads from the section makes it difficult to judge whether conditions otherwise would be suitable for colonization by juveniles. In one instance a single coral head of the species Pocillopora meandrina was found growing two feet off the bottom on the fluke of an old anchor. It was found that this head, which afforded relatively poor protection because of its small size as well as its widely separated branches, always had an associated population of juvenile Dascyllus albisella. Figure 21, taken off Waikiki at a depth of 70 feet, shows this coral head. The head was essentially out of the

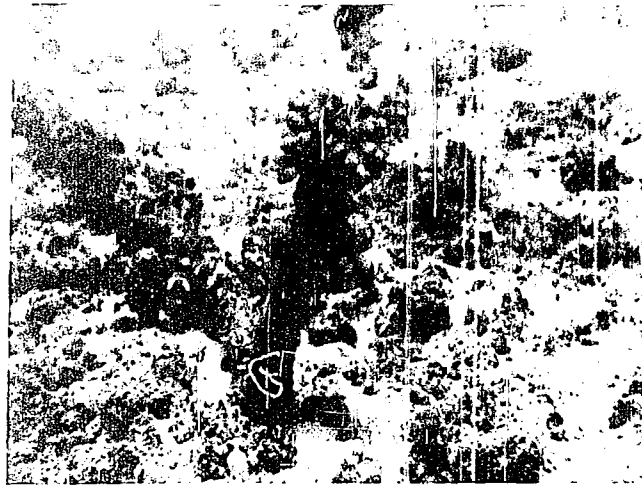


Figure 21. Pocillopora meandrina coral head growing on fluke of encrusted anchor. This coral head was continually populated by juvenile Dascyllus albisella throughout the period of observation.

area of predation (Section 3.16), which is an indication that young could survive in the section as far as hydrographic features are concerned. The very large aggregations of fish that resulted from the planting of coral heads in the section proves that fish can live there (Section 3.12.1).

It should be noted that individuals or small groups of Dascyllus albisella are occasionally found associated with isolated rocks or other conspicuous objects. However, because of the continual presence of fish, the situation noted above indicates that conditions were favorable for colonization by an aggregation of fish.

Section B, in the surge zone, also appears to be devoid of juveniles. Apparently suitable coral heads are present in the section, but are uninhabited. Many hours of observation in this section as well as in more or less identical surroundings farther up and down the reef along the Waikiki area have failed to disclose any fish. Therefore, it is concluded that the section represents an unfavorable habitat for young of this species.

3.3 LENGTH DISTRIBUTION OF JUVENILES

Fish were usually captured by placing a net over an occupied coral head which was then brought to the surface intact with fish. In some cases it was necessary to catch fish individually when they were found occupying cavities

in rocks, etc. Few catches were made in this manner for it was time consuming and relatively unrewarding. Fish occupying sea urchins were caught by rapidly swinging the urchin through the water and catching the fish in a net when they swam out. A plastic bag was used to hold the fish until shore could be reached and the fish could be transferred into buckets.

During the summer months, collections were made sporadically in many different localities while working on other phases of the problem. During the months of November through April, the Waimanalo area was visited each month, but no fish were found. Fish collected during these months were caught during irregular visits to Coconut Island. Collections were made outside of immediate test areas and areas under observation. They were occasionally made by placing coral heads on the reef near Waimanalo and collecting fish that came to occupy them.

Figures 19 and 20 show length frequency distributions of fish caught during 1960 and 1961. An examination of these figures, formed by grouping fish lengths by 3 mm. intervals, shows that juveniles were found in coral heads during most of the year. Greatest numbers of very small juveniles were found during the late spring and early summer months. These periods indicate that juvenile Dascyllus albisella tend to enter inshore areas later than Abudefduf

abdominalis, which appears in the early spring months in greatest abundance (Helfrich, 1958). However, sampling of Dascyllus albisella was inadequate to establish this as a fact.

In some species, it is possible to trace the influx of new groups of fish and to determine average growth rate by the progression of modes in the length frequency distributions from time-series samples. No modal progression appears in Figures 19 or 20. The modal groups show that new fish appeared throughout a period of over a month during the summer of 1961 (Figure 20). Such constant increases lead to a potential blending of modal groups such as appear in Figures 19 and 20. Undoubtedly there is also an interaction between recruitment and loss of fish through predation together with normal movements from one head to another, that further obscure the picture. In addition to this, although juvenile Dascyllus albisella are not uncommon, they are not abundant enough to furnish sufficient numbers for accurate population analyses. They occur in many different areas, but areas of dense, accessible concentrations are relatively scarce. There is a possibility that modal groups could be studied by attracting aggregations to certain areas such as was done at Waikiki (Section 3.12.1).

3.4 INITIAL ENTRY OF JUVENILES INTO CORAL HEADS

In the spring months coral heads became populated by juvenile Dascyllus albisella which appeared to be about the same size in different locations on the reefs. It is likely that at that time of the year, the condition of various physical and biological factors combined to produce a movement of juvenile fish from the pelagic environment of the ocean to the inshore reef areas. In order to determine the size of newly arrived fish, it was necessary to find new aggregations in coral heads that were known to be uninhabited at some previous date. A number of observations of this kind were made and were included in Figures 19 and 20.

These aggregations are shown in Figure 20 by collections made on June 20, July 1 (no. 1), and July 14, 1961. The coral heads in which these fish were collected were known to be without fish one week prior to the time that the fish were collected. The distribution shown for June 23 represents another newly arrived population that was sampled from sea urchins uninhabited a week earlier. The February 20 distribution in Figure 19 represents a new population of fish that was caught adjacent to a piling in Honolulu Harbor. The fish in these collections ranged from 12.8 mm. to 21.1 mm. and the average length was 14.7 mm. Data for these collections are summarized in Table 10.

TABLE 10. LENGTH FREQUENCY DISTRIBUTION OF
 JUVENILE DASYLLUS ALBISSELLA WHEN FIRST
 COLONIZING CORAL HEADS.

		<u>Frequency</u>				
		1960	1961	1961	1961	1961
		<u>Feb.</u> <u>20</u>	<u>June</u> <u>20</u>	<u>June</u> <u>23</u>	<u>July</u> <u>1</u>	<u>July</u> <u>14</u>
	12	-	1	-	-	-
	13	-	1	4	1	3
	14	5	6	5	8	1
	15	1	5	8	12	6
	16	4	2	3	3	-
	17	-	2	1	1	-
	18	-	-	-	0	-
	19	-	-	-	2	-
	20	-	-	-	0	-
	21	-	-	-	1	-
Mean	Length	15.0	14.7	14.6	14.9	14.2
Total	Number	10	17	21	28	10

Average length = 14. 7 mm.

The question of how newly arrived fish locate coral heads is difficult to answer. It could be argued that juveniles being swept into the shallow reef habitat merely settle out in various places and those that happen to reach coral heads survive while others have less protection and are eaten by predators. However, as will be shown later (Section 3.9), the existence of surge probably drives newly arrived fish off the shallow portions of the reefs and the fish congregate in the deeper portions of the reef. The constant association of juveniles with coral heads strongly indicates that they are attracted to them in some way in the field. On two occasions juvenile fish associated with glomerate coral heads almost immediately swam to ramose coral heads placed close to them. In the absence of coral heads, they have been seen to occupy other objects such as sponges or clusters of sabellid worm tubes which essentially present an arborescent or ramose appearance. In aquaria, juveniles will occupy coral heads to the exclusion of other objects that are introduced.

Macfadyen (1957) pointed out that animals having patchy distributions must have highly specialized methods for detecting their habitats. It is probable that coral heads act as visual sign stimuli to juvenile Dascyllus albisella, but laboratory experiments designed to shed further light on this hypothesis were inconclusive. It is

possible that the coral heads as a whole might represent a configurational organization of certain sign stimuli, or "gestalt", which is the usual situation encountered in the field (Tinbergen, 1951). It is likely that the regular pattern presented by the light branches and dark interstices would offer a "recognition mark" that could be seen by a fish from a considerable distance, thus offering a first "sign" in guiding fish to adequate shelter.

The type of terrain on which a coral head is located might have an important bearing in relation to a fish's orientation to its characteristic shelter. This could be one factor influencing the build-up of populations in calmer waters. In such areas, sand tends to settle out and form pockets or a smooth sandy bottom. Areas of this kind have interspersed stretches of flat rock bottom on which coral heads grow. Under these conditions it becomes relatively easy for a human observer and presumably a fish to visually detect coral heads as they tend to stand out from the sandy surroundings. Juveniles coming into an inshore area might more easily detect the heads and thus build up the large aggregations that are found in such locations.

Coral heads are less evident on more jumbled stretches of rock bottom both because their color tends to blend with the surroundings and also because of the presence of rocks and non-ramose coral heads with which the ramose types may

be confused. Under these circumstances, young Dascyllus albisella might not be able to detect the presence of a head as readily and might be prone to move elsewhere until an area is reached where coral heads are more easily seen. Such interactions are influenced by surge which drives fish from more turbulent areas where coral heads are actually more conspicuous on the wave swept bottom.

In view of these considerations, it is probable that the development of an association with coral heads might involve, among other things, an interaction between surge (or surge associated factors) and an orientation to coral heads. Juvenile Dascyllus albisella might arrive in surge zone areas from the pelagic region and be immediately swept away from coral heads in the area. They might then be transported by currents to milder shallow areas where they are able to tolerate the conditions of surge for varying lengths of time. A certain proportion of these fish might leave such areas and eventually arrive in the quieter, deeper areas where conditions result in greater survival and where there are fewer rheotactic stimuli that might cause them to leave. The photographs in Figures 22 and 23 show the isolated nature of coral heads that may build up large aggregations of juvenile Dascyllus albisella. Figure 22 shows juvenile Dascyllus reticulatus with the coral Pocillopora eydouxi and Figure 23, Dascyllus aruanus with



Figure 22. Pocillopora sp. coral head on intermittent sand-rock bottom that isolates it from surrounding coral and rock. Head is populated by juvenile Dascyllus reticulatus.



Figure 23. Acropora sp. coral head on intermittent sand-rock bottom that isolates it from surrounding corals and rock. Head is populated by juvenile Dascyllus aruanus (middle right).

Acropora echinata. Although the photographs were made at Eniwetok Atoll at a depth of 6 feet, they well illustrate the situation that is found in Hawaii.

3.5 ABUNDANCE OF FISH IN RELATION TO SIZE OF CORAL HEADS

An effort was made to determine whether or not a correlation existed between the size of coral heads and the numbers of fish inhabiting them. Accordingly, the volume of the internal spaces was determined and used as a criterion for the size of the head. This was accomplished by placing the head in a plastic bag, and immersing it so that the outside water pressure forced the bag against the periphery of the head. Measured amounts of water were then poured into the bag, thus filling up the spaces between the branches of the coral. The numbers of captured fish that had been associated with the coral head in the field were then compared with this volume.

Two such comparisons were made; one utilized 17 coral heads chosen at random from Kaneohe Bay and reef areas near the town of Waimanalo, and the other utilizing 20 heads that were observed near the Waimanalo study area. In the latter comparison, average numbers of fish that appeared throughout the summer of 1961 were compared with the volumes of the coral heads with which they were associated. The volumes of the latter coral heads were judged by

comparing them with coral heads of known volume held alongside them.

The scatter diagrams in both Figures 24 and 25 show no significant relationship between total or average numbers of fish and volume. The scatter of the points shows a more or less random distribution with a slight increase in numbers of fish with increase in size of coral head in the Kaneohe data. There appeared to be some increase in average numbers of fish with larger coral heads at Waimanalo. It should be noted that in the latter case fewer heads of a larger size were examined.

These results do not preclude the possibility that such a correlation might exist. However, they support the impression that if a correlation does exist, it is not of a magnitude that permits easy recognition in the field.

3.6 ABUNDANCE OF FISH IN RELATION TO LOCATION OF CORAL HEADS

Figures 17 and 18 show that the size of fish populations in coral heads is related to the area in which the head is located. In 1960, the heads in section A at Waimanalo were populated by greater numbers of fish than those in section B. It is most interesting to note that those heads having the most fish in section B (heads 1, 4 and 8) were located at the deeper edges of the section where the surge

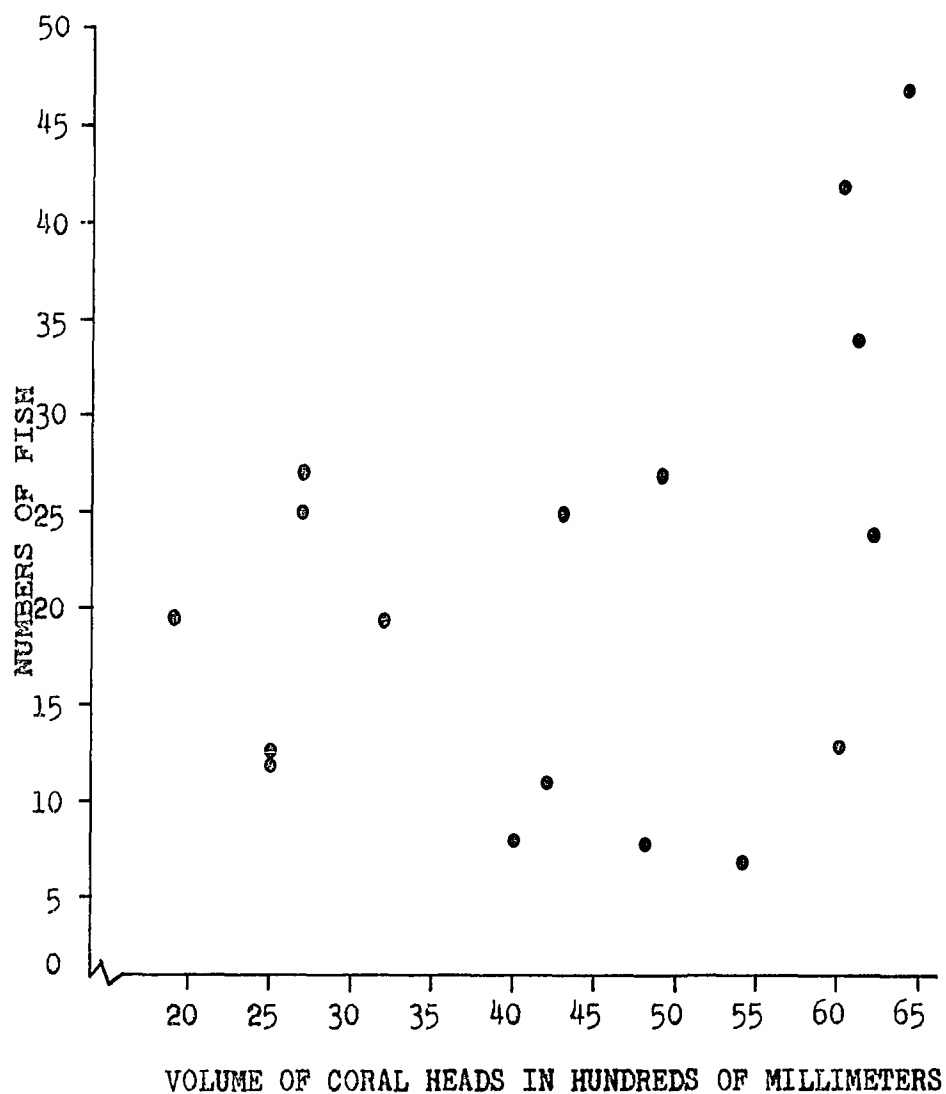


Figure 24. Relationship between numbers of fish and volumes of coral heads from which they were captured in Kaneohe Bay.

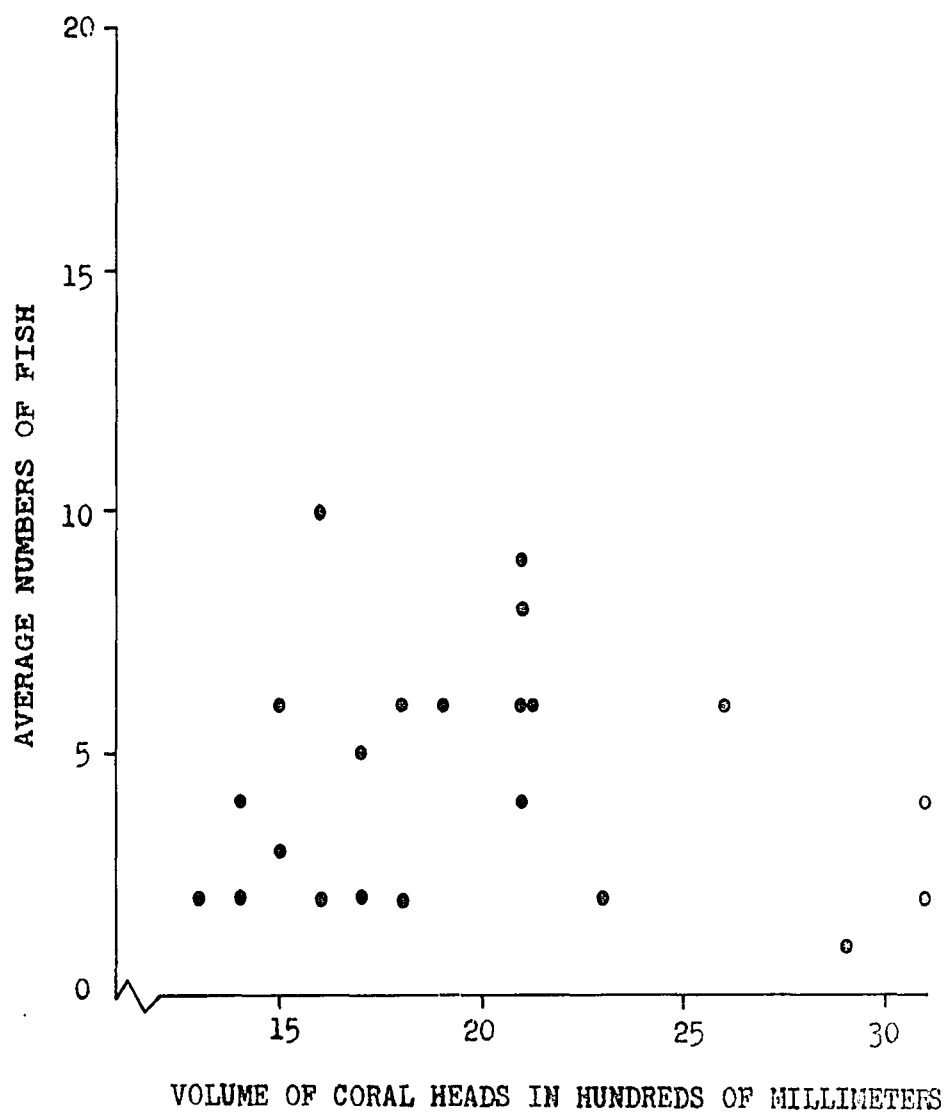


Figure 25. Relationship between average numbers of fish observed at Waimanalo during 1961 and volumes of coral heads in which they were living.

was reduced (Section 3.9.3). Head number 1 was at the sloping north edge of the section where the water was deeper and heads number 4 and 8 were in still deeper water at the edge of section C. Section A on the basis of surge velocities appeared to be a less rigorous habitat than section B. In 1961, the situation was similar with section A having much greater numbers of fish.

Sections C and D, which had relatively calm water and coral heads isolated in the sand, had heads that were populated by considerable numbers of fish as seen by the few observations made there in 1960. In 1961, numbers of fish at C and D far surpassed numbers found in sections A and B. The tendency for flat areas with isolated coral heads and relatively little surge to build up large populations of fish is also shown in Figure 35 for section A at Waikiki. Figure 19 shows the sizable numbers of fish captured at Kaneohe Bay, an area that also fits the above description.

3.7 BEHAVIOR OF FISH IN RELATION TO CORAL HEADS

3.7.1 General Behavior

Juvenile Dascyllus albisella show a very definite behavior in relation to their coral head habitat. The fish spend practically all of the daylight hours feeding outside of the coral head. However, they remain very closely associated with it, and are able to regain quickly the safety of

the interstices between the branches when they become frightened. This behavior pattern is made up of a number of components.

Juveniles tend to cluster in the immediate neighborhood of coral heads in a pattern that varies with a number of factors. The shape and dimensions of an aggregation change with the velocity of the current. When current or surge is strong, the individuals of an aggregation group together and maintain their position within a few inches of the coral head on the upcurrent side. This position, which is usually about midway below the top of the head and above the side, strongly contrasts with behavior during periods of slack water. In still or slow moving water, fish tend to fan out in an umbrella shape on all sides as well as over the top of the head.

The composition of the aggregation has a definite organization that is related to the size of the fish. The largest fish maintain positions up to two feet from the head whereas the distance that progressively smaller fish maintain decreases with the size of the fish. In this position, the largest fish extend farthest into the current and thus are first to come into contact with the planktonic organisms on which they feed. It is evident that these fish would be more vulnerable to attacks by predators.

Some aggressiveness of larger fish toward smaller fish is evident when the aggregation is feeding. This indicates that the order of the aggregation is maintained, partially at least, by size. During those short periods when fish have taken refuge within a head, they vigorously chase each other with quick darting movements. As the larger members begin to make quick exploratory darts outside the head, the aggressiveness decreases and practically ceases with the full establishment of the feeding complex.

The distance that fish maintain between themselves and the shelter of the head is modified by the current to which they react by staying closer as the velocity increases. For the first month or so they slowly increase the distance at which they feed from the head while maintaining a more or less normal feeding pattern. As they grow larger in size, they sometimes cease to feed when they are two feet or more from the head and descend to the bottom. At this time single larger fish or small groups of larger fish may continue to another nearby head where they may remain for a short time, or they may immediately return to the former head. These movements occur as fish begin to leave the commensal stage of their existence and become free-living. The reduced numbers of larger juveniles in collections presumably result from this type of behavior.

In areas where the coral head is located over a sandy

bottom, juveniles of a given size normally stray much farther from the head. Occasional sorties after particles of food may take an individual a foot or more beyond the rest of the aggregation. Under such conditions, the entire aggregation may gradually begin to stray farther away from the head.

The increase in distance between fish and coral head serves a number of functions. As fish grow larger it is apparent that they literally outgrow their shelter, becoming too large physically to fit into the interstices of most coral heads. This reduces the effectiveness of coral heads as shelter. Fish apparently relocate in areas where more effective kinds of shelter are available.

The greater distance between individuals that results from this behavior helps to reduce the effects of certain density-dependent factors such as fighting and shortage of food, which otherwise might result in a more rigid control of numbers of fish. When currents and surges are reduced as a result of changes in the weather or by fluctuations in the tidal cycle, the amount of water that flows past a coral head is also reduced. The compensatory activity of fish that leads to greater dispersal under such conditions allows each fish a larger volume of water from which to seek food. This would be of particular benefit to very small fish that tend to stay closer to the head, and eat what food

is left after the larger fish have sorted out the plankton (Section 3.8)

3.7.2 Distance Maintained Between Fish and Coral Head

Distance measurements were made using heads 3, 4 and 6 at section A at Waimanalo since they were relatively close together and did not require the use of diving apparatus. The distances maintained by the largest fish were measured since they offered a better reference point than the inner members of the aggregation and also because they represented those fish that were in the stage of transition between a commensal and free-living state. Measurements were made by placing a ruler on the bottom under the coral head and recording the distance in inches between fish and coral head. Recordings were made at 10 second intervals over a total period of five minutes. A sufficient time was allowed to enable the fish to resume their feeding activity before measurements were made. There were no indications that the behavior of the fish was influenced by the observer.

The distance between fish and coral head varied because of the presence of unusually strong series of surges, which fish could not always effectively swim against. The distance during back-surges was not measured since these occurred during a relatively small percentage of the time. These variables were excluded from the data by halting the

observations during the time when they were operating.

Observations were made between June 4 and August 11, 1961, and the distances were plotted against time (Figure 26). The significant regression ($P < 0.01$) shows the increasing distance between fish and coral heads with time that eventually results in the transition from commensalism to the free-living state. As shown by the low average distance on July 27, and by the large average distance on August 11, there are times when fish remain closer to the head and times when they move farther away. Such deviations result from differences in water velocity with fish remaining closer to the heads in swifter water.

3.8 SELECTIVITY IN FEEDING

The established fact that larger fishes eat larger organisms applies also to Dascyllus albisella. The examination of stomach contents showed that larger organisms eaten by the larger juveniles were also eaten in reduced numbers by smaller fishes in the same aggregations. Therefore, the question arose as to whether or not the smaller fish would eat more larger organisms if the larger fish were not present to "screen" them out of the plankton before the smaller fish could eat them. To find an answer to this question, it was necessary to sort fish collections into two groups for stomach analysis.

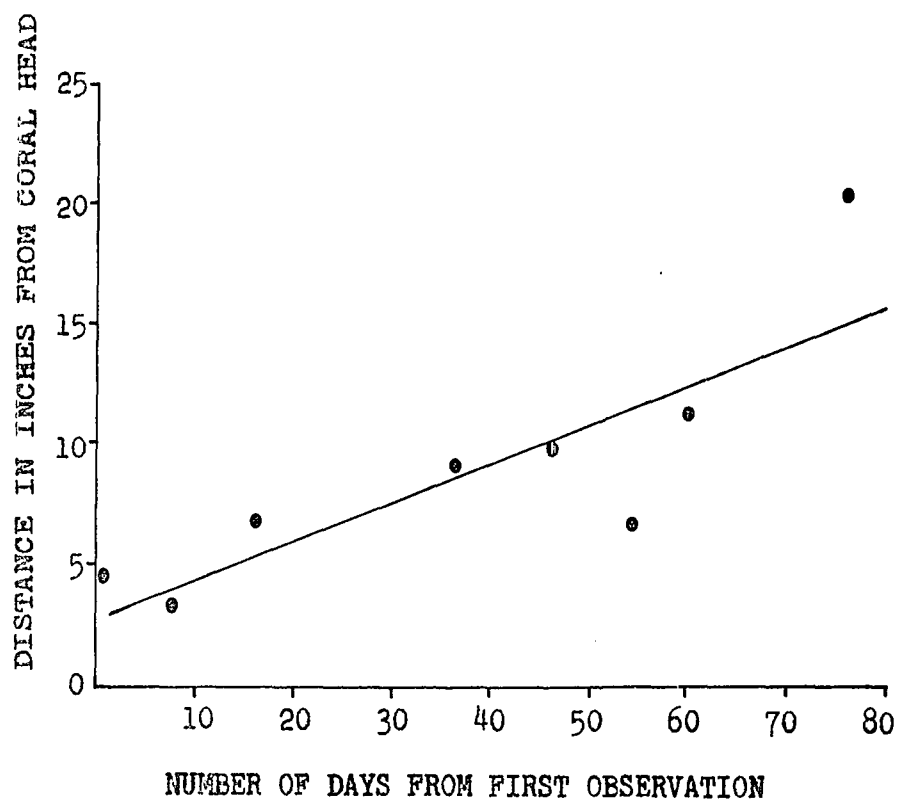


Figure 26. Increasing distance from coral heads maintained by juvenile Dascyllus albisella during the summer of 1961.

Individual aggregations collected from single coral heads that contained relatively small fish that were few in number were sorted into one group. In these small aggregations, fish would have had less competition from the few larger individuals and therefore would have been free to select larger organisms. If these fish had selected larger organisms, their stomachs should have contained greater percentages of larger organisms than smaller.

The second group contained aggregations collected from single coral heads that contained many larger fish, as well as smaller ones. In this case, it was expected that the larger fish would have selected the larger organisms leaving the smaller ones for the smaller fish which should have contained a relatively small percentage of larger organisms.

The stomach contents of 232 juveniles were analysed by determining the kinds and weights of organisms consumed. Similar organisms were grouped for each collection and weighed on a chainomatic balance after excess moisture had been removed. The data were arranged in Table 11 to show the percent of each type of organisms that was contained in the stomachs of fish of different length classes.

The data for both groupings show a more pronounced trend for copepods than for the other organisms. In both groups the larger fish ate a smaller percentage of copepods

<u>Collections Containing Mostly Smaller Fish</u>									
Standard Length in mm.	Weight in Grams Copepods	% by Weight	Weight in Grams Ascidians	% by Weight	Weight in Grams Shrimp-like Organisms	% by Weight	Weight in Grams Annelids	% by Weight	Total No. of Fish
11-15	0.105	68	0.057	17	0.027	14	0.002	1	46
16-20	0.472	70	0.136	20	0.043	6	0.019	4	46
21-25	0.313	54	0.211	36	0.037	6	0.018	4	24
26-30	0.287	58	0.113	23	0.091	18	0.005	1	16
31-35	0.193	54	0.084	23	0.066	18	0.016	5	9
<u>Collections Containing Mostly Larger Fish</u>									
11-15	0.048	82	0.002	3	--	--	0.009	15	13
16-20	0.186	93	0.013	7	--	--	--	--	16
21-25	0.275	74	0.084	23	0.004	1	0.006	2	18
26-30	0.505	66	0.134	18	0.069	9	0.051	7	25
31-35	0.999	62	0.423	26	0.107	7	0.079	5	26
36-40	0.552	33	0.895	53	0.166	10	0.073	4	20
41-45	0.316	24	0.668	52	0.202	16	0.108	8	13
46-50	0.160	22	0.484	65	0.095	13	--	--	6

TABLE 11. WEIGHT AND PERCENTAGE BY WEIGHT OF VARIOUS FOOD ORGANISMS
FOUND IN STOMACHS OF JUVENILE DASCYLLUS ALBISSELLA.

which means that a concomitant increase occurred in percentage of other larger organisms eaten. However, in the collections containing mostly smaller fish with few larger individuals for competition, the smaller fish ate considerably less copepods and more larger organisms than did fish of comparable size in collections where many larger individuals were present. It is evident, therefore, that when considerable numbers of larger fish were present, they "screened" larger organisms from the plankton, leaving the smaller ones for the smaller fish.

It is reasonable to suppose that smaller fish would have to eat smaller organisms because of physical limitations in the size of the mouth. An examination was made of the size of the gape of juvenile Dascyllus albisella in relation to the size of the larger organisms ingested. It was found that the smaller sized juveniles used in this work had no physical limitations in mouth size.

The method by which Dascyllus albisella select their prey is difficult to evaluate. There would seem to be little doubt that this species is a visual feeder. Its quick reactions to surge in maintaining its position relative to the coral head as well as its ability to dash quickly in and out of confined spaces indicates a very well developed visual system that is most likely important in feeding. The importance of olfaction in feeding in such a turbulent

environment would seem to be negligible, although Randall (1955) performed a brief experiment in which another pomacentrid fish, Abudefduf abdominalis, appeared to be able to detect odors in the water. Hiatt and Strasburg (1960) referred to several species of pomacentrids as having selected their food by visual means, although these observations were apparently made in the field. Since juvenile Dascyllus albisella remain close to coral heads, there would seem to be little utility connected to a sense of smell because the fish could not move far enough to find the source.

Although juvenile Dascyllus albisella living in coral heads cannot be compared in every respect with free-living plankton feeders, it is apparent that they are confronted with a number of similar problems in relation to their predator-prey relationships. The actual catching of prey is probably related to abundance of particular organisms that happen to be present in the water. This tendency among clupeoid fishes is referred to by Lebour (1919), Bigelow (1926), and Shelbourne (1953) who agree that fish probably feed on those organisms that are most plentiful in the water. There is little doubt that this is the case in connection with copepods, and with young Dascyllus albisella, it might also apply to larvaceans which are abundant in their stomachs.

Other factors no doubt play a part in these relationships. It is reasonable to suppose that the vulnerability of the prey would be related to its size, structure and behavior as well as the efficiency of the predator. Shelbourne (1953) states that "the number and efficiency of sense organs, conspicuousness, special escape reactions, secretion of repellents, and the swarming habit are but a few of the factors which might well decide how far a particular prey is open to attack by a particular predator." He goes on to say that "with the concept of vulnerability in mind, it is easy to see why the soft-bodied, slow moving, but conspicuously vibratile Oikopleura (Larvacea) should fall a ready victim to a visual feeder."

The change in food habits of juvenile Dascyllus albisella appears to be a general pattern that is followed by other plankton feeders. In general, copepods are the major food of young fish, with greater numbers of other crustacea being consumed as they grow older. Bigelow (1926) wrote that larger herring in the Gulf of Maine took copepods and euphausiids while fish under four inches took chiefly copepods. Bigelow and Welsh (1925) add in reference to the same body of water that herring over 12 mm. depend exclusively on copepods for a time, and as they get larger they feed on larger prey, turning to the larger amphipods, shrimp and decapod crustacean larvae. Hildebrand and Schroeder

(1927) say that mysid shrimps appeared to be the principal food of adult anchovies (Anchoa mitchilli Cuvier and Valenciennes), while copepods were apparently the sole food of the young. In any of these species, the advantage is apparent of having adult fishes utilizing different food than the young. However, it might be even more important in connection with young Dascyllus albisella that will not move from a restricted area to obtain their food.

The influence of food on distribution was not studied in detail. Because of the mixing of reef water by currents and surge, it is presumed that the planktonic food organisms of Dascyllus albisella were uniformly distributed, although plankton tows to verify this were not made. A lack of local concentrations of plankters would remove an influence that might cause juvenile Dascyllus albisella to concentrate in their vicinity. In addition, the scarcity of empty stomachs suggests that food is almost always available. If fish congregated in places where food was plentiful, then one would expect to find large numbers of fish on shallow flats because of the greater flow of water that would bring more plankters to them. It was apparent that such large concentrations did not exist.

3.9 HYDROGRAPHIC FEATURES OF THE ENVIRONMENT

3.9.1 Characteristics of Current

An attempt was made to study surge velocities by the use of flow meters of the Rigosher type kindly loaned by the U. S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii. This equipment was modified by the addition of a large fin that kept the meter pointed into oncoming current or surge. The equipment was first used in the calmer portion of the Waikiki area and it was found that in spite of a very free-spinning set of blades, it would not always record. In other areas where current and surge were mild, the blades often would fail completely to respond. It became apparent that the rapid changes in direction and the short duration of most surges in the shallow reef area would necessitate the design of special equipment. This problem presents a magnitude of difficulty that has resulted in a lack of commercial gear designed for such studies. Therefore, this approach to measuring current and surge was abandoned.

An attempt was made to employ a drift bottle that was hydrostatically buoyed in such a fashion as to float just off the bottom. It was hoped that watching such a device would make it possible to measure the current close to the bottom where fish live. However, local turbulence close to the bottom tended to alter the hydrostatic balance of the

bottle, thus causing it to rise or descend out of the area of interest.

The method finally adopted utilized naturally drifting particules in the water. The procedure was to locate a small particle of suspended matter and to watch the way in which it moved as an index to the motion of the water. If the observed particle settled to the bottom, other nearby particles were always available.

The observer carried a handful of 1 x 1 inch lead squares that were painted white. Since numbers were painted on them, they could be dropped when ever necessary to leave a consecutively numbered trail along the bottom. The distance between the squares was measured by means of a metal rod marked off in 6-inch lengths or a one-foot ruler depending on whether current or surge was being measured. The time it took particles to travel a measured distance was read from a watch sealed in a bottle. Time measurements were made independently of distance measurements because of difficulties inherent in doing two things simultaneously under the conditions encountered in the field. By combining time and distance measurements it was possible to determine velocities of currents and surge.

To measure current independently from surge was an extremely difficult task. The problems arose because of the

complicated patterns of surge that are superimposed on a more or less steady current. A discussion of surge can be found in the section dealing with that subject; however, it is necessary to include a word about surge as it applies to current so that a definition of current as used here can be given.

There are two general types of surge. One is an alternating type that pulses toward shore and then immediately reverses to pulse in the opposite direction. This type of surge is of no concern here because such pulses were not included in current measurements. The other type of surge pulses in a shoreward direction only. This type is difficult to measure because a considerable amount of subjectivity is involved. A strong shoreward pulse can be recognized as such, but a gradation of intensities of pulses exists that makes it difficult to determine the onset or cessation of activity. Instruments could probably be designed to measure such one-way pulses, but this problem alone is quite formidable.

The current that was measured was the more or less steady flow of water in a given direction plus a component of one-way pulses of surge that were traveling in the same direction as the current on the incoming tide, but which were traveling against it on the outgoing tide. The resulting current velocities were therefore higher than they

should have been on the incoming tide and possibly lower than they should have been on the outgoing tide.

In making measurements on a particular day, it was necessary to wait for a current change to take place so that both tides could be measured. Accordingly, measurements were made two hours before the change and two hours after the change. Measurements were made in one section of an area and then the observer immediately swam to the other section and repeated the measurements. This procedure was followed on both tides.

Figure 27 summarizes the current velocities that were measured at Kaneohe Bay, Kualua, and in the Waimanalo areas. Measurements were made at each place on two different days and at comparable stages of both the outgoing and the incoming tides. The data are meant only to show that differences exist between recognized rougher and calmer sections of the areas studied, as well as to give an idea as to the magnitude of current velocities on two days when wind and sea conditions appeared to be about average for the season. Measurements were made on different days in the different areas as it was not possible to cover all of the areas in one tidal cycle to make the measurements comparable. For this reason, it was decided that the valid comparisons that could be made were between tides and sections of reef within areas on a particular date.

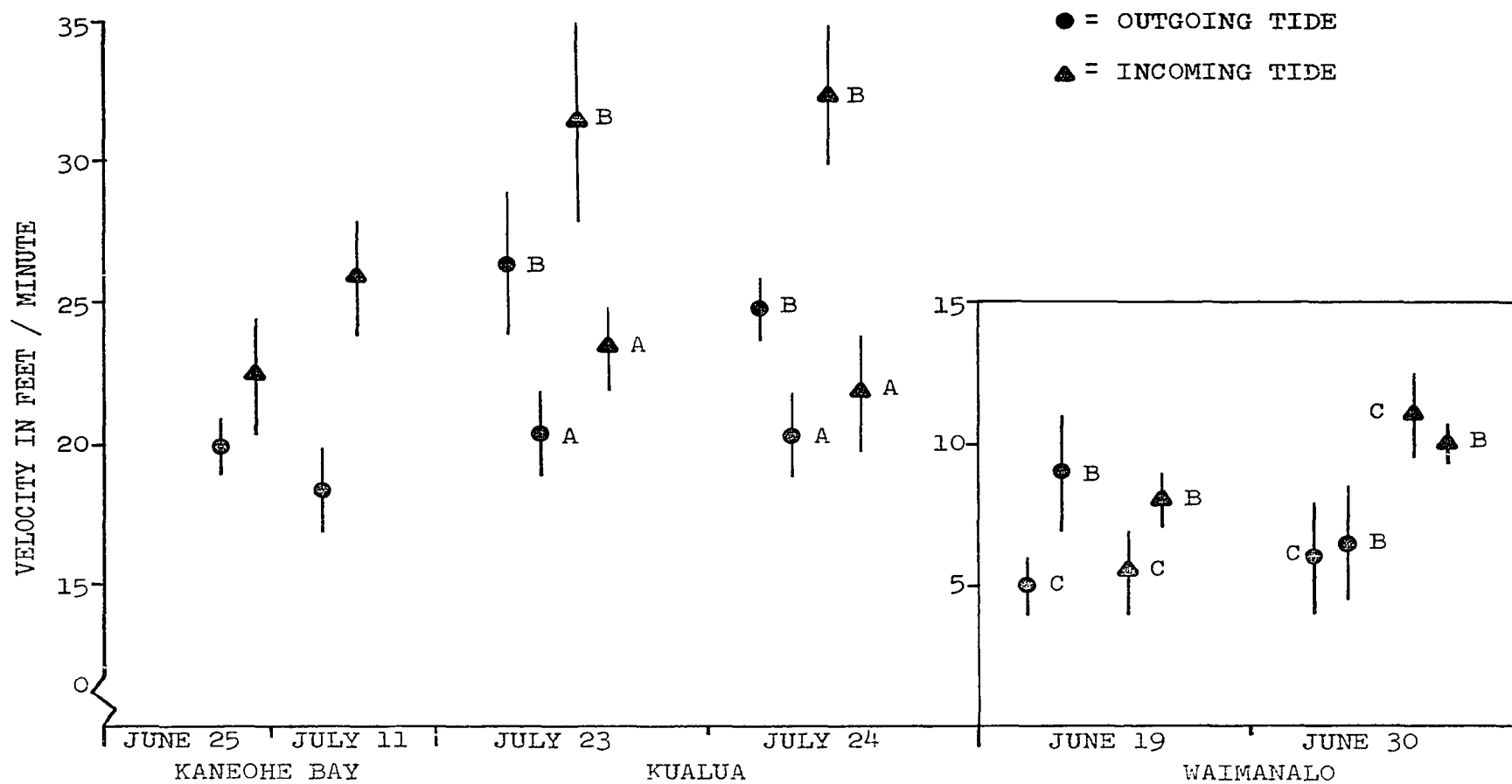


Figure 27. Average and ranges in current velocity observed in sections of three study areas during the summer of 1961.

The data in Figure 27 show that stronger currents occurred on the incoming tides. This was particularly noticeable at Kualua where the velocity of the current on the incoming tide averaged as much as 11 feet per minute faster than the outgoing tide in the surge zone, and as much as 6 feet per minute faster on the outgoing tides. On both of the days during which observations were made, the current had a greater velocity in section B.

Although the two measurements at a given spot during a given tide produced a rather wide range, it can be seen that the ranges for outgoing and incoming tides did not overlap to any extent except at Kualua on July 24. Therefore, a real difference appears to have existed on the days during which the observations were made.

The greater velocity in section B has a hydrographic as well as a topographic basis. The rather constant flow is caused partly by the incoming waves that follow each other in rapid succession, the result being what might be termed a "surge-related current." In addition to this, the outer edge of the reef in the surf zone rises to within 2 or 3 feet of the surface, thus causing a shallow barrier to the deeper reef flat toward shore. To fill the resulting inshore basin the water must flow over this barrier and the result would be a faster current. These two factors could thus be expected to function together in producing

a stronger velocity on the incoming tide.

The currents in Kaneohe Bay appear to be less strong than in section B at Kualua and the variation between measurements is less. Although the measurements with the Kaneohe Bay and Kualua areas were made on different days, they are consistent with the strong impression one gets that the outer reef at Kualua is swept by much stronger currents as well as surge. This idea is also supported by the fact that the Kaneohe Bay area is considerably deeper than the outer flat areas at Kualua. Current velocities are greater at the surface than at the bottom -- particularly in deeper waters.

The currents at the Waimanalo area were much weaker than those in the other two areas. Section B had a pattern that was similar to Kaneohe Bay and Kualua with the stronger components appearing during the incoming tides. The ranges in the measurements, however, show more of a tendency to overlap than in the other areas. Section A had very little current which tended to flow in various directions. Although section C was deeper than B, the currents were comparable. It was noticed that currents close to the surface were much stronger than those near the bottom. This was particularly noticeable in the deep areas (C and D). Section D had a slight current that was apparently weaker than the other sections at Waimanalo.

In addition to having weaker currents than the other windward areas studied, it was observed that the currents present in section A and B flowed in a direction that almost paralleled the shore. Both of these differences are explainable on the basis of the proximity of the area to shore as well as to wave direction. In section A as well as the surrounding sections, waves tended to sweep at an angle to the shore which probably influenced current direction. In addition, the Waimanalo area is situated within 100 yards of the shore so that the tidal flow has very little distance to travel. The Kaneohe Bay and Kualua areas are located about half a mile or more from shore where the water is still traveling rapidly as it fills the inshore parts of the reef.

Currents in the Waikiki area were not measured. A slight current appeared in the surge zone and paralleled the shore somewhat as at Waimanalo. During times when other work was being carried out in the area, the velocity was estimated at less than 5 feet per minute and it was often hardly perceptible at all, as indicated by the pattern of distribution of markers that were being used to study surge. Currents offshore were rarely observed at all and were very slight when encountered in the study area. Heavier currents were sometimes noticed near the surface, but they were considerably reduced near the bottom.

3.9.2 Characteristics of Surge

Surge is defined here as an increase in the velocity of water over a short period of time which usually lasts from about 1 to 4 seconds. If an area is kept under observation for a time before measurements are made, it soon becomes apparent that water movements that fit the above description come predominantly from a direction corresponding to the direction from which the waves are traveling. Such increases may be of two types: 1) a surge from the direction of the approaching waves; 2) a back surge that travels in the opposite direction. In many cases, surges come in a series which cause the water to oscillate back and forth for about a minute. Such back and forth water movement seems to be caused by series of waves that are larger than others. In many instances, surges can be seen that travel only toward shore. They apparently result from waves that are smaller in height than those that cause alternating surges. Some of these surges are easy to detect while others are so weak or are of such short duration that they are difficult to identify. The shallow reef environment is characterized by moving water that predominantly flows in relation to waves and tides, but cross-currents, eddies and other turbulences are present.

The observations on surge were made in much the same way as were those on current. Numbered markers were laid

down on the bottom at the limit of a particular surge just as the water began to move in the opposite direction. After a series of surges the distance between the tags (i.e., the distance of the surges) was measured in inches. Only those surges that alternated their directions were measured.

Since one-way surges are difficult to measure, the first surge of a series that was measured was a back surge, or one that was traveling away from the shore. Correspondingly, the last surge measured in a series was also taken as a surge that was traveling away from shore. Such alternating surges almost always came in groups, or series, and appeared to be of a stronger nature than the one-way surges.

Time could not be measured simultaneously with the measurement of surge because of the joint tasks of dropping tags and keeping oriented in the water. Therefore, the individual surges of a series were timed using the same criterion of beginning the measurements with back surges.

Observations were made at Waimanalo on July 7, 8 and 9, 1961, during conditions of normal trade wind weather. Measurements were similarly made at Kualua on July 23 and 24, and in Kaneohe Bay on July 22 and 25. The incoming tide alone was measured at Waikiki on May 13 and 14. Each time and distance measurement was based on 25 surges.

An analysis of variance was carried out to determine

whether or not the measurements made on the various days differed significantly. Since the differences were not significant, the days were combined to give a single average distance for surges within each section within each area. The average was divided by the average time for surges to give the average velocities shown in Figure 28.

3.9.3 Velocity of Surge

An examination of this figure shows in all instances that the average velocity of surges was greater during the incoming than the outgoing tides. It should be noted that only the incoming tide was measured for surge at Waikiki. The increase in velocity during flooding tides ranged from about 100 percent within section A at Waimanalo to about 300 percent within section D. It can be seen that the areas having the least surge were sections C and D at Waimanalo, which represent the deeper and quieter portions of the areas studied. Section A at Kualua, although not as deep as those mentioned above, represents the relatively sheltered inshore portions of the reef in that area. It can be seen that the velocity in the inshore section (A) was much less during both tides than that in the section (B) near the surf zone. The velocities in Kaneohe Bay differed considerably between the incoming and outgoing tides. Since this area had no rougher and calmer sections for comparison, the figures can only be taken as tidal differences for the area, which had

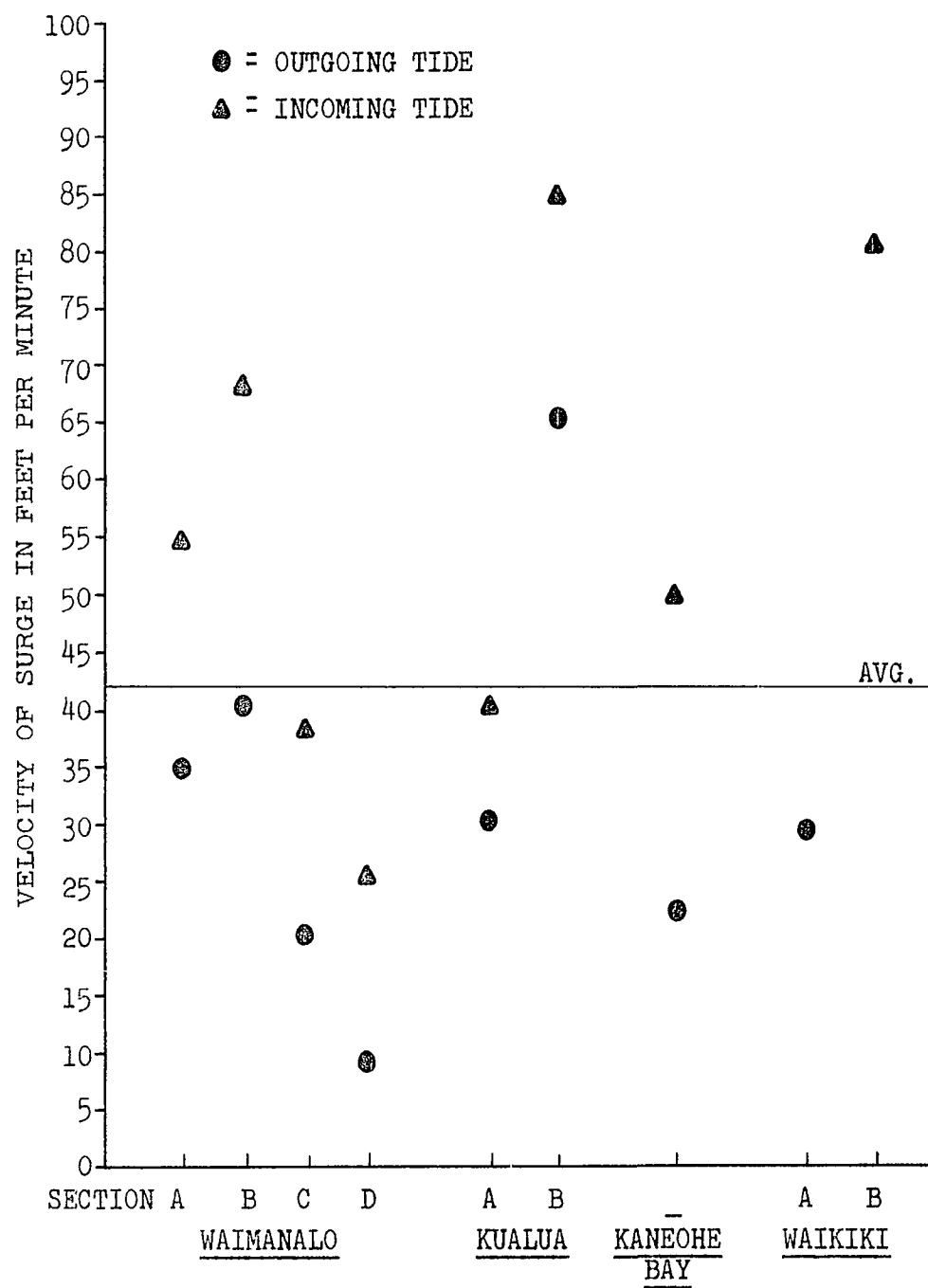


Figure 28. Average velocities of surges observed in study areas during incoming and outgoing tides in 1961.

less surge when compared with places like section B at Kua-lua. The deep offshore section (A) at Waikiki also showed velocities that averaged only about one-third of those found in the surge zone (section B). Although section A at Waikiki is an entirely different area from D at Waimanalo and was measured at different times, it is quite apparent from repeated contact with both areas that both their surge velocities were far lower than those found in other areas.

From the data presented here it is apparent that surge velocities in the rougher sections of the areas were continually stronger than in the calmer sections. The differences persisting during both incoming and outgoing tides were often two or three times greater in the rougher areas. It is most interesting that a section of relatively great surge velocity existed far inshore of the actual breaker zone where surge was the strongest. This section (B at Waimanalo) was the shallowest place in which surge was measured and illustrates the type of situation in which localized shallow areas are subjected to greater surge velocities than deeper areas. This idea was reinforced by viewing the reef from a high vantage point. It could be seen that actual breaker areas existed in various locations within the reef where the bottom closely approached the surface. Swimming in these areas left little doubt that surge zone conditions existed where the water was shallow. The bottom

in such areas generally had a bare "swept-clean" appearance, that was characteristic of Hawaiian reef front surge zones and only fish adapted to living in swiftly moving water were found there. A gradation of surge intensities existed between such breaker areas and deeper areas where the bottom was little disturbed by the influence of surface waves. The four sections at Waimanalo represented such a gradation. As was shown in Section 3.2, numbers of juvenile Dascyllus albisella increased with increasing depth. Since surge decreased with depth, surge and numbers of fish were inversely correlated.

3.9.4 Frequency of Surge

After a number of observations, it became apparent that surge had another component. This was the frequency, or number of surges per minute, that occurred in a particular section or area. Some sections, such as D at Waimanalo, seemed to have a low frequency, while others such as B at Waimanalo seemed to have a high frequency. Suspended particles in the water were watched to determine the motion of the surges. The number of back and forth surges per minute were counted for five 1-minute periods and an average number per minute was determined. As in measuring surge velocities, the first and last shoreward surges of a series were not measured because of the subjectivity involved.

Figures 29 and 30 show the frequencies of surge as

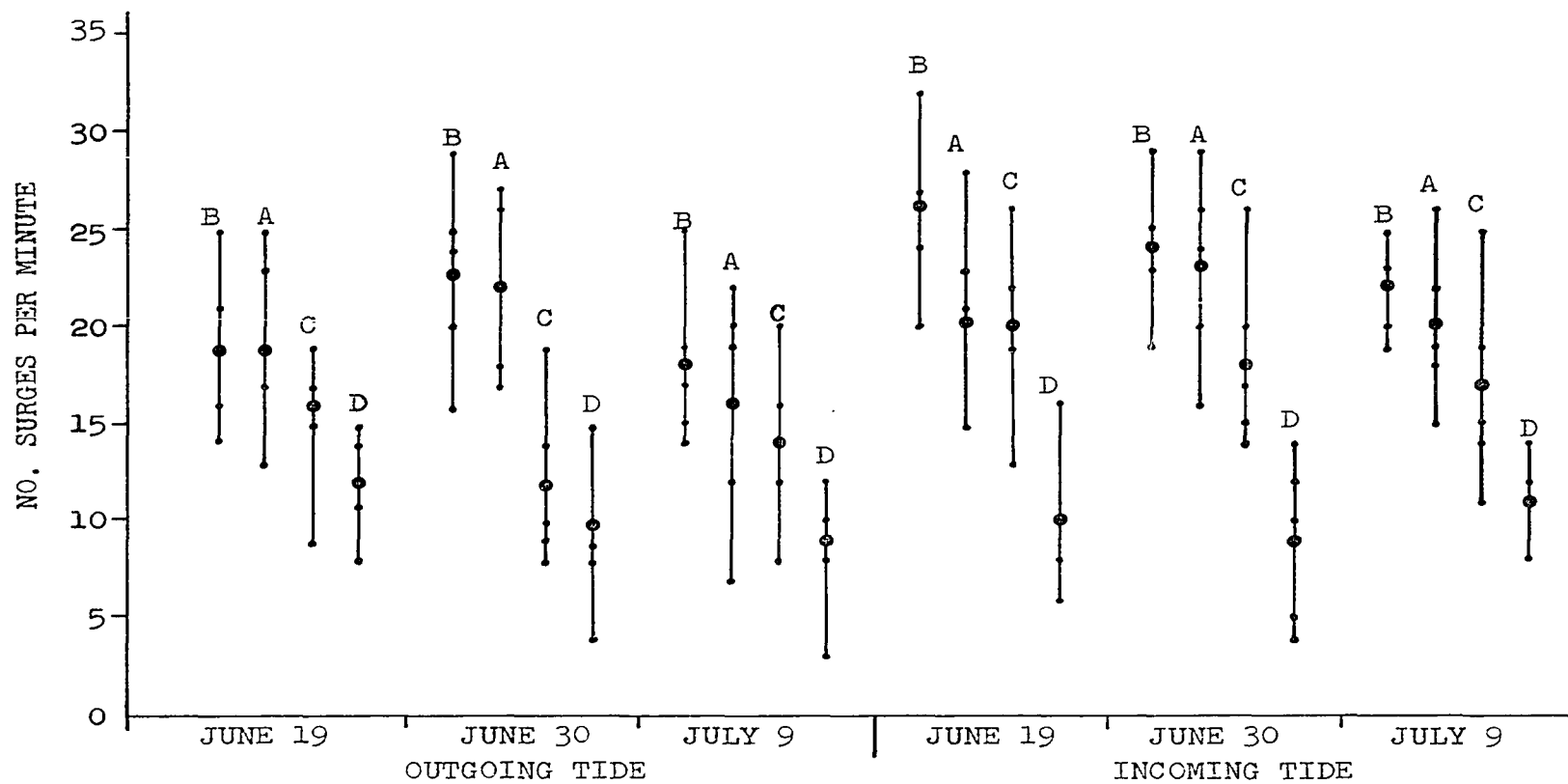


Figure 29. Number of surges per minute observed in the 4 sections of the Waimanalo study area during 1961.

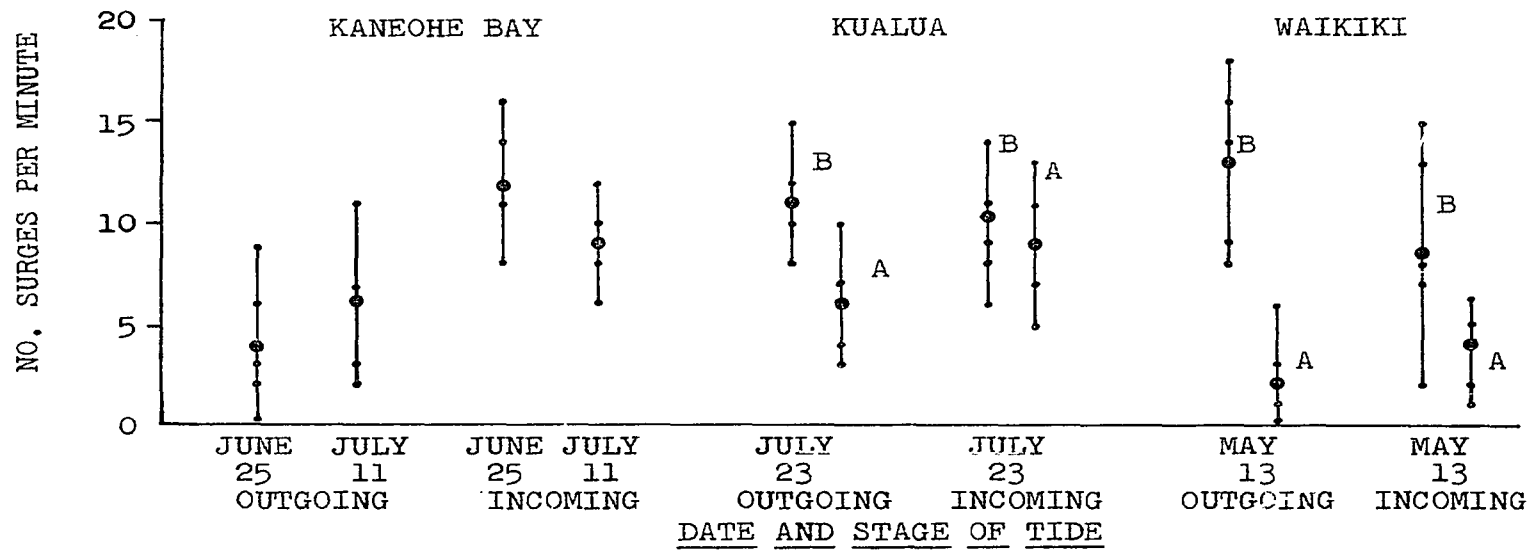


Figure 30. Number of surges per minute observed in the Kaneohe Bay, Kualua and Waikiki study areas during 1961.

measured in the different areas and sections on 7 different days. Individual measurements are indicated by the small dots on the straight lines that represent the ranges and the large dots represent the averages of a particular set of measurements. An examination of the data for the Waimanalo area for both incoming as well as outgoing tides shows a definite reduction in numbers of surges per minute from the roughest area (B) to the calmest area (D). To determine whether or not this trend was statistically significant, a contingency χ^2 test was performed on the data. Although two different tides were involved, the data were all grouped together since the trend was very definite during both the incoming and the outgoing tides. The test showed that the hypothesis of independence, i.e., that frequency of surge was independent of area, was unacceptable ($P < 0.01$). Thus, it may be concluded that the shallower areas here were subjected to more alternating surges per minute than the deeper sections.

As surge in shallow waters seems to be definitely related to the action of waves, these results are readily explainable on the basis of the depth of the water. In shallow waters, the actions of more waves reaches the bottom and in deeper waters, only the stronger surges caused by the largest waves exert their influence on the bottom.

The outgoing and incoming tides on July 23, 1961, show

little difference at Kualua. The data are so limited that it is not possible to make any statements about possible differences in numbers of surges per minute between sections A and B. The May 13 data for Waikiki indicate a possibly greater number of surges per minute in the surge zone (section B). Again, however, the data are too scant to allow a statement as to real differences that might exist between the sections. The number of surges in Kaneohe Bay were fewer on the outgoing than on the incoming tide, and like the Kualua and Waikiki areas, they were fewer than those on the shallow sections at Waimanalo (i.e., sections A and B).

It is possible that in the Kualua and Waikiki areas, the velocity of the surges might be the component of surge that affects the distribution of juvenile Dascyllus albisella. However, at Waimanalo both velocity and frequency of surges might be instrumental in affecting distribution. In any event, there are many possible ways in which surge could affect fish that were exposed to its action. Whether fish are overtaxed by surges of certain velocities or frequencies, or whether some combination of factors occurs such as fish being thrown against coral heads by surge at night, is not known. On one occasion juvenile Dascyllus albisella were seen inside a coral head shortly after dawn at Kewalo Basin. However, it is not known whether or not juveniles

enter coral heads at night in areas where there is surge.

The measurements of the velocity and frequency of surges were made during conditions of normal summer trade wind weather. The average wind velocities on the days during which the observations were made varied between 7.8 and 11.6 knots and the tides varied between -0.2 and ~~2.0~~ 2.0 feet. Although these variations might have resulted in increased or decreased surge velocities, etc., such were not of sufficient magnitude to be apparent to the observer during frequent visits to the areas. Stronger winds increase the velocity of surges on reefs because surges are related to waves that are in turn related to the ocean waves that cause them. Stronger surge probably would drive juveniles off the shallower parts of the reefs, thus narrowing the pattern of distribution to include only the more protected shallow and deep areas. Conversely, periods of very reduced winds might allow aggregations to build up in areas where they would not be found under normal conditions. If such conditions coincided with periods during which large numbers of juveniles were coming into the reefs, distributions could be affected for a whole season.

3.10 SALINITY

Due to the effects of breaking waves, currents, surge, irregular bottom contours, etc., it was expected that little

differences in salinity would be encountered in most of the areas studied because of the great amount of mixing. The deep water areas at Waikiki were not expected to vary since they are covered by ocean water that normally has a very constant salinity. However, a number of water samples taken at Waikiki and Waimanalo were tested to determine the salinity. The Waikiki area received the most attention since observations were made in connection with the study of reproduction.

Samples at Waikiki were taken within two feet of the bottom by opening an empty bottle at that depth. The first filling was flushed out by inserting a tube and filling it with compressed air. The bottle was then refilled and stoppered underwater before it was brought to the surface. The temperature was recorded at the same time that the water sample was taken.

Samples were taken in the same way at Waimanalo along with temperature readings. Salinities throughout the water column were determined from a series of samples taken from the top and bottom of the water column in both the deep and shallow sections of Waimanalo. The resulting comparison was expected to give an idea of the completeness of mixing based on the degree of uniformity of the salinities and temperatures.

Salinities were determined from the water samples by the conductivity method, the the work was carried out by the Honolulu Biological Laboratory of the United States Fish and Wildlife Service.

Figure 31 shows that there was very little variation in the bottom salinities at Waikiki in 1960. Although no determinations were made in the inshore surge zone area, there is no reason to suppose that bottom salinities would vary from the locality tested.

The three determinations made at Waimanalo in 1960 show a variation of only 0.07 parts per thousand between the deep and shallow areas, indicating the rather complete mixing of the water mass. On August 16, 1961, four samples were taken to determine whether or not differences existed between the upper and lower parts of the water column. The greatest variation, which occurred in section A, was only 0.03 parts per thousand between the top and bottom of the water column which were separated by about four feet. These results again show the uniform salinity conditions in the area.

3.11 TEMPERATURE

Temperatures were measured to tenths of a degree using an ordinary centigrade thermometer, and were recorded on a

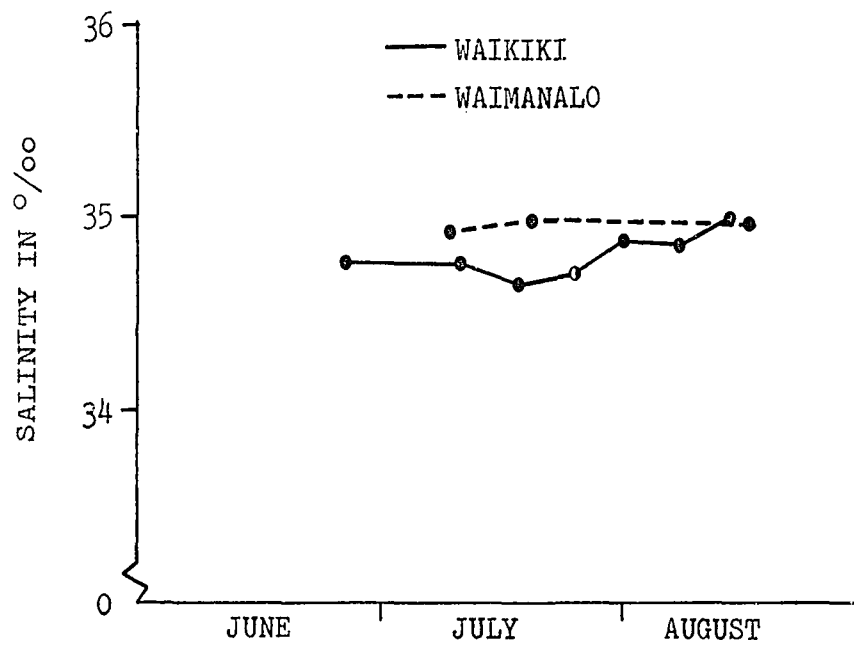


Figure 31. Average salinities in the Waikiki and Waimanalo study areas during summer of 1960.

plastic sheet while underwater. As with salinities, the recordings were made close to the bottom where the fish live. When salinities were taken the temperature was also recorded.

Figure 32 shows the temperatures recorded from both the Waikiki and Waimanalo areas. The temperatures at Waikiki in 1960 show a very gradual rise throughout the summer and a gradual decrease during early winter. Changes over a number of days are in the order of tenths of degrees rather than in whole degrees. As with salinities, the differences in temperatures between offshore study areas were slight with the greatest differences being only 0.2 degrees.

Bottom temperatures observed at Waimanalo during 1961 were for the most part rather uniform between the shallow flats of sections A and B and the deeper waters of section D. The three comparisons made during July and the one on August 18 show somewhat more fluctuation, although the variations were still of the order of magnitude of tenths of one degree. The figures indicate that the temperatures at section A were higher in late summer than in early summer.

3.12 FIELD EXPERIMENTS WITH AGGREGATIONS OF FISH

Experiments were carried out in which fish and coral

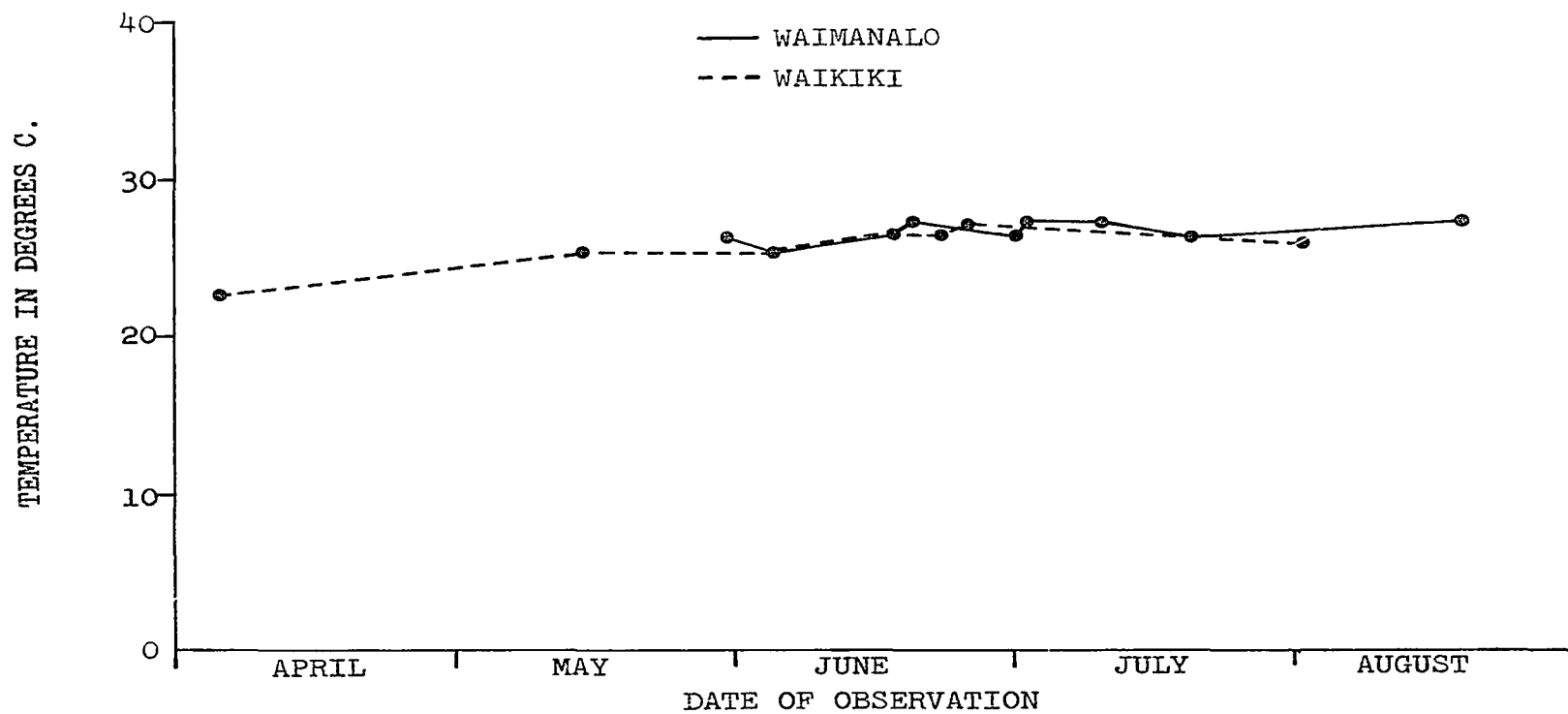


Figure 32. Average temperatures observed in the summer of 1961 at Waimanalo and in the spring and summer at Waikiki.

heads were transplanted in the field to areas that appeared to represent both suitable and relatively unsuitable habitats for juvenile Dascyllus albisella. It was hoped that observation of these aggregations would give additional information concerning the increase and decrease of numbers of fish in such areas. The areas chosen for this work were sections B and D at Waimanalo and section A in the offshore area of Waikiki. The main reason for choosing the latter area was to determine whether or not the presence of coral heads, which were naturally absent, would attract juvenile fish.

Coral heads were transplanted to the study areas and were made fast to the bottom by wiring them to boards that were mounted on iron stakes driven into the bottom. In this way, the head became situated in a more or less natural position close to the bottom in such a way that wave action could not sweep it away. Juvenile Dascyllus albisella were captured and introduced into the coral heads after they were placed on the bottom.

3.12.1 Experiments at Waikiki

Since few live ramose coral heads were available in the Waikiki study area, they had to be brought from the surge zone area close to shore. Pocillopora meandrina coral heads were common in the area and were used in this study.

Four live coral heads were placed over rock bottom

(9, 10, 11 and 12 - Figure 33), and four live heads were placed over sandy bottom (1, 2, 3 and 4). In addition, four dead coral heads were placed over rock bottom (13, 14, 15 and 16), and four were placed over sandy bottom (5, 6, 7 and 8). The dead coral heads were the same species as the live ones and, judging from the amount of algae growing in the interstices, had been dead for some time.

Because of the difficult working conditions, fish could not be introduced to all of the coral heads at the same time. On June 11, five fish each were introduced in heads 1, 2, and 9, 10, which consisted of two live heads over rock bottom and two live heads over sand. On June 15, heads 3, 4, and 11, 12, and 13, 14, 15, 16 received five fish each, which were comprised of two more live heads over sand, two more live heads over rock bottom and four dead coral heads over rock bottom. Head 5 was a dead coral head that was placed over the sand on June 15 without any fish and was found to have a natural aggregation when examined on June 22. On that day, three more dead coral heads were placed on the sand and five juvenile Dascyllus albisella were introduced into each.

The first twenty fish introduced into heads 1, 2, 9 and 10 on June 11 were obtained from sea urchins in the area. However, since sea urchins and associated aggregations of fish were kept under observation from that date (Section

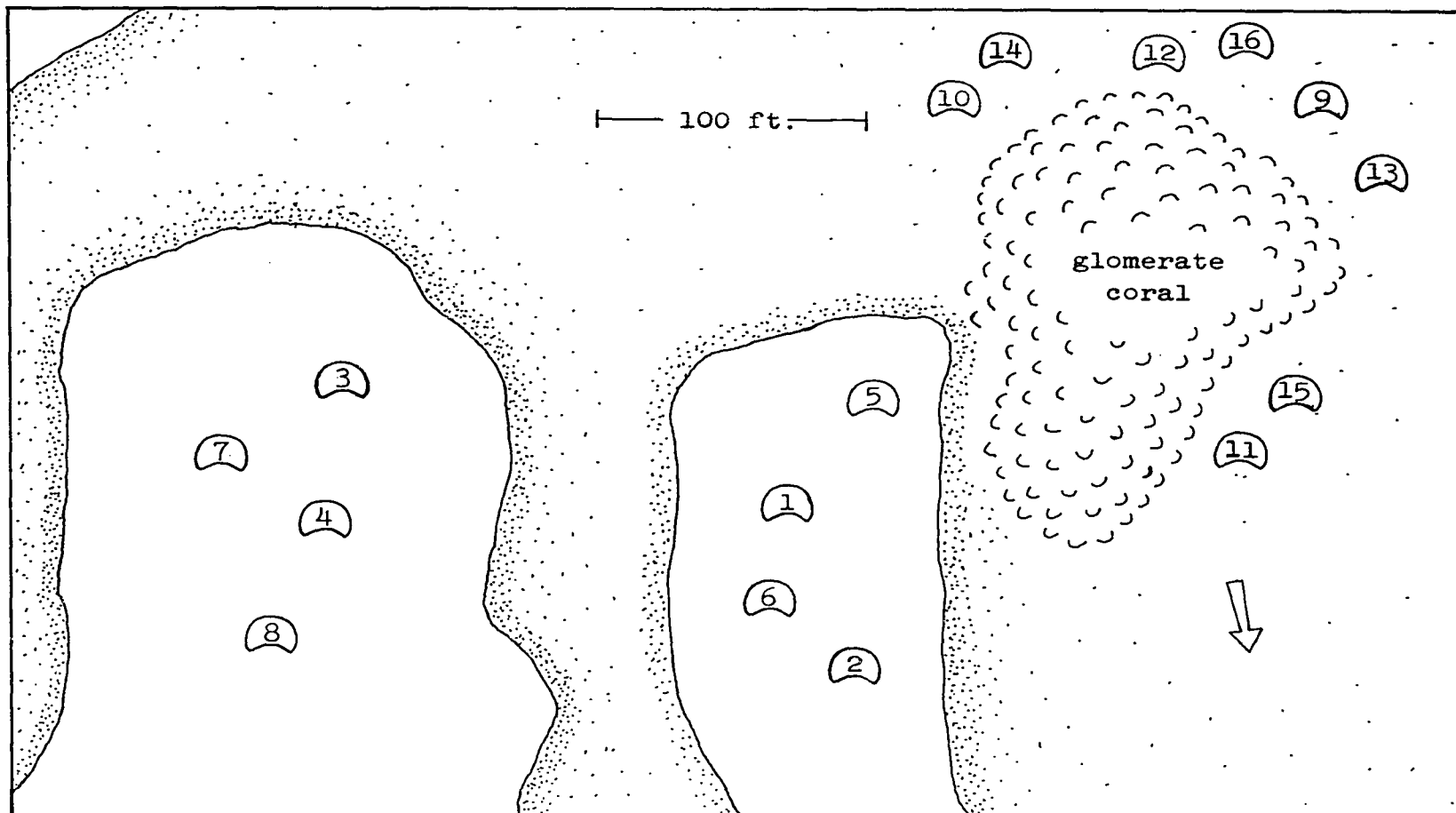


Figure 33. Map of section A, Waikiki study area, showing location of coral heads and other geographic features.

3.13), no more fish were obtained from that source. Fish introduced into the remaining 11 coral heads were obtained from a general area off the town of Waimanalo. These fish were captured the day before introduction into the field and were slowly brought to the same temperature as the sea water before release.

Figure 34 shows the resulting increases and decreases in the numbers of fish in the experimental coral heads transplanted at Waikiki. The histograms topped by a bar represent estimates of the abundance of fish present since numbers were so great as to prevent accurate counts (which could be made up to about 30 fish). The extreme right-hand histogram in each set of observations represents the final observation of July 30. Fish were captured at that time and were brought back to the laboratory for measurement.

The large build-up in numbers in the live coral heads on the sand is evident (Figure 34 - 1, 2, 3 and 4). The numbers of fish were so great that all the interstices between the branches of the coral were filled when they retreated into the coral heads. Although these heads were only about 8 to 10 inches in diameter, there was still room for the fish to retreat deep enough within so that they were not exposed beyond the periphery of the head. The dead coral heads on the sand (5, 6, 7, 8) also contained large concentrations of fish although the quantities were

considerably less than in the live heads. Numbers of fish in live heads that were placed over the rock bottom (9, 10, 11, 12) tended to increase slightly although the numbers in head 10 tripled. In only one instance did the four dead coral heads over hard bottom (13, 14, 15, 16) increase in numbers of fish and this increase was slightly less than double the original number placed there. In two instances, the introduced aggregations were reduced while the remaining coral head contained the same number of fish that was introduced. Figure 10, taken off Waikiki at a depth of 70 feet in the study area, shows experimental coral head #9 over the rock bottom and Figure 11 shows head #1 over the sand. The greater number of fish in the head over sand is evident.

The large numbers of fish in the live heads on sand make it difficult to gain information concerning the mechanics of recruitment. Heads 1 and 2 showed a great increase in numbers of fish between June 15 and 22, while heads 3 and 4 showed similar increases between June 22 and 25. If these increases were part of the same influx of new fish, then it is reasonable to assume that the increase might have occurred sometime around June 22. With one exception, it appears from these data that only one large increase in numbers of fish occurred. However, head #7 gives an indication that another increase occurred between July 5 and 30.

Figure 35 shows the length frequency distributions of

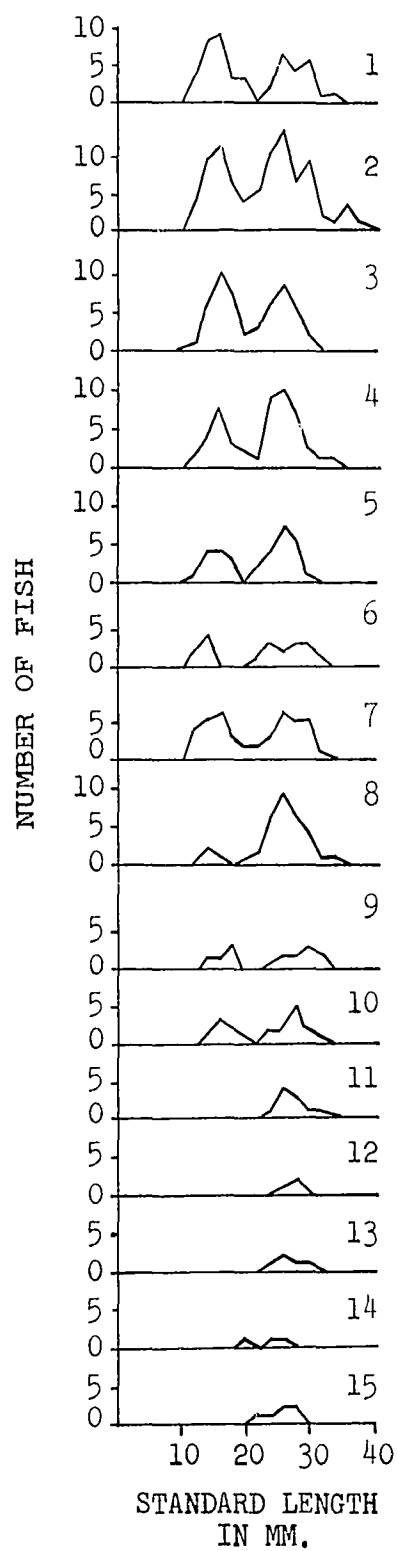


Figure 35. Length frequency relationships of fish captured from experimental coral heads at Waikiki in 1961.

fish captured from the experimental coral heads at Waikiki on July 30. Fish lengths were grouped by 2 millimeter intervals to produce the curves. The data show 2 distinct modal distributions which probably represent the influxes of fish noted in Figure 34. The peak formed by the larger fish probably represents those that appeared about June 22, but which had increased in length by the time of capture. The other peak probably represents the influx of juveniles that occurred between July 5 and 30.

3.12.2 Experiments at Waimanalo

Pocillopora meandrina coral heads were secured from nearby areas and were transported to the study areas, where they were affixed to the bottom as already noted. Fish were captured on other sections of the reef and were transported in nets to the study area without having left the water.

Four coral heads were randomly placed in section B over the rock bottom and four were similarly placed in section D over the sand bottom (Figure 16). Five fish were released into each head on June 19, 1961, and each head was watched to make sure that the fish entered and remained therein. In all cases, fish were responding normally shortly after release.

Figure 36 shows that numbers of fish tended to increase on the sandy section at Waimanalo, whereas they decreased on the hard bottom. Thus, the results are similar to those at

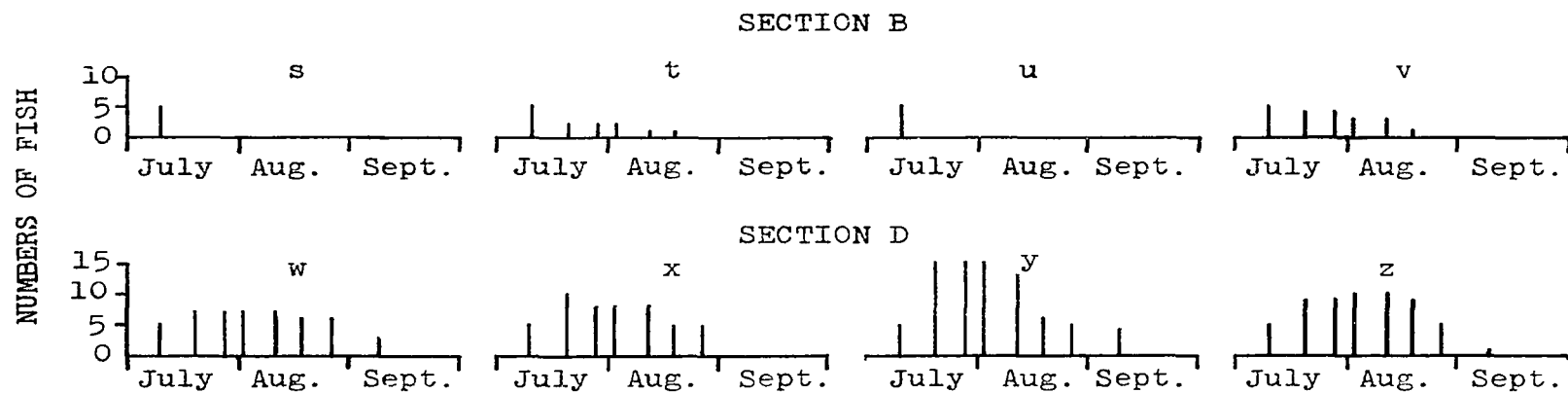


Figure 36. Observations of numbers of fish colonizing experimental coral heads at Waimanalo in the summer of 1961.

Waikiki, although the aggregations did not become so large. It is important to emphasize the fact that the aggregations introduced on the rock bottom of section B, where there was a great amount of surge, did not maintain their numbers whereas those on the rock bottom section of Waikiki where the water was very calm did maintain their abundance. This again shows that surge plays an important part in determining the distribution of juveniles.

The experimental data confirm the observations made on fish under natural conditions, i.e., juvenile Dascyllus albisella build up large aggregations in coral heads in calm water over sand. However, heads associated with hard bottom (in both a shallow, surge-prone section as well as a calm, deep section) contains very few fish. As will be seen in the section on predation (Section 3.16), the scarcity of aggregations on the hard bottom in the calm, deep section of Waikiki is thought to result more from predation than surge, although the latter is doubtless important in the shallow section at Waimanalo.

3.13 ASSOCIATION WITH SEA URCHINS

Young Dascyllus albisella were first observed living among the spines of the poisonous sea urchin, Echinothrix diadema, along the sea wall at Honolulu Harbor in July of 1959. One urchin had a population of three fish and the

other, five fish. One other similar observation was made in deep water off Waikiki in 1959 in which the urchin had an associated aggregation of 16 fish. It was not possible to catch any of these fish, but it was recognized that all of them were of a very small size.

On June 11, 1961, considerable numbers of juvenile Dascyllus albisella were observed associating with Echinothrix in section A of the Waikiki study area. From this time until the study was terminated, urchins were kept under observation and counts were made to determine the magnitude of the fluctuations in numbers of associated fish.

Table 12 shows the results of observations made of the numbers of juvenile fish in relation to numbers of urchins. From both the total numbers of fish found in the urchins and the percentages of inhabited urchins between June 11 and July 30, it appears that there were three influxes of juveniles. One of these occurred on or prior to June 11, another between June 15 and 22, and another between July 5 and 30.

The data indicate a cyclic influx of juveniles during which the fish temporarily inhabited the spines of the sea urchins. Two of the periods during which considerable numbers of fish occupied the urchins were shortly followed by periods when few or no fish could be found. This sudden

TABLE 12. RELATIONSHIP BETWEEN NUMBERS OF SEA URCHINS
 (ECHINOTHRIX DIADEMA) AND NUMBERS OF JUVENILE
DASCYLLUS ALBISSELLA ASSOCIATED WITH
 THEM DURING SUMMER OF 1961.

<u>Collection Date</u>	<u>Total No. Urchins</u>	<u>Total No. Fish</u>	<u>No. Urchins Inhabited</u>	<u>% Urchins Inhabited</u>
June 11	80	58	14	17
June 15	108	7	5	3
June 22	89	81	23	26
June 23	77	75	20	26
June 25	75	5	3	4
July 5	73	0	0	0
July 30	87	39	18	21

disappearance resembles that which occurred in coral heads at Waimanalo in both 1960 and 1961, and supports the idea that juvenile fish may set up a temporary association with either coral heads or urchins (and perhaps other objects) before moving to other locations.

3.14 ASSOCIATION WITH ANEMONES

Commensal associations between pomacentrid fishes of the genus Amphiprion and large anemones of a number of genera have received considerable attention since they were reported by Collingwood (1868). Details of the behavior of these fishes toward their carnivorous host and aspects of their life histories have been reported by Verwey (1930), Gohar (1948), Abel (1960) and Eibl-Eibesfeldt (1960). Gudger (1947) has reviewed the literature up to that time.

The acclimation process whereby the fish is enabled to swim freely among the tentacles of the anemone without being seized and devoured is of the utmost importance to the survival of the animal. Davenport and Norris (1958) gave physiological evidence that a factor in the skin of Amphiprion percula raised the threshold for nematocyst discharge, thus blocking the stimulus necessary to induce the anemone to seize the fish. They also described in detail the behavior of the fish that resulted in the production of the necessary protective factor. However, the possible origin

of the behavior pattern has not been explained.

Although juvenile Dascyllus trimaculatus have been reported to remain in the vicinity of large anemones (Harry, 1953; Eibl-Eibesfeldt, 1960), it has not been reported hitherto that juvenile Dascyllus albisella are sometimes found as a commensal with the small anemone, Marcantbia cookei. Unlike Dascyllus trimaculatus which flees beneath the oral plate but does not touch the tentacles, Dascyllus albisella takes refuge among the tentacles of its temporary anemone host. Although this species belongs to a different genus from the generally recognized anemone fishes, and although the anemone is much smaller and belongs to a different genus than those associated with anemone fishes, the acclimation process is similar. Observations of the behavior of this species not only toward its anemone host but also toward corals and other objects has suggested a possible origin of sea anemone commensalism which will be discussed below.

Studies of the behavior pattern of juvenile Dascyllus albisella toward both coral and anemones were conducted primarily in aquaria. Field observations of fish and anemones showed agreement with those made in aquaria. The fish that were observed varied in length from 15 to 18 mm. The anemones varied in width from 100 to 125 mm. The sizes of both fish and anemones approximated those observed in the

field.

When first introduced to an anemone, juvenile Dascyllus albisella show the same type of behavior as reported for Amphiprion percula by Davenport and Norris (1958). Fish approach the anemone and usually swim around and over it for a short time before contacting the tentacles. They sometimes settle down near the stoma for a few seconds and then continue their "investigation". Unlike Amphiprion percula which touches the anemone with the lower margin of the caudal fin or the ventral edge of the anal fin while swimming over the disc, Dascyllus albisella usually comes to a halt at the side or over the top of the anemone and backs into the tentacles. Actual contact with the anemone takes place along the posterior or anal edges of the caudal fin or anywhere along the anal fin. The anemone usually adheres to the fin at which the fish violently jerks loose and turns to face the anemone. This latter activity is thought to have important significance in the evolution of the behavior of anemone fishes and will be discussed later. The anemone does not always adhere to a fish at every contact, which may indicate either that different areas of the fish cause different responses or that the tentacles may respond differently at different loci along their length. The fish may either wander away from the anemone for a few minutes, or it may remain close to it and continue to make

contact. Occasionally fish approach the anemone headfirst and nip the tentacles. Judging from the vigorousness of the action, this is apparently not a response to food particles. Similar activity is well known among anemone fishes which actually feed on the tentacles.

The initial contact is usually as described above, but occasionally the fish first contacts the anemone with its body. However, this type of behavior usually occurs later in the acclimation process when the fish may bend its body while backing into the anemone, or when it settles down on the disc and leans against one or more tentacles which usually do not adhere to the fish.

As acclimation proceeds, the fish back deeper among the tentacles and lie on the sides but the tentacles seldom adhere to them. At this time all motor activity, except respiration, usually ceases for periods up to 30 seconds or more after which the fish right themselves and remain finning in one spot or else move over the anemone again or away from it. Such cessation of motor activity is unusual among fishes and is shown by Dascyllus albisella only after contact with the anemone or during "sleep" when the fish lean against the branches within coral heads. This behavior is different from that of Amphiprion percula which at this time during the acclimation process dashes back and forth across the disc among the tentacles (Davenport and Norris,

1958).

Dascyllus albisella do not remain close to the anemone for very long periods in the aquarium, but spend most of their time swimming elsewhere. Verwey (1930) noted similar behavior in Amphiprion percula that had become tame in the Onrust Aquarium in Batavia. When acclimated Dascyllus albisella return to an anemone after having spent 5 or 10 minutes away from it, they back into the tentacles without hesitation and sometimes remain in the vicinity nipping them or touching them with the caudal fin. In the field, they may take refuge among the tentacles, or may hide instead among rocks adjacent to the anemone. It would seem from these observations that the anemone might not offer the fish as much of a "feeling" of security as some other objects such as coral heads.

Whether or not the tentacles of the host react to the presence of the fish has been the subject of discussion by a number of authors. Crespigny (1869) and Herre (1936) both reported that the tentacles of the host moved apart in response to the presence of acclimated fish. However, Davenport and Norris (1958) could detect no such movements and suggested that those witnessed by Crespigny and Herre were the result of water movements. The tentacles of Marcanthia cookei showed a definite reaction to Dascyllus albisella both in the laboratory and in the field. Fish that

lay quietly among the tentacles were often rocked back and forth by the action of the tentacles, which actively curled around them. At other times when fish were immobile or finning quietly in one spot, individual tentacles were seen to curl around and seemingly touch the fish with their tips and then quickly withdraw by both contracting and swinging away. The action strongly suggested contact by the tentacles with an agent that definitely repelled them. Whether or not the "agent" was chemical in nature or whether the tentacles were showing a thigmotactic response is not known.

The degree of commensalism existing between Dascyllus albisella and Marcantbia cookei appears to be much less intimate than between Amphiprion sp. and the larger anemones they usually inhabit. Sluiter (1888) and Verwey (1930) observed that anemone fishes in aquaria picked up pieces of food that had been thrown in and deposited them on the tentacles of the anemone, which thus benefited by receiving food not normally available. Gohar (1934) asserted that Amphiprion bicinctus in the Red Sea hunted food and "dragged" living fish almost their own size to the anemone which devoured them. He also observed that fish cleaned out the gastrointestinal cavity of the host.

The anemone fishes benefited from the protection afforded them by the tentacles and numerous observations confirmed that they not only ate the tentacles, but also picked

from them organisms that had been caught by the anemone.

It is doubtful whether fish as timorous as small juvenile Dascyllus albisella that feeds on plankton would bring food to the anemone and judging by their small size while inhabiting anemones (15 - 18 mm.), they would not be large enough to feed on the tentacles. Care of the anemone by "preening" the tentacles was never observed. Incidental fanning of the anemone by the fish, which some authors interpret as functioning to bring a fresh oxygen supply to the anemone or to remove waste products, would be of doubtful benefit to Marcantbia which lives close to the surface on reef flats that are almost continually washed by small waves.

It is apparent that the behavior of Dascyllus albisella toward an anemone is unusual when it is compared with the behavior displayed toward coral heads which are more frequently inhabited. When first exposed to a coral head, juvenile Dascyllus albisella either swim slowly over its surface or immediately enter the interstices and swim slowly around. Within a few minutes the swimming speed increases and they dash around among the interstices occasionally stopping to face outward, after which they continue their high rate of activity. This may continue for five minutes after which they swim more slowly and leave the confines of the coral head to begin feeding outside it. "Tail-touching"

may occur after the fish are fairly well acquainted with the coral head. It was observed only in rare instances, and was seldom repeated as with anemones. Fish occasionally pick vigorously at the coral branches, but the cessation of motor activity that occurs with anemones was never seen.

It might be briefly mentioned here that juvenile fish associated with the long-spined urchin, Echinothrix diadema, in an aquarium often displayed a characteristic fluttering of the caudal fin that is associated with "tail-touching". It is thought that this activity might be released by the sign stimulus presented by relatively sharp-pointed objects such as sea urchin spines and Marcanthia tentacles.

3.14.1 Origin of Commensal Association

The development of commensal associations between animals is based on changes that occur in one or both of the partners. Such changes result from the interactions between the animals and also from the influence of environmental factors such as the type of available shelter, the presence of other animals, etc. In addition, one or both of the partners may have had certain behavioral, physical or physiological characteristics that would make them partially suited for a mutual existence. The following discussion points out some of these characteristics.

Fishes of the family Pomacentridae, as well as other fishes, are strongly influenced by their immediate

surroundings. Although the adults of some species of the genera Chromis, Dascyllus and Abudefduf feed at a considerable distance above the bottom, most species remain in close contact with some kind of bottom cover. All of the species that have been observed to spawn have laid their eggs on the bottom in places which they have first prepared by fanning away or picking off loose materials. Many species develop commensal associations with other organisms. At Eniwetok Atoll, juvenile Dascyllus reticulatus are most often found living with the coral species Acropora nasuta and Pocillopora eydouxi or forms that appear much like these (personal observation). In the same area, juvenile Dascyllus aruanus are most often found with Acropora echinata and Acropora nasuta, whereas adults become associated with the staghorn coral, Acropora accuminata. Franzisket (1959) who worked in the Indian Ocean, showed a photograph of juvenile Dascyllus aruanus with Acropora echinata or a similar form of coral. Cott (1940) related the disruptive coloration of this fish with staghorn coral which is generally referred to by other authors as the habitat of this fish. However, Smith (1960) observed that Dascyllus aruanus was usually associated with weeds in shallow water; this is doubtless an unusual response to local conditions. In Hawaii, juvenile Dascyllus albisella is most often found with either Pocillopora ligulata or Pocillopora meandrina and occasionally with the less common anemone, Marcanthia

cookei, and with the long-spined urchin, Echinothrix diadema.

In addition to forming commensal associations, pomacentrids show other intimate relationships with their surroundings. Limbaugh (ms.) observed the reproductive activity of the garibaldi, Hypsypops rubicunda, which makes its nest by cleaning off the surface of rocks, but "cultivates an elliptical patch of velvety red algae" on which the eggs are eventually placed. Pomacentrus leucostictus commonly lays its eggs in old conch shells (Brinley 1939) and Breder and Coates (1933) observed that a pair of breeding adults carried mouthfuls of sand which they blew at the nesting site apparently scouring the surface. Breder (1949) observed that Pomacentrus leucostictus, which had become acclimated to an aquarium, carried away stones that were placed near an aerator which the fish frequented. Verwey (1930) observed a specimen of Premnas biaculeatus in the Onrust Aquarium in Batavia which "deepened out a hole under its anemone by loosening pieces of coral shingle of the tank bottom with its mouth, removing them to a small distance and depositing them there". The latter author also observed that Amphiprion polymnus, Premnas biaculeatus and Amphiprion ephippium carry food particles to their anemones but with varying degrees of development of this trait among the species.

It is apparent from these observations that fishes of

this family react toward objects in their environment both by congregating within or near them and by making physical contact with them. Many hours of observing Dascyllus albisella have shown that they have great curiosity toward objects that are placed in the aquarium with them. They slowly approach a foreign object and appear to inspect it from a distance which shortens until they have reached the object. At this time they almost always turn and "fan" the object with the caudal fin and many times appear to touch it. Only occasionally do they rapidly dart a short distance away and turn to inspect the object as do fish in the presence of an anemone. Their curiosity is usually quickly satisfied and they leave the object. The "tail fanning" behavior is displayed not only toward inanimate objects such as stones, aerator tubes, etc. but is also directed toward other fish, either of the same or different species. When directed toward other fish "tail fanning" may serve as a form of fighting behavior. During such activity, the caudal fin may be directed toward the head end of an opponent or the fish may assume a position almost parallel to the other fish and slowly approach it sideways while fanning. Breder (1950) observed that Pomacentrus leucostictus engaged in such activities by fanning away sand from the nest as well as "invertebrate marauders".

The motions used by adult fishes in fanning the nest serve to remove foreign particles as well as to aerate the

eggs (Helfrich, 1958; Shaw, 1955). Nest "fanning", however, appears to employ a more vigorous use of the main body musculature than the "fanning" of miscellaneous objects. The body motion of fish engaged in nuptial display is more accentuated than the body motion of fish that are "fanning" eggs, but is less vigorous or absent in fish that are merely "fanning" various objects with the caudal fin. It appears that Dascyllus albisella are prone to display a particular type of motor activity when engaged in various kinds of behavioral activity, and it is expected that the particular type that has developed in relation to "tail-first" investigations of strange objects may have been instrumental in developing relationships between pomacentrids and anemones.

The release of the tail-fanning and tail-touching response by sign stimuli from all kinds of objects, along with the natural curiosity of the fish toward objects in its environment, is a possible basis for the origin of the commensal behavior of pomacentrids with anemones. The adhesion by the tentacles of the anemone to the edges of the caudal or anal fins of "curious" fish that were inspecting them could have great significance in the formation of the association. Since the tentacles stick to such edges, the fish has to jerk itself loose much as Dascyllus and Amphiprion do early in the acclimation process. Whereas touching most objects evokes no response from juvenile Dascyllus, the momentary adhesion of the tentacles acts

as a stimulant. After jerking loose, they immediately turn around to face the anemone and after a short period of time begin to approach it again. It is conceivable that a number of such experiences might have induced certain fish to remain in the vicinity of anemones until behavior patterns and physiological processes associated with the anemone were evolved.

3.15 ASSOCIATION WITH OTHER CORALS AND ANIMALS

Young Dascyllus have been observed associating with coral of the genus Porites. However, the frequency of such associations is low compared with the number of Pocillopora heads that are colonized. The heads involved in such associations are almost always found under conditions similar to those surrounding Pocillopora heads. Porites heads often grow close to each other and tend to form clumps that may extend over many square yards. However, those with associated fish have always been individual heads growing at least two or more feet from others of the species. In addition, they have always been located in deeper waters where the surge is reduced. Such associations have been observed on a number of occasions in the entrance channel to the Coconut Island Marine Laboratory, on flats about 200 yards inshore of the study area. Associations with Porites pukoensis have been mentioned in connection with section 3.2.

Small aggregations were occasionally found at Ala Moana Beach Park living within clumps of the bivalve mollusc Ostrea sandvicensis. The fish were hard to catch in such places and they did not seem to persist there for long periods of time. Since Ala Moana is a popular collecting area, it is not known whether the aggregations disappeared from natural causes or whether they were caught by people.

Occasionally, clusters of calcareous tubes of annelid worms (Serpulidae) attached to pilings in Honolulu Harbor were found to have associated aggregations of juvenile Dascyllus albisella ranging in size from 15 to 25 mm. The tubes were mostly in the intertidal zone and the fish remained close to them at all times, rising and falling with the tides. As many as 80 to 90 fish have been observed congregating around a few clusters of tubes which apparently afford good protection. The tubes, which were up to 3 inches in length, clustered closely together and somewhat resembled a coral head in appearance. It might also be mentioned that no predatory species of fish were seen in the vicinity of the worm tubes.

3.16 PREDATION

The nature and extent of predation of juvenile Dascyllus albisella is difficult to evaluate. Since juveniles are normally only a short distance away from the protective

confines of a coral head, it is likely that it would be difficult for a free swimming predator to catch them. Potential predators are difficult to catch for stomach analysis. Moreover, Dascyllus albisella are relatively scarce compared with other potential prey such as anchovies and silversides, thus decreasing the probability of finding them among the stomach contents of predators. The available information on this question is based on observations in the field.

3.16.1 Invertebrate Predators

Of the invertebrate animals observed only the mantis shrimp was seen to display any interest in juvenile Dascyllus albisella. This animal is well equipped for the role of predator since it has large raptorial chelipeds for grasping as well as the ability to move quickly. Mantis shrimps were seen to catch juvenile fish on two separate occasions, although the conditions under which they occurred were not wholly natural. On one occasion, a juvenile fish that had recently been released was seized by a two-inch shrimp as it struggled close to the bottom near the coral head in which it had been released. The fish was in an obvious state of physiological stress, and was not behaving normally. On the second occasion, a young fish was seized by a shrimp about $2\frac{1}{2}$ inches in length as it swam close over the surface of a coral head. The fish was one of a group of 6 individuals that had retreated close to the head

apparently in response to the presence of the observer. On another occasion, a mantis shrimp was seen attempting to catch a young fish that had recently been released. The fish was apparently under no stress, and was swimming around about 4 inches from a coral head. The shrimp was seen to dash out from the head and to strike at the fish which eluded it.

These observations are not presented as proof that the mantis shrimps are normal predators on juvenile Dascyllus albisella. However, some species are normal inhabitants of coral heads and the fact that they are able to catch fish under certain conditions indicates that they might sometimes prey on them.

3.16.2 Vertebrate Predators

During the course of the studies, it was noticed that many coral heads were inhabited by small fishes of the family Scorpaenidae. Because of the predatory habits of fishes of this family as well as their favorable location in relation to juvenile Dascyllus albisella, they were suspected of feeding on them. Therefore, 15 of these fishes were captured and identified as to species -- Scorpaena ballieui (11 specimens) and Scorpaena conlorta (4 specimens). The captures were made from areas near Waimanalo during the course of other work.

Neither the stomachs nor the intestines of these fish

contained recognizable remains of Dascyllus albisella. However, comparing the number of stomachs containing food with the number of intestines containing material in a later stage of digestion, it would seem that the fish fed some hours before capture. Since many fishes of this family are nocturnal feeders and since most of the fish contained food in an advanced stage of decomposition, it is reasonable to assume that they might feed at night. This raises the possibility that they might prey on juvenile fish at night when they return to the coral head. More information might be gained on the particular question by making collections very early in the morning. Although some Dascyllus albisella in aquaria "sleep" within coral heads at night, others do not. Although observations were not made at night in the field, it is probable that juvenile fish remain close to or within coral heads during the night.

In 1960, observations were made of the number of scorpaenids that were seen in coral heads in sections A and B at Waimanalo and also on the number of Dascyllus albisella inhabiting the heads at intervals over a two-week period. These data are presented in Table 13. It is apparent that large fluctuations in numbers of fish took place in heads 1, 2 and 3 of section A and in head 1 of section B in the absence of scorpaenids. The decrease in numbers between July 20 and 22 could well have been due to some factor other than predation since it occurred in a number of heads at the

HEAD NO.	SECTION A										SECTION B									
	JULY										JULY									
	16	17	18	19	20	22	23	24	27	30	16	17	18	19	20	22	23	24	27	30
1	$\frac{7}{0}$	$\frac{9}{0}$	$\frac{10}{0}$	$\frac{12}{0}$	$\frac{20}{0}$	$\frac{8}{0}$	$\frac{4}{0}$	$\frac{6}{0}$	$\frac{5}{0}$	$\frac{5}{0}$	$\frac{6}{0}$	$\frac{6}{0}$	$\frac{8}{0}$	$\frac{14}{0}$	$\frac{13}{0}$	$\frac{8}{0}$	$\frac{5}{0}$	$\frac{5}{0}$	$\frac{4}{0}$	$\frac{3}{0}$
2	$\frac{2}{0}$	$\frac{4}{0}$	$\frac{5}{0}$	$\frac{5}{0}$	$\frac{9}{0}$	$\frac{8}{0}$	$\frac{9}{0}$	$\frac{10}{0}$	$\frac{9}{0}$	$\frac{6}{0}$	$\frac{1}{1}$	$\frac{2}{1}$	?	$\frac{2}{1}$	$\frac{7}{1}$	$\frac{2}{1}$	$\frac{2}{1}$	$\frac{3}{1}$	$\frac{1}{1}$	$\frac{0}{1}$
3	$\frac{9}{0}$	$\frac{7}{0}$	$\frac{7}{0}$	$\frac{10}{0}$	$\frac{23}{0}$	$\frac{16}{0}$	$\frac{18}{0}$	$\frac{16}{0}$	$\frac{12}{0}$	$\frac{7}{0}$			$\frac{1}{0}$	$\frac{3}{0}$	$\frac{3}{0}$	$\frac{1}{0}$	$\frac{1}{0}$			
4	$\frac{5}{1}$	$\frac{8}{0}$	$\frac{6}{1}$	$\frac{7}{1}$	$\frac{25}{0}$	$\frac{24}{1}$	$\frac{12}{1}$	$\frac{12}{0}$	$\frac{5}{0}$	$\frac{3}{0}$	$\frac{6}{1}$	$\frac{5}{1}$	$\frac{6}{1}$	$\frac{11}{1}$	$\frac{15}{1}$	$\frac{7}{1}$	$\frac{4}{2}$	$\frac{5}{3}$	$\frac{4}{1}$	$\frac{2}{1}$
5		$\frac{1}{3}$		$\frac{2}{2}$				$\frac{1}{1}$					$\frac{2}{1}$	$\frac{3}{1}$	$\frac{4}{1}$	$\frac{1}{0}$	$\frac{1}{0}$	$\frac{1}{0}$		
6	$\frac{1}{0}$	$\frac{1}{0}$	$\frac{1}{0}$	$\frac{1}{0}$	$\frac{2}{1}$	$\frac{2}{1}$	$\frac{3}{1}$	$\frac{1}{0}$	$\frac{0}{1}$	$\frac{0}{2}$					$\frac{2}{1}$	$\frac{1}{1}$	$\frac{1}{1}$	$\frac{1}{1}$	$\frac{1}{1}$	
7	$\frac{2}{1}$	$\frac{2}{1}$	$\frac{1}{1}$	$\frac{1}{1}$	$\frac{3}{1}$	$\frac{2}{1}$	$\frac{1}{1}$	$\frac{1}{1}$					$\frac{3}{0}$	$\frac{3}{0}$	$\frac{1}{0}$	$\frac{1}{0}$				
8	$\frac{1}{0}$	$\frac{2}{0}$	$\frac{2}{0}$	$\frac{3}{0}$	$\frac{1}{0}$	$\frac{5}{0}$	$\frac{2}{0}$	$\frac{3}{0}$			$\frac{3}{0}$	$\frac{4}{1}$	$\frac{7}{1}$	$\frac{16}{1}$	$\frac{24}{1}$	$\frac{6}{0}$	$\frac{8}{0}$	$\frac{5}{0}$	$\frac{4}{0}$	$\frac{2}{0}$
9	no data										no data									
10				$\frac{5}{0}$	$\frac{5}{2}$	$\frac{8}{2}$	$\frac{12}{0}$	$\frac{16}{0}$	$\frac{10}{2}$	$\frac{8}{2}$			$\frac{3}{0}$	$\frac{2}{0}$	$\frac{1}{0}$	$\frac{1}{0}$	$\frac{1}{0}$			
11	no data												$\frac{3}{2}$	$\frac{3}{2}$	$\frac{3}{2}$	$\frac{4}{2}$	$\frac{4}{2}$	$\frac{3}{2}$	$\frac{2}{2}$	$\frac{2}{2}$
12						$\frac{2}{0}$	$\frac{2}{0}$								$\frac{2}{0}$					
13													$\frac{2}{0}$	$\frac{2}{0}$		$\frac{1}{0}$				

TABLE 13. NUMBERS OF JUVENILE DASYLLUS ALBISELLA (NUMERATOR) IN RELATION TO
NUMBERS OF SCORPAENID FISHES (DENOMINATOR) ASSOCIATED WITH THE SAME
CORAL HEADS AT WAIMANALO DURING THE SUMMER OF 1960.

same time (section 3.2.1). The decrease also occurred in other heads that had associated scorpaenids. The fact that scorpaenids were not observed in coral heads in which numbers of fish decreased does not imply that predation did not take place, since scorpaenids might visit different heads at night. However, it does imply that relatively large decreases in numbers of fish can take place in heads that are not populated by these predators. What appear to be the same scorpaenids can be repeatedly seen in the same head and often in the same spot, thus indicating that they remain in specific heads at least during daylight hours.

It can be seen from Table 13 that scorpaenids were not plentiful in either section. On any single day the most that were found were 5 individuals in section A and 7 in section B.

An indication that scorpaenids prey on Dascyllus albisella is suggested by the situation encountered at head #24a in section D at Waimanalo. This is not a single coral head, but a 4 x 7 foot mass of an arborescent form of Porites lobata. The patch when first discovered on May 29, 1961, had an associated aggregation of 25 juveniles, which gradually disappeared until none remained by June 30. When first seen, the juvenile Dascyllus albisella had singled out a conspicuous clump of coral that stood out among the general mass and the fish were feeding at this

locus. A 5-inch scorpaenid fish of the genus Dendrochirus was also associated with the mass of coral. On three of the four subsequent observations of the Dascyllus albisella at this head, this scorpaenid (or one of similar proportions) was seen lying motionless at the base of the particular locus over which the fish were feeding. On each visit, the fish were feeding at a different locus, and the scorpaenid had changed its position accordingly so that it remained below the Dascyllus.

A number of other observations indicate that other species of scorpaenids prey on juvenile Dascyllus albisella. On two occasions in section A of Waikiki, large scorpaenids of the genus Dendrochirus were seen lying motionless at the bases of rocks where small juvenile Dascyllus albisella were living. The juveniles were feeding on a particular side of the rocks and the scorpaenids were lying directly beneath them. One of these fish, a 4-inch specimen of Dendrochirus brachipterus was captured, but its stomach was empty.

Three other species of predatory fish appeared to adopt a "stalking" attitude similar to that of the scorpaenids. On one occasion, a cornet fish (Fistulariidae) 2 feet in length, was seen floating motionless alongside experimental head #5 in section A at Waikiki. Although this head was in a sandy section, it was within 10 feet

of the periphery of an area that was populated by coral heads and other fish. Several trumpet fishes (Aulostomidae) were seen hovering around experimental coral heads at Kewalo Basin where juvenile Dascyllus albisella had just been released. The absence of some of the juveniles strongly indicated that the trumpet fish had eaten them. On another occasion, a 12-inch lizard fish (Synodontidae) was seen lying beneath the same coral head. The final observation of apparent stalking was made about 40 yards to the southwest of head #5 where a 6-inch flounder (Pleuronectidae) was observed lying on the hard bottom facing head #10, and about one foot from it. The fish was initially seen as it approached the head from a distance.

With the exception of the scorpaenids, all of the predatory fish referred to above show essentially the same type of behavior in relation to the actual seizing of the prey. This consists of an extremely quick darting motion when the prey reaches a particular point in reference to the predator. The scorpaenids show a somewhat different behavior in this respect by typically waiting until the prey approaches to within a critical distance at which time they ingest it by creating a quick suction of water into the mouth. From the above observations, however, it appears that these species (and probably others as well) actively seek juvenile Dascyllus albisella and other species and lie in wait for them close to the coral heads in which they live.

It must be emphasized that the evidence to date is all circumstantial and Dascyllus albisella have never been identified from the stomachs of predatory fish.

3.16.3 Abundance of Predators

Since predators represent an integral part of the environment of juvenile Dascyllus albisella, some evaluation of their abundance and distribution is necessary to bring this factor into perspective in relation to surge. A great deal of experience in underwater observing over a number of years in the various types of marine environments has enabled a general analysis of this factor. Areas of considerable surge activity and areas of relatively quiet water each present rather well defined fauna that can be expected in such areas, providing the topographical features of the bottom and associated factors are the same.

Sections of relatively strong surge in the Kualua, Waimanalo, and Waikiki areas appeared to be devoid of the types of predators mentioned above, with the exception of Scorpaena ballieui and Scorpaena conlorta. Since none were seen during the normal course of observations, specific searches were made which included looking into crevices whenever possible. Predaceous fish still were not seen in spite of this extra effort. The coral heads in these sections did harbor the two species of small scorpaenid fishes mentioned above, but a comparison of their relative

abundance between rough and calm areas was not made. It is doubtful whether the presence of these species alone could eliminate aggregations of juvenile Dascyllus albisella so quickly that they would seldom be seen in these areas.

The surge areas were rather devoid of small fish in general. The wrasses, chaetodonts, pomacentrids, apogonids, and other species that can almost always be seen in areas of quieter water were very scarce or nonexistent. It is probable that surge activity was also responsible for their absence. Whether or not the absence of predators is a reflection of the absence of prey species is difficult to say. It is probable that these species also cannot tolerate such hydrographic conditions. Most likely their absence results from a combination of these two factors.

The calmer areas can be divided into two types of habitats in relation to predator distribution. One of these types is typical of most of the Kaneohe Bay study area as well as sections C and D at Waimanalo and the sandy parts of section A at Waikiki. Such types of bottom are either sandy or are characterized by a flat, bare hard base of coral rock interspersed with patches of sand. Sand from the patches drifts into crevices in the harder parts of the bottom, thus filling up possible hiding places for bottom feeding predators. Predatory species have not been seen in such sections in Kaneohe Bay and with the exceptions

noted earlier in this section, have not been seen near Dascyllus albisella in sandy patches of bottom. The exceptions are those discussed earlier in this section where a lizard fish and a cornet fish were seen lying beneath the same coral head at different times. Although the head in question was isolated on sand, the bottom around it that led to a nearby patch of coral was strewn sparsely with small rocks that probably afforded enough cover for the predatory fish to work their way to the head. The movement of the sand might be a more important factor than lack of cover in restricting the movements of relatively quiescent species of predators into such areas. The sand is often in motion to a greater or lesser degree and would tend to cover up a fish lying on the bottom. Possibly it would also interfere with the vision of the fish, which have no eyelids.

The second type of habitat involves calmer areas with rock bottoms such as those found in section A at Waikiki. Predatory species of fish in such areas are very numerous and include a number of different species of the types mentioned above. In addition, hawk fishes (Cirrhitidae) are very common and some species habitually "perch" on top of the few coral heads that were found in such areas. Other predators such as angler fishes (Antennaridae) and some wrasses (Labridae) are also present, but are less abundant. Although accurate counts were not made, it

is conservatively estimated that at least 10 to 15 individuals of predatory species of fish were seen incidentally during each dive.

A more precise study of the distribution of juvenile Dascyllus albisella in relation to predator distribution was made in an area about one mile northwest along the coast from Nanakuli. An isolated coral mound with an area of about 50 square feet was found in a large area of sand about 150 feet from the nearest hard bottom. Associated with the mound were six live and four dead coral heads of the species Pocillopora meandrina. Five of the six heads had aggregations of juvenile fish that ranged in size from about 15 to 25 mm. in length. The five heads contained 3, 5, 12, 13, and 22 fish. A careful search of the mound failed to reveal a single fish of a predatory species. Not all of the crevices could be thoroughly explored, so the possibility exists that predators might have been present.

A nearby stretch of rock bottom was well populated by coral heads of the species Pocillopora meandrina. Small coral mounds with associated coral heads were also present in sand pockets and were as close as four to five feet from the main area of rock bottom. Thirty-eight individuals of predaceous species of fish were counted in the area within a ten minute interval. The dominant species belonged to the families Scorpaenidae and Cirrhitidae which

are considered as having the greatest potential as predators of juvenile Dascyllus albisella. No juveniles were seen either on the main area of hard bottom or on the small coral mounds closely associated with the main area.

Hiatt and Strasburg (1960) also considered the problem of predation in relation to bottom living fishes in the Marshall Islands. They state that: "Hawkfish are small, solitary, demersal carnivores which lie in wait for their prey which consists mostly of crustaceans and small fish closely associated with living corals . . . The larger members of the family usually lie motionless on the top and sloping sides of living coral heads rather than partially concealed . . . " Their stomach analyses of these fishes show a high proportion of small fish including Chromis caeruleus, a small pomacentrid fish that inhabits coral heads. Randall (1955) observed a lizard fish (Synodontidae) catch a juvenile manini, Acanthurus triostegus sandvicensis, and also found them in the stomachs of moray eels. He also mentioned that squirrel fishes (Holocentridae), jacks (Carangidae), scorpaenids, hawkfishes, barracudas (Sphyraenidae) and possibly certain of the larger nocturnal crabs probably feed on manini. Although the manini is not a coral fish, it is a bottom living form as is Dascyllus albisella and is often exposed to the same kinds of predators.

3.17 DISCUSSION OF FACTORS INFLUENCING DISTRIBUTION

Examination of the various physical and biological factors in the environment of juvenile Dascyllus albisella show the complex nature of the individual components. The individual factors in the environment vary in quality and intensity, but their effect on a fish may be modified by other factors. For instance, the velocity of surge may increase or decrease which causes the distance a fish maintains between itself and its coral head to increase and decrease. However, older fish maintain a greater distance between themselves and coral heads which offsets to a certain extent the effects of the surge. The distance is also influenced by the type of bottom over which the coral head is located. Fish located over rock bottom strewn with pieces of coral, algae, etc., remain closer to their coral head than fish located over sandy bottom. In view of such considerations, it is apparent that many difficulties are involved in attempting to relate such a complex of factors. However, with the information available from this study, it is possible to create a general picture of the interaction of pertinent factors in relation to the distribution of juvenile Dascyllus albisella.

Environmental factors at Waimanalo, such as surge, bottom topography and composition, show a gradation of intensities and characteristics between the four sections

studied. The differences between the extremes of the area are well-defined and form a definite basis for comparison. The area is composed of one section in which fish are concentrated in coral heads in deeper water and one section in which fewer fishes are found in shallower water. Abundance of coral heads is not a factor causing the differences in numbers of fish, since more coral heads are present in the shallow section where fish are more scarce. Certain species of predators are somewhat more abundant in the shallow section, but fluctuations in numbers of fish occur independently of their presence. Predation in the more populated deeper section also appears to be reduced both because of the absence of potential predators and because of the survival of fish associated with glomerate type coral heads which offer less protection than the ramose type that are usually colonized.

Salinity and temperature vary only slightly at Waimanalo due to the mixing action caused by surges and currents. Since these factors are rather uniform they probably have little influence on distribution of fish.

Differences in distribution of fish are unlikely to be caused by differences in distribution of food, since the same factors that result in an even distribution of temperature and salinity also result in an even distribution of plankters. The behavior of particular species of plankters

as well as certain local conditions might tend to form concentrations in certain spots, but such phenomena would be difficult to evaluate. If anything, there might be a greater abundance of food in the shallow areas where fish are scarce because more water passes a given location in a given period of time. Juvenile Dascyllus albisella taken from different areas rarely have empty stomachs, which indicates that food is available most of the time.

The greatest differences were found in the velocity and frequency of surges. The shallow section was subjected to surges of considerably greater velocity than the deep section. The number of surges in a given period of time were also greater. In terms of energy expenditure, there can be little doubt that a fish living in the shallow sections must do more work to maintain a constant position in relation to a coral head. The orientation problems are relatively simple in relation to a constant current since a fish can take a position on the upcurrent side of a coral head and swim at a pace that will keep it an even distance from the head. However, the presence of surge causes the fish to almost constantly change its pace of swimming to meet the resulting increase and decrease in velocity of the water and change in direction of the surges. At one time the fish must swim hard to keep from being swept toward the coral head, and in as little time as one second or less, it

may have to turn and swim hard in the opposite direction to keep from being swept away from the head. Such activity can persist for periods of time up to 30 seconds during which the fish is struggling constantly to maintain its orientation with the coral head. Isolated surges also occur frequently along with occasional cross surges, all of which require some compensating motion on the part of the fish.

By watching the behavior of fish in both sections, it became apparent that the fish in the deeper quieter section were having much less difficulty maintaining their positions in respect to the coral heads. They were not constantly being pushed toward or away from the heads by the surges before they were able to compensate, as were the fish in the shallows. Nor did they undergo interrupted periods of feeding as did fish in the shallows when they apparently could do nothing but swim hard to maintain a stationary position in the water.

It is possible that juveniles initially colonizing a coral head might leave after a period of exposure to such conditions. In this event, they would have another chance of resettling in a more favorable area. This type of behavior could represent a response to a lack or an excess of certain stimuli that result in an integration of the fish with a particular type of habitat. Under these conditions, the motivation for migrating might become dominant

so that the fish would leave the shelter. This type of situation could account for the sudden disappearance of fish from urchins in which they had been living, as well as their disappearance from coral heads in turbulent areas. In the former case, the spines of the urchin could represent an inadequate visual stimulus while in the latter case, the velocity of the surges could represent an excess of a rheotactic stimulus. The high level of motivation for migrating would probably become reduced the longer a fish remained associated with a shelter such as a coral head.

The experimental coral heads placed in the two sections support the conclusion that fish tend to concentrate in calmer waters. It is significant that the numbers of fish decreased or were barely maintained on the more turbulent flats at Waimanalo while they increased in the calmer sections both there and at Waikiki where the topography of the bottom was very similar. In the latter place, the increase occurred despite the presence of many predatory fish.

Whether it is the velocity or frequency of surge that exerts the greatest influence on distribution is difficult to say, since the data at hand do not allow a comparison between these components. Both are inextricably bound together and act jointly on the fish in the field. Comparing the velocities of currents that are tolerated by fish with the velocity of individual surges is of little

value since the surge is essentially a current of varying velocity. For the moment, at least, the important thing to note is that either the frequency or the velocity of the surge or both are potentially important in the early life history of this species.

The Kualua area, as at Waimanalo, shows little variation in temperature between the inshore section which is populated with fish and the turbulent surge zone section which lacks fish. The surges and currents no doubt serve to more or less completely mix the water, producing a uniform temperature. Although salinities were not determined in all locations, there is little reason to expect that they would vary to any great degree.

The predator situation appears to be quite different in the two sections. Only a few individuals of potentially predatory species were seen in the rougher section at Kualua, although numbers were greater in the calmer portions where most of the Dascyllus albisella were found. In respect to numbers, there would seem to be a greater potential for predation in the calmer section, but in total numbers of individuals as well as species of predators in the two sections, the potential is slight when compared with an area such as Waikiki. Predation undoubtedly operates in the area, but it is probably not the most important of the factors regulating distribution.

Currents in the two sections at Kualua are relatively strong and are persistent during periods when tides are flowing. Steady current, however, is probably not an important influence on the distribution of the fish since Dascyllus albisella are relatively abundant in the middle sections of this area. Observations made in other areas also point to a minimal role of current in influencing distribution. Juvenile Dascyllus reticulatus, which behave much like Dascyllus albisella, were found in large numbers at Eniwetok Atoll in areas where currents were as great as two knots. However, these areas were either on the lee sides of islands or were located in deep water where surge was not detected.

As at Waimanalo, the contrast in velocity of surges is very pronounced between the two sections at Kualua. The surge zone section is a very difficult one in which to work because of the high velocities of the surges. Very few fish of any kind are present although coral heads are rather abundant. Fish living in this section would be subjected to all of the problems of orientation discussed above.

It is difficult to integrate the Kaneohe Bay area into the general picture because of the uniform conditions found there, and also because there is no section where surge is pronounced to serve as a comparison. The area lies deeper underwater where surge has less effect on fish than in

shallow water. Currents in the area are relatively strong, but as noted above, they are probably a relatively unimportant component of the habitat. Potential predators are practically nonexistent in the area possibly because of the lack of adequate shelter. The temperatures and salinities would be expected to vary little and are probably not a significant influence to distribution. In comparison with other areas, the Kaneohe Bay area gave the general impression of being one in which there was a moderation of the influences under discussion. The great abundance of fish no doubt results from a reduction of one or more of these factors.

The situation at Waikiki is somewhat unusual. The two sections were compared on the basis of the features dealt with in this study despite the relative lack of juvenile fish. No juveniles were ever seen in the surge section while those found in the calm section offshore were present under unusual conditions. A few were seen hiding in crevices in dead coral rocks and considerable numbers were seen temporarily associated with sea urchins.

It was recognized early in the study that the offshore section had many of the features of other areas where Dascyllus albisella were most abundant. However, ramose coral heads were almost totally absent in the section. In addition, predators were particularly numerous and were

found closely associated with the two ramose coral heads that were present. A single small Pocillopora meandrina head was found growing on an anchor fluke about two feet off the bottom which effectively removed it from the predators below. Probably because of its widely separated branches and small size, numbers of fish associated with it fluctuated with the numbers of fish in sea urchins, but at least 8 juveniles of varying sizes were always associated with it.

The introduction of coral heads into the area resulted in the build-up of large numbers of associated fish. The increase in numbers of fish was noticed in heads placed on rock bottom as well as in those placed on sandy bottom, but it was much more pronounced in the latter. On the basis of these observations and experiments, it was concluded that the calm area would be a more or less optimal habitat for juveniles from the standpoint of the very slight surge found there.

As in the Kualua and Waimanalo areas, the greatest differences noted were in the velocity of surges between the two sections. The surge section had much greater average velocities than the calmer section and there was an indication that the number of surges per minute were also greater. Of all of the areas measured, the Waikiki surge section had the strongest surge and probably the greatest

potential surge since the section is located outside the breaker zone where the height of the waves can become relatively great.

Temperatures and salinity differences are quite uniform throughout the area and would not be expected to have important effects on distribution.

Relatively few species of fish were seen in the surge section, including potential predators. Among those species that apparently were able to tolerate conditions in the section were the active swimmers. These species, which included mostly scarid (Labridae) and goat fishes (Mullidae), apparently were able to survive there because their swimming behavior allowed them to be swept back and forth by the surge. Fish in this area were restricted to browsing for food during periods of relative calm which reduced their energy expenditure in resisting the surge. It is probable that other species maintain themselves in the area by finding crevices or other cover that offers protection from the strong surge.

Certain species of fishes are found in "characteristic habitats" which offer sufficient protection against surge. Strasburg (1953) pointed out that the scouring and filling of tide pools by sand, which was moved around by surge, may act to keep many fish inhabitants including blennies away

from such areas. As a result, most species of fish are found in more sheltered locations. Helfrich (1958) found that juvenile Abudefduf abdominalis were more abundant in tide pools that were sheltered from the direct surge by ridges, outcroppings of rock, or solution benches. It appears that juvenile Dascyllus albisella "adjust" to surge by congregating in restricted portions of the reef where surge action is relatively slight. By showing this in greater detail, this study further supplements the observations of Gosline and Brock (1960) who stated that "repeated collecting and observation of Hawaiian shore fishes over a number of years have made it increasingly clear that in shallow water, the primary factor governing zonation is wave action", which is responsible for surge.

SECTION IV
SUMMARY AND CONCLUSIONS

1. The life history, behavior and ecology of the pomacentrid reef fish Dascyllus albisella Gill were studied in the waters around the island of Oahu. The investigation was conducted with two goals in mind. The first was to gain more information concerning the life history and behavior including reproduction, growth and food. The second was to relate distribution to physical and biological factors in the environment including temperature, salinity, water movement and predation.

2. An analysis of the ratio of ovary weight to body weight showed that spawning occurred during the late spring and summer months. Spawning was observed only on the leeward side of the island of Oahu where the length frequency mode for adult fish was 115 mm. No spawning was observed in Kaneohe Bay, and on the basis of smaller fish captured there, it was concluded that either sexually mature fish did not enter traps or were not present in the areas sampled. The average ovary contained 25,000 spawnable eggs and size distribution of ovarian eggs indicated that spawning may take place more than once each year. Sex ratios from fish caught in both Kaneohe Bay and off Waikiki show that there were more females than males present. This

condition could have resulted from the absence of nesting male fish in the aggregations sampled.

3. Nesting occurred over a wide area off Waikiki where adult fish were common. Male fish made nests on the bottom by fanning away sediment with a vigorous swimming motion. Numbers of nests increased during the spring and summer thus corresponding with the time of maximum reproduction as shown by gonad analysis. Eggs in the field required an incubation period of 4 days at temperatures that ranged from 26.2 to 27.5 degrees C. Eggs were apparently all laid on the same day since they all hatched within one day. Comparisons between numbers of spawnable ovarian eggs and numbers of eggs in nests showed that more than one female fish may spawn in a particular nest.

4. Male fish showed a characteristic pattern of reproductive behavior around the nest. They assumed a bright white coloration and performed a series of loops in which an exaggerated anguilliform motion apparently added emphasis to the color. The male swam in front of the female and led her to the nest where the eggs were laid and fertilized. After spawning, the female left the nest and the male continued to fertilize the eggs. The male continued to drive away intruders and fanned the eggs until they hatched.

5. Dascyllus albisella larvae are described and were compared with the larvae of Abudefduf abdominalis. The former had an oval yolk sac, a line of yellow material (probably fat) along the trunk, and the pupil of the eye appeared to be colorless. The latter had a triangular yolk sac, no yellow line and the pupil of the eye appeared to be black. The gradual development of oriented movements during the first few days after hatching is described.

6. Growth rate was studied by periodically measuring the length of fish introduced into coral heads transplanted in the lagoon at the Coconut Island Marine Laboratory and at Kewalo Basin. In the former area, 8 juveniles showed an average daily growth rate of 0.17 mm. over a 14 week period. In the latter area, 4 juveniles grew an average daily rate of 0.14 mm. over a 35 day period. Observations on feeding behavior indicate that growth rate might vary with the location of the fish. In lagoons and other areas with relatively little current, fish fed at a slow pace, whereas in areas of current and surge, feeding activity was greatly accelerated. It was apparent that the planktonic organisms on which fish fed were more plentiful in the latter areas, probably because of the increased flow of water that brought more food past the fish.

7. An analysis of the weight of various kinds of organisms in stomachs showed that the most abundant

plankters were copepods, larvaceans, shrimp-like crustaceans and fragments of polychaet worms. Adult fish in Kaneohe Bay fed close to the bottom, whereas adults off Waikiki fed up to 50 feet above the bottom. Juveniles fed close to the coral head and occasionally darted beyond their normal range after food. Stomachs of fish were seldom empty and indicated that food was plentiful.

8. Attempts to study migration by tagging fish were largely unsuccessful. However, a total of 38 adult fish were tagged off Waikiki and subsequent observations over a 3 month period indicated that movement was slight between 2 aggregations separated by a distance of 70 yards. Observations also showed that some tagged fish remained together in small groups without dispersing individually throughout the aggregation. A number of tagged fish showed abnormal behavior by remaining among coral on the bottom for about a week after receiving the tag.

9. Three kinds of coloration were recognized and they appeared to be correlated with the state of activity of the fish. Male fish in nuptial coloration were white except for a black caudal and anal fin and a black distal edge on the dorsal fin. Nuptial coloration was almost identical to feeding coloration except that the former appeared to be brighter due to the lack of pigmentation on the edges of the scales. Although fish displaying nuptial coloration

were in a state of reproductive activity, they were not continually active. This may account for their similarity in color to slow-moving fish in feeding aggregations. In contrast to the above, some fish were dark gray or black with a light area in the middle of the body. Such fish were usually in a relatively high state of activity and the related color was termed excitation coloration. The darker or lighter coloration developed within a few minutes, and changed with the activity of the fish.

10. Ecology of juveniles was studied by observing concentrations of fish in relation to various environmental factors. Studies were carried out on reefs near Waimanalo, Kualua, in Kaneohe Bay and off Waikiki. Most fish were concentrated in the inner portions of reefs away from the surge zone. However, it was apparent that all gradations existed within the reef from surge conditions to calm water. Periodic counts of numbers of fish in coral heads at Waimanalo were used as a basis for comparison with the different environmental conditions encountered. In that area, fish were less abundant on shallow flats, but were more numerous in the deeper channels. Comparisons between the other study areas also showed that fish were relatively scarce on shallow flats, but were more abundant in deeper channels and other depressions.

11. Some relationships between juveniles and coral

heads were studied. An analysis of length frequency distributions showed that fish entered coral heads when they were about 15 mm. in length. An aggregation of fish showed a characteristic behavior toward its coral head. In moving water, the fish remained together on the upcurrent side of the head where they fed actively on plankters that drifted past. In calm water the aggregation became umbrella-shaped around the coral head. In this formation, the individuals became widely spaced and also moved somewhat farther from the head. The aggregations had a definite organization in which the larger fish remained farther from the head, and the smaller fish remained closer. As fish grew larger, the distance they maintained between themselves and the head increased until they became independent of the head. Stomach analyses showed that large fish "screened out" certain planktonic organisms that probably would have been eaten by smaller fish in the absence of the larger fish.

12. A number of hydrographic features of the environment were compared between the areas. The similarity of temperatures and salinities in areas where fish were relatively scarce as well as in areas where fish were comparatively abundant indicated that these factors were probably not major determinants of distribution. Comparable numbers of fish in areas where current was strong as well as in areas where current was weak, indicated that this factor

was of little importance. However, measurements of the velocity and frequency of surges showed a wide variation between different areas. Both velocities and frequencies were relatively strong in shallow areas where fish were least abundant and both factors were relatively weak in deeper water where fish were most abundant. The effects of surge on the orientation of fish to coral heads were discussed along with the broader aspects of the way in which surge and other factors might affect distribution.

13. Although Dascyllus albisella were not found in stomachs of predatory species of fish, a number of potential predators were observed. Certain behavioral traits of fishes of the families Scorpaenidae, Aulostomidae, and Fistulariidae indicated that they might prey on Dascyllus albisella.

14. Field experiments were conducted in which juvenile fish were introduced into transplanted coral heads off Waikiki and Waimanalo. Large aggregations of fish accumulated in the coral heads in the deep waters off Waikiki and in the deep channel at Waimanalo. However, no build-up in numbers occurred in the shallow flats in the latter area where surge was strong. This build-up in numbers of fish in relatively surge-free areas was interpreted as further evidence that fish were not able to remain in places where surge was strong. The large numbers of fish that

accumulated in transplanted coral heads at Waikiki showed that the absence of naturally occurring coral heads was one reason why few juveniles were found there.

15. Associations between juveniles and sea urchins were observed on three occasions off Waikiki. In view of the fact that numbers of fish associated with urchins fluctuated from zero to over 80 fish, it was apparent that urchins were a temporary habitat. Fish associated with urchins were very shy and mostly remained between the spines.

16. In Kaneohe Bay, juveniles were sometimes observed among the tentacles of the sea anemone Marcanthia cooki. Aquarium observations showed that fish gradually became acclimated to the anemones by repeatedly touching the tentacles with the caudal fin. The fish were eventually able to lie motionless among the tentacles and to swim freely among them. In the presence of the anemone, the fish undergo a more or less set pattern of behavior similar to that of true anemone fishes (Amphiprion). The evolution of commensal associations between pomacentrid fishes and anemones is discussed.

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