AGGREGATION BEHAVIOR OF THE HERMIT CRAB *Clibinarius tricolor*.

Carol and George:

A very nice study! Excellent presentation of data and discussion.

John

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ABSTRACT

Aggregation behavior of the hermit crab _Clibenarius tricolor_ was studied at Discovery Bay, Jamaica, West Indies. The crab is found in large aggregations during the day (up to 300 individuals) in sediment pockets on the reef flat. Experiments were performed to investigate evolutionary advantages of aggregations and the various mechanisms involved. Aggregations were found to vary in size, location, and individual composition. Experimental crabs were found to orient positively toward light, ~~p~~ groups of empty shells, and water flowing from conspecifics. These behaviors are probably employed in the daily cycle of aggregation. In addition, clustered crabs could withstand desiccation significantly better than lone crabs, providing a possible evolutionary explanation for aggregation behavior important in earlier intertidal environments. The variation of shell fit was significantly greater for individuals not associated with an aggregation, than for those in a cluster. It is possible therefore that aggregations serve to facilitate mutually beneficial shell exchanges, ~~to~~ in an environment where shells are a limiting resource.

INTRODUCTION

Hermit crabs are prominent members of the invertebrate fauna of Caribbean shores and coral reefs. They are well-known for their body form: the abdomen is elongated and quite soft, curving to fit into the spiral interior of a gastropod shell. The crab has lost its own hard exoskeleton and relies on the protection of an aquired shell.

Thirteen species of hermit crabs are indigenous to Jamaica, at least seven of which occur in Discovery Bay (Hazlett personal communication). The crabs may be found in the intertidal zone as well as on the reef flat on coral, on algal growth, and in bare pockets of sediment. Several species are solitary or occur in small groups, others defend territories, and several species are involved in large aggregations — as many as 300 individuals — in interstices of sediment in the reef flat. Clibanarius tricolor is the dominant member of these conspicuous clusters; individuals of Pagurus miamensis may occasionally be associated with C. tricolor, or form small independent aggregations. Calcinus tibicen, although never in the latter large aggregations, can be found in small groups, especially on coral outcroppings where it may share depressions or pockets with Diadema sp.

Hermit crab aggregations are noticable in sediment pockets only during the day; at night the animals disperse, moving into the surrounding coral outcrops to feed on algal growth. Interspersed with crabs, day and night, on the sediment and in algae, are the gastropods, Cerithium sp., from which most individuals of C. tricolor and P. miomensis obtain their shells.

Why some species aggregate is not entirely understood. In Discovery Bay C. tricolor occurs mainly at depths greater than half a meter, but elsewhere in the Caribbean it inhabits shoreline areas exposed by low tides. It has been proposed that in areas subject to tides, clusters of crabs may serve to ~~retain~~ conserve necessary moisture at low tides to prevent desiccation. This behavior may have evolved initially in the intertidal zone and may have been retained as the crabs later expanded their range onto the deeper reef flats (Hazlett pers. comm.)

It has also been suggested that aggregations may serve to facilitate mutual exchange of shells between individuals. In areas where empty shells are rare, shells constitute a limiting resource for crab populations. The abundance and size of shells can determine the density of crabs in a given area as well as population size (Vance 1972); crab growth rate may be influenced by shell sizes available

(Hazlett pers. comm.). Under conditions of limited shell supply, as in Discovery Bay, contact with other members of the species would enhance circulation of shells to increase the probability of obtaining a better shell fit. Studies by Vance (1972) in Washington indicated that if large shells are in short supply, many crabs must occupy shells smaller than preferred. Hazlett (pers. comm.) has shown that in some species significant numbers of individuals inhabit shells either smaller or larger than preferred. [Ideal shell fit is measured in the laboratory by offering crabs a variety of shell sizes.]

Hazlett has also documented shell "negotiations" in which an initiating crab presumably "sees" a desirable occupied shell. It then commences tapping manoeuvers with its own shell, that may test the other shell and/or impart information about shell quality to the recipient crab. If the crabs eventually exchange shells, ~~both~~ the result is often a better fit for both individuals. These negotiations occur intraspecifically and possibly interspecifically as well (Hazlett work in progress).

Several cues are likely to be involved in the control of aggregations. Crabs may orient tactilely toward a particular substrate – in this case, sediment during the day, and algae at night; certain specific sites, especially in the sediment, may be sought out by individual crabs, resulting in a cluster.

Perhaps a thigmotaxis as well?

Although not documented, it is possible that crabs employ visual cues to form aggregations, using positive phototaxis at the outset to locate light areas of sediment, then detecting and joining crabs already present. Lastly, pheromones may be involved in aggregation behavior; large groups of crabs might concentrate a chemical attractive to other individuals, or a pheromone might be released during shell exchanges that entices more exchangees to the site.

The aim of this study was to investigate the factors controlling aggregation behavior in Clibinarius tricolor, in particular, what purpose the aggregations actually might serve. The following experiments attempted to assess the importance of specific locations of aggregations, effects of predators, the role of pheromones, phototaxis, and visual cues in group detection by individuals. Desiccation tolerance by single and clustered crabs was investigated, as was goodness of shell fit within and outside of aggregations.

why test this? explain

Proximate and ultimate factors responsible for aggregations should be separated more clearly in your introductory comments.

List of Species - Discovery Bay, Jamaica

fam. Diogenidae:

1. Calcinus tibicen
   Dark red; white claw and leg tips.
   Inhabits *Cerithium* sp. shells, and others often covered with red-encrusting algae. Often on coral, algae growth. Small aggregations.

2. Clibinarius atelensis
   light-colored; black and cream stripes
   Inhabits *Cerithium* sp.

3. C. tricolor
   Blue legs and claws; red and white stripes on jionts and leg tips. Found in large aggregations on sediment pockets.
   Inhabits *Cerithium* sp.

fam. Paguridae:

4. Pagurus marshii
   Light tan; fuzzy, detritus covered - both crab and shell.
   In rubble areas, algae on coral. Does not aggregate

5. P. miamensis
   Whiteish; light-brown speckles on legs.
   Often found in *C. tricolor* aggregations or small independent groups.
   Inhabits *Cerithium* sp.

6. Paguristes ssp. (grei)
   Largest species.
   Dark red; white speckles
   Inhabits quite large shells up to Queen conch.

METHODS

Field Studies

Five sites were marked on the West Back Reef in Discovery Bay where hermit crab populations - mostly of *C. tricolor* - were found in aggregations.

Aggregation Dynamics

1. The five study sites were observed over a ten day period. During five of the day observations (between 11:00 and 15:00, February 20 - March 2) numbers of hermit crabs in each aggregation were noted and the locations of the aggregations were mapped. An observation was also made in the early evening (17:30) and another at night (21:00).

2. 42 *C. tricolor* were taken from a cluster in site #2; the shells were labeled with waterproof blue pen and then returned as a group to where they were collected. These shells were then tracked over the next few days.

3. 58 *C. tricolor* were collected from site #4 and labeled with red nail polish. The crabs were released in two aggregations. During two subsequent observations the distance from the release site was recorded for each red shell found.

Shell Availability

1. In three areas within aggregation sites,

samples were made of the bottom sediment to determine the abundance of available shells.

2. Two groups of 40 labeled, empty shells of a wide range of sizes were released next to aggregations in site #2. Immediate observations of hermit crab behavior were recorded. The marked shells and their ~~co~~ occupants if any were collected over the next two days and catalogued.

<u>Shell Fit in and out of Aggregations</u>

Two groups of 43 <u>C. tricolor</u> and shells were collected: the first group was composed of individuals from an aggregation; the second group was composed of individuals not associated with an aggregation. For each of the two groups the shell for each crab was analyzed: The length of the shell was first measured with calipers to 1/20 of a millimeter. Perfect shells were chosen where possible. The crabs inside each were removed by cracking the shell. The crabs were blotted to remove surface water and then weighed to 1/1000 of a gram. Regressions were made using a power curve fit and then compared for significant differences. [The basis for this curve choice is mentioned in the discussion.]

Predation in the Field

The following experiment tested the consequences of remaining aggregated on the sediment by night. A possible risk is predation by nocturnal gastropod predators: lobsters, crabs, octopi, and rays.

One group of five glass petri dishes, each containing 20 C. tricolor were placed in the aggregation area (sediment). Another group of four dishes, each with 20 C. tricolor, were placed in the algae where C. tricolor were found at night. The dishes were just high enough to prevent hermit crab escape and heavy enough to remain upright in the currents. The following morning the dishes were collected and counted.

Laboratory Experiments:

Desiccation

The effect of aggregation on desiccation was measured by placing 2 groups of 26 C. tricolor with shells in the sun. One group was clustered; the other group was composed of separated individuals. Survival was noted for each of the groups after one hour.

Lobster Predation

Hermit crabs (C. tricolor) in their shells were offered to spiny lobsters (Panulirus argus).

Phototaxis

The ability to orient towards light surfaces was measured in a series of choice experiments. These were preformed between 5:00 and 7:00 in the morning when C. tricolor would be aggregating in nature. C. tricolor were placed individually in the center of a 15 cm wooden trough; one end of which was white, the other black. The crabs were timed in their movement toward either end from the center of the trough. The colored ends were removed and exchanged periodically to control for possible confounding factors. (Figure 11)

Clustering By Vision

A similar experiment was performed to test whether crabs can use vision to aggregate. Crabs of C. tricolor were placed individually in the center of a 25 cm trough - one end consisted of empty shells (Cerithium) behind a glass slide. At the other end was only a glass slide. The ~~em~~ empty shells were also switched periodically from end to end. [At first, live crabs in shells were used instead of empty shells, with the water current flowing from the center of the trough towards the ends. (Figure 11)

Pheromones

The presence of an aggregation pheromone was tested with several apparatuses. (Figure 10)

1. *C. tricolor* individually were allowed to choose between two forks of a Y-maze. Wire cages were placed at both ends: one contained an aggregation of *C. tricolor*, the other was empty. The water currents flowed from the ends of the forks towards the center.

2. *C. tricolor* were placed individually in the center of a trough bounded with two plastic cups, each with water flowing out of the side. In one cup was placed a group of about 30 *C. tricolor*; the other cup was empty.

3. *C. tricolor* were placed individually into a trough and allowed to choose between water flowing from a *C. tricolor* aggregation and fresh sea water. The individuals being tested could not see the source of the water.

4. A similar test was performed to determine whether the chemical cue was a specific pheromone and not the product of respiration. Water flowing from a container of *P. marshi*, which does not aggregate was substituted for the fresh sea water ~~of~~ the previous experiment. (Figure 10)

RESULTS

Aggregation Dynamics

1. The maps of the study sites show that aggregations do not return to exactly the same locations, although some spots are prefered over others (figs 1-5). The frequency of aggregations versus aggregation size peaked at about 30 individuals (fig. 6). Group sizes varied greatly from 4 to 300 individuals. The numbers of aggregations per site also varied from day to day; they were composed mainly of Clibinarius tricolor, although Pagurus miomensis was found as well.

At night there were no aggregations in sediment pockets; crabs were found feeding in the surrounding algae.

2. The crabs marked blue did not all aggregate together on the days following release, and became further dispersed in separate aggregations as more days passed. (~~table~~). 39 crabs were located the next day, 23 in one aggregation, 16 in another. Later, 17 were found distributed among 8 aggregations. Some were found singly as well.

3. A histogram for frequency of hermit crabs (marked red) for a given distance from the release site over two days' time is shown in fig. 9. A large number of individuals was found between .30 and .60 m from the point of release; some were found as far away as 4.5 m. Again, the

red-labelled crabs did not stay within the same aggregation. These crabs were also found singly and in small groups (2-3 individuals).

Shell Availability

1. Sampling in the three sites showed available shells to be extremely rare – in fact, no vacant shells were found.

2. When the two groups of empty shells were released, the adjacent crabs immediately began to investigate them. There was much movement within the aggregation. One crab abandoned its shell for a new one in less than 10 seconds. Another crab was seen to pull a dead crab out of a new shell before occupying it.

Most of the marked shells found the next day were occupied (38 of 40) and nearly all contained C. tricolor.

Shell Fit In and Out of Aggregations

1. Regressions for power curves of shell length to crab weight are shown figs. 7 and 8. The best fit power curve has been drawn in. The best fit for those within a population was: shell length = $41.97(\text{crab wt.})^{.343}$ ($r^2 = .91$; $n = 41$); for those outside of the aggregations: shell length = $35.86(\text{crab wt.})^{.246}$, ($r^2 = .72$, $n = 43$)

Both curves had regression coefficients significantly different from 0 ($p < .001$), although the difference in regression coefficients (.343, .246) was not significant. However, the two correlation coefficients ($r_{in} = -.954$; $r_{out} = -.847$) were significantly different, showing a difference in variation of shell fit between the two samples.

Predation in the Field

Significantly more crabs were gone from the petri dishes left in algae, than those in the sand. The results of this experiment were nevertheless deemed inconclusive, because it could not be determined whether removal of crabs was due to predation or to other causes.

such as?

Desiccation

After one hour only four of the single crabs had survived; all 26 of the aggregated ones survived, even though some had crawled out of their shells. This difference was significant (X^2 test $p < .005$). The single crabs that crawled out of their shells died within five minutes. Those naked ones in the aggregation were able to seek shelter under other crabs, thereby reducing effects of the sun.

Lobster Predation

Lobsters in the lab did not eat the hermit crabs offered (C. tricolor).

Phototaxis

At 5:00-7:00 the crabs showed positive

phototaxis. In all 11 trials the crabs selected the light end of the trough (χ^2 test $p < .005$). (~~table~~).

Visual cues

The crabs could orient to shells by vision alone. In 10 trials out of 15, the test crabs moved toward the shells (χ^2 test $p < .05$) (~~table~~)

Pheromones

1. When the aggregation was in the wire cages the crabs tested moved away from the group 9 out of 11 times. This was significant (χ^2 test $p < .05$).

2. However, crabs chose hose water flowing from the tank of aggregated crabs significantly more than the sea water hose: 17 out of 24 trials (χ^2 test $p < .05$)

3. When sea water was replaced with water flowing from a holding tank of P. marshii, crabs oriented toward C. tricolor waterflow 13 out of 14 times. This was significant (χ^2 test $p < .005$).

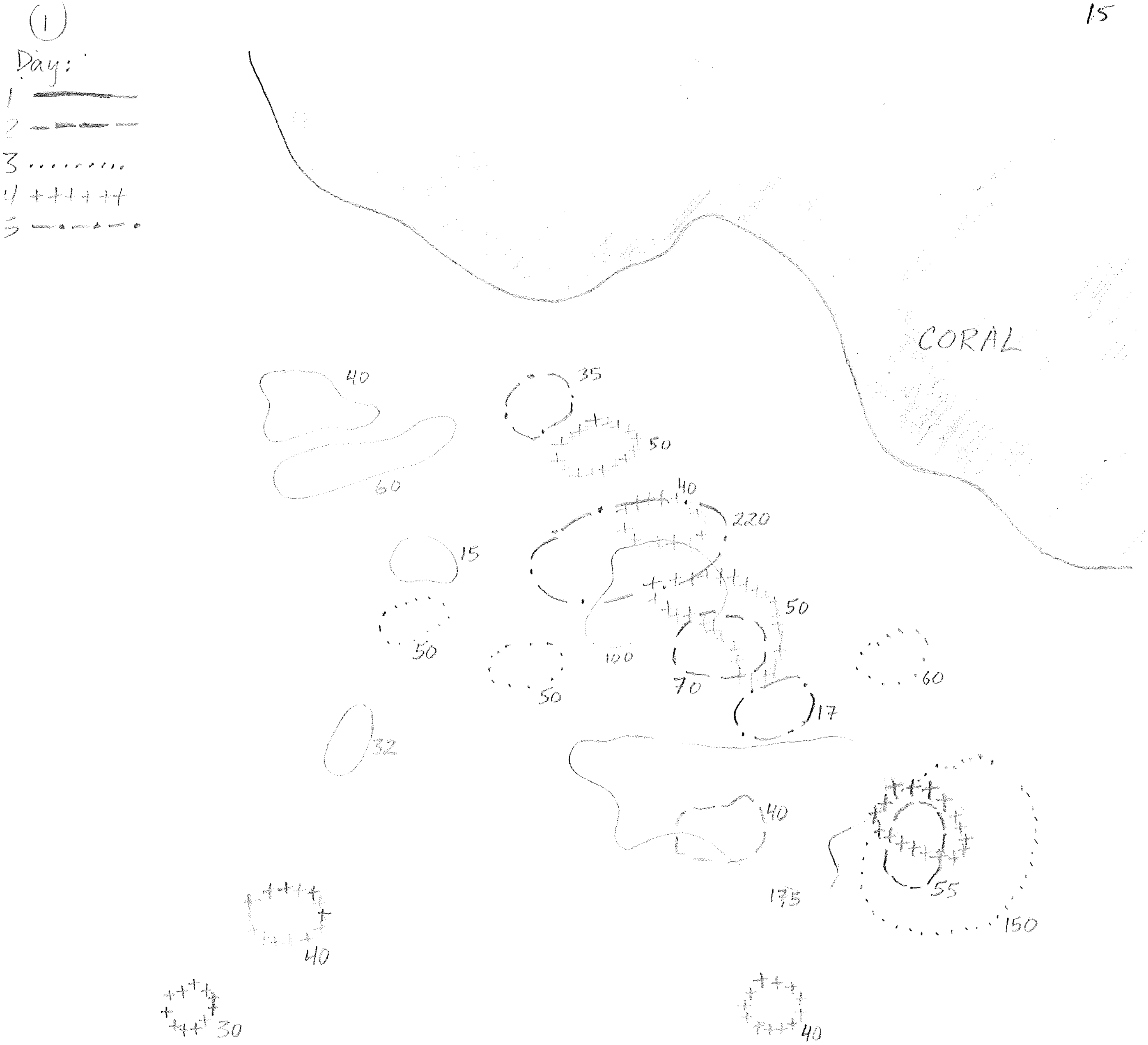


Fig. 2: Map of study site 1.

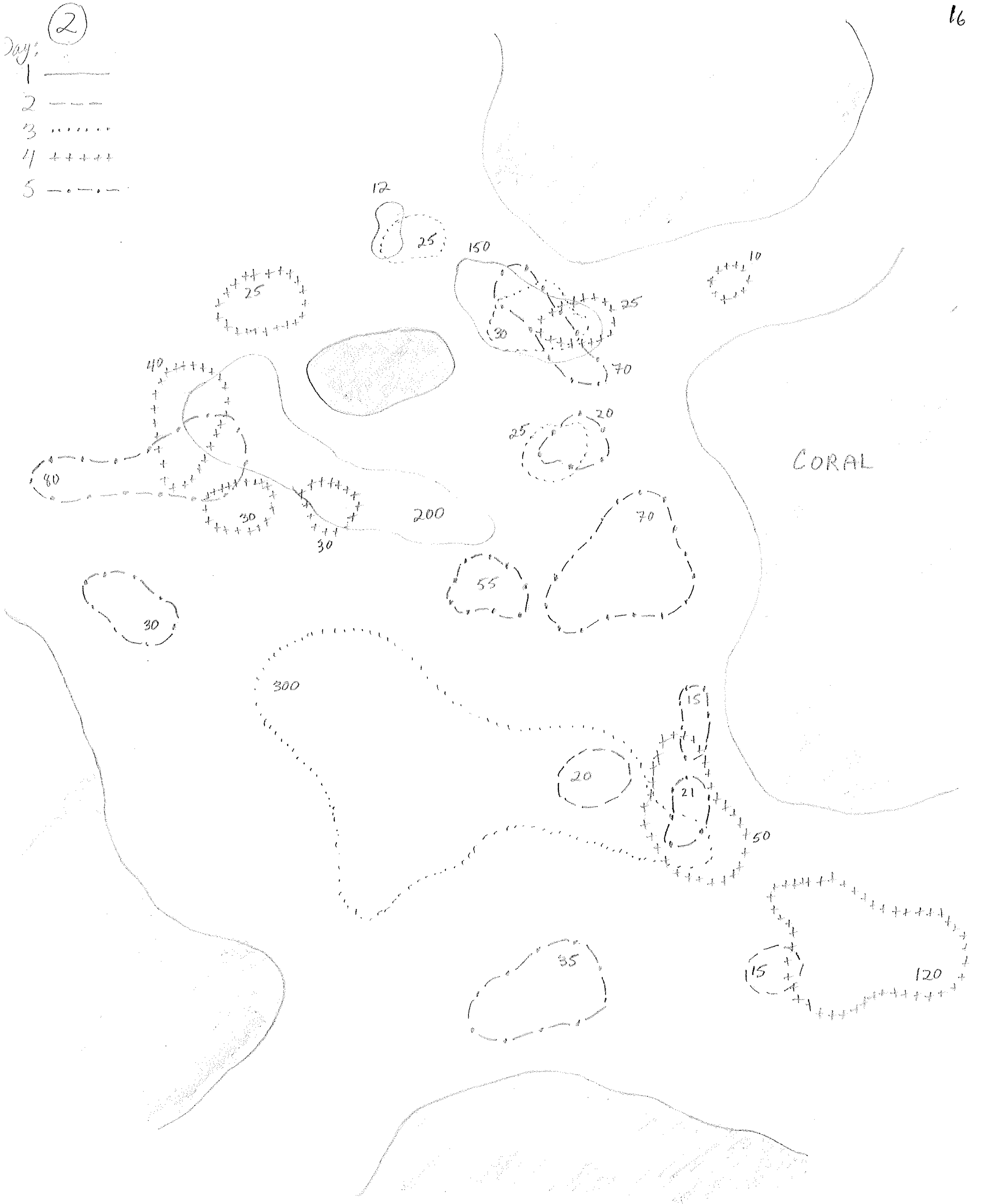


Fig. 2. Map of Study site 2

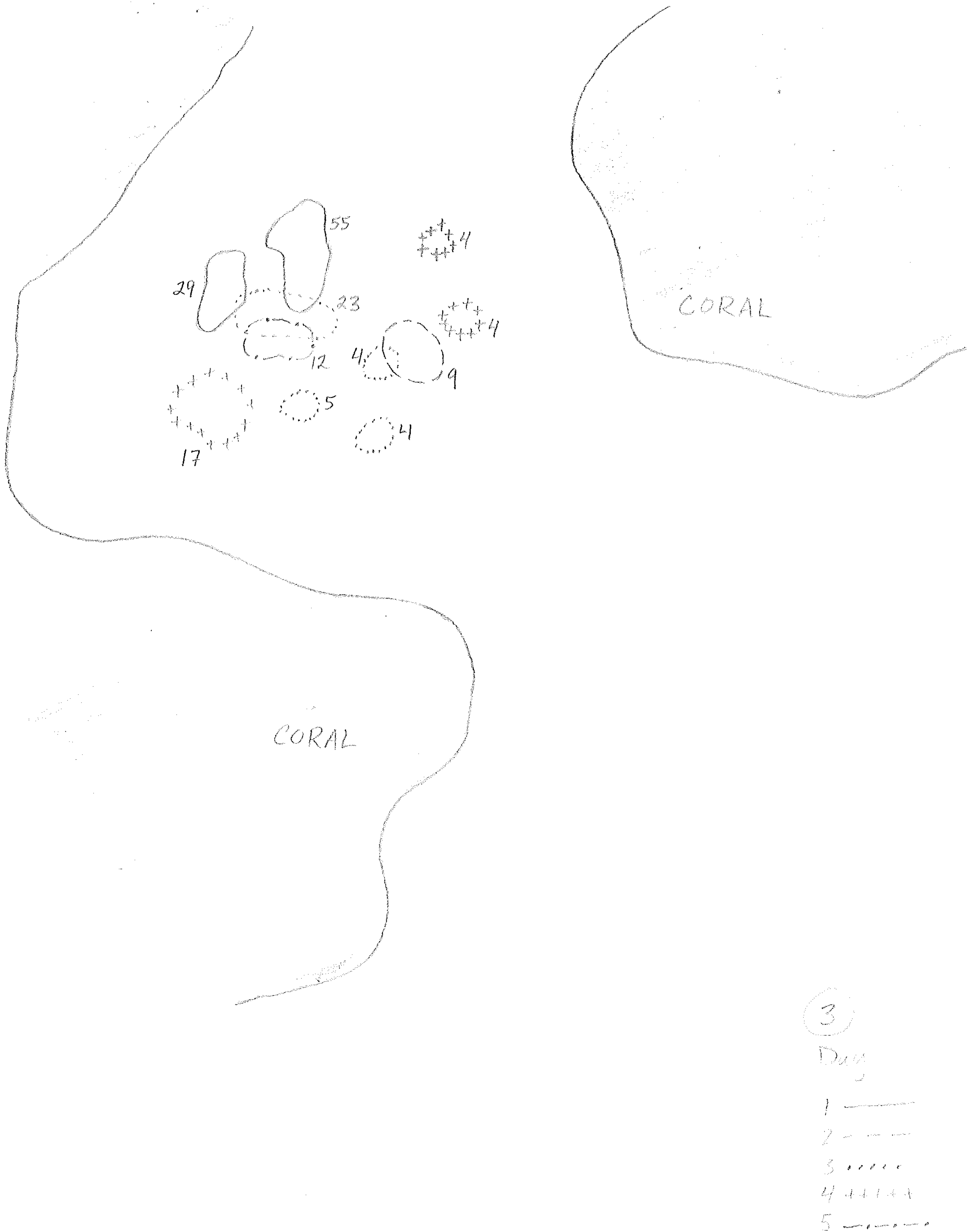


Fig. 3: Map of study site 3

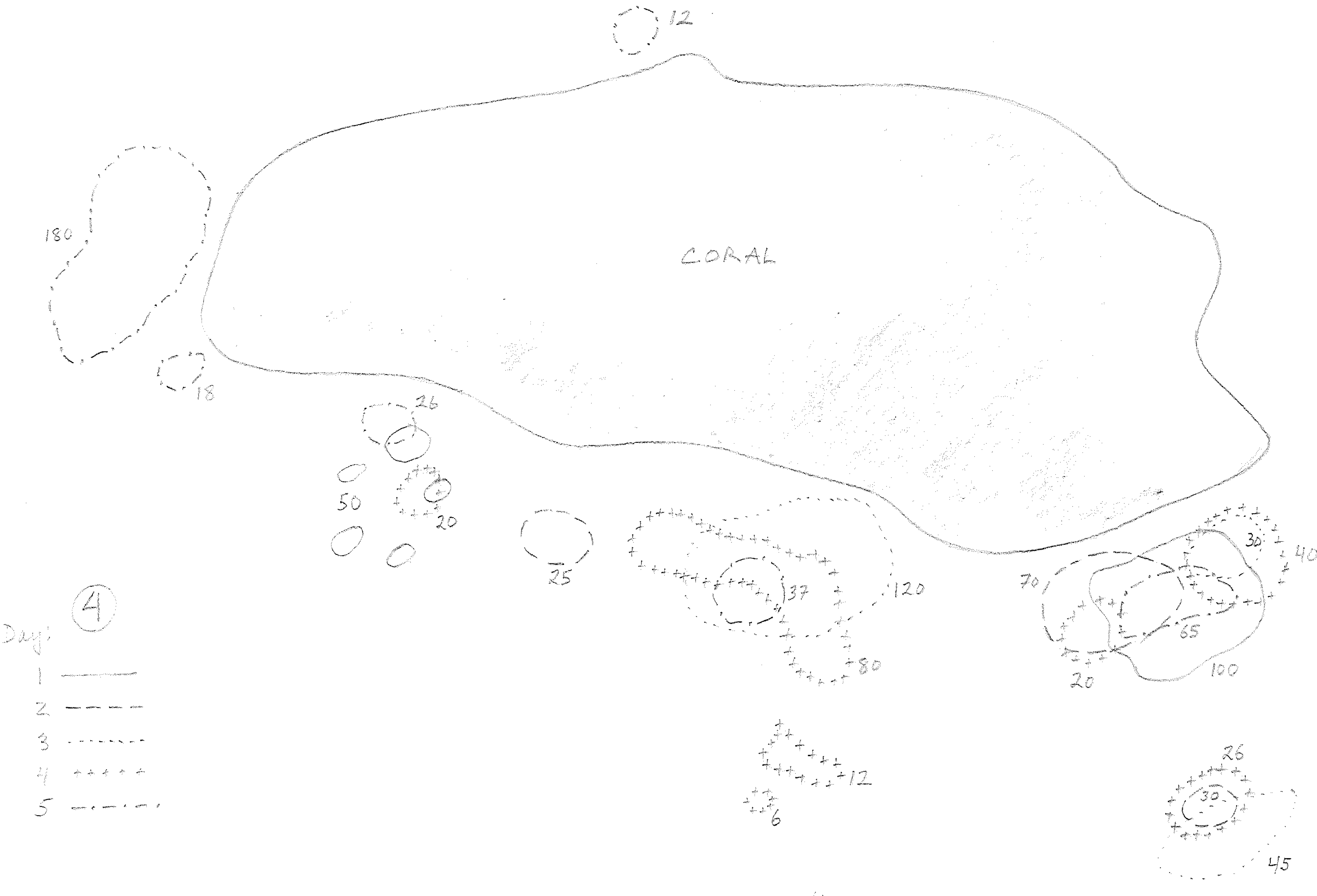


Fig. 4: Map of Study site 4

Fig. 5: Map of Study Site 5

mode 30 median 70 n = 41 $\bar{x} = 58$ s - 60

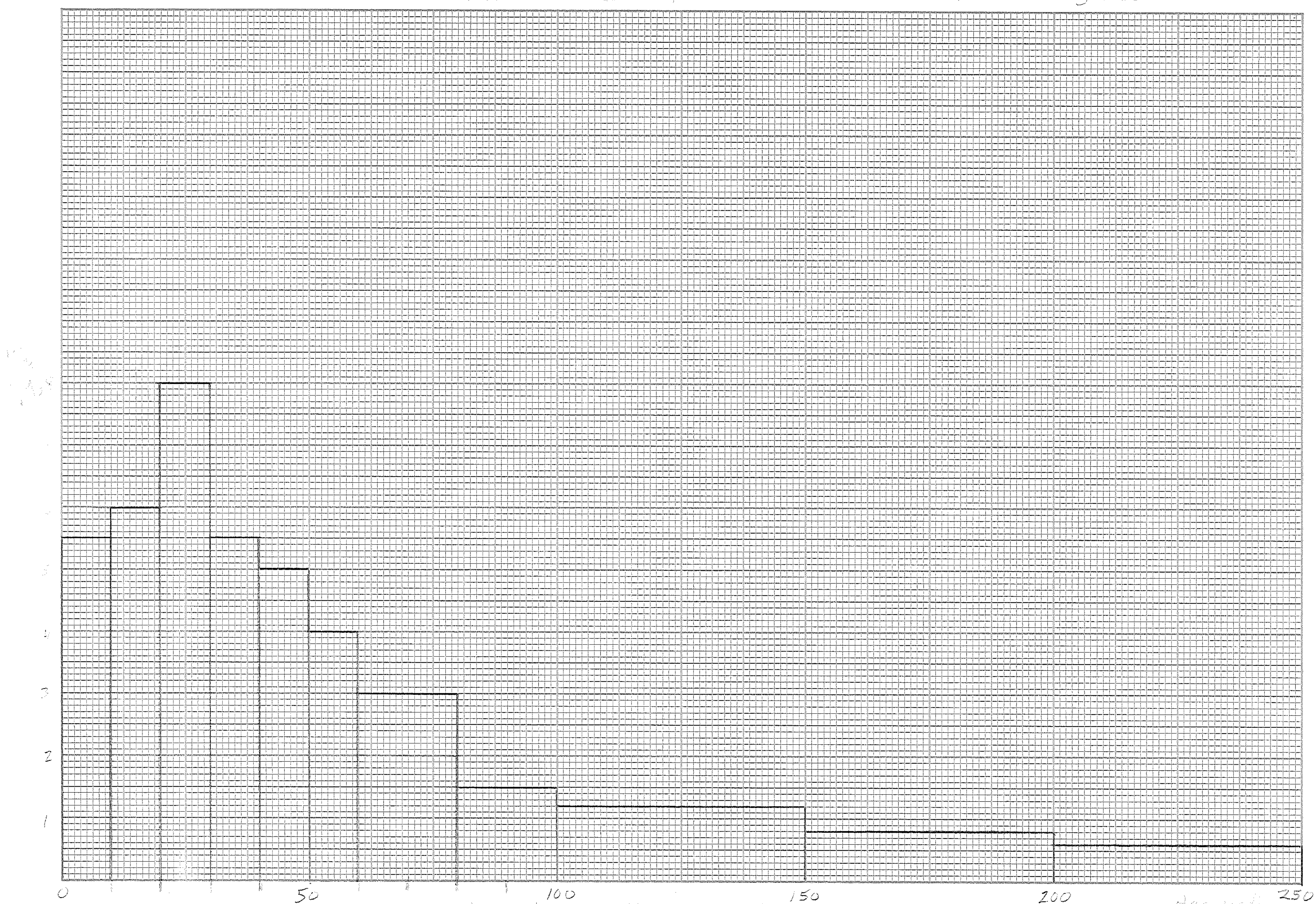


Fig. 6: Frequency of Aggregation size within study sites

K+E 20 X 20 TO THE INCH 46 1240
7 X 10 INCHES MADE IN U.S.A.
KEUFFEL & ESSER CO.

n=45 a=35.86 b=2.46 r² = .717 y = ax^b

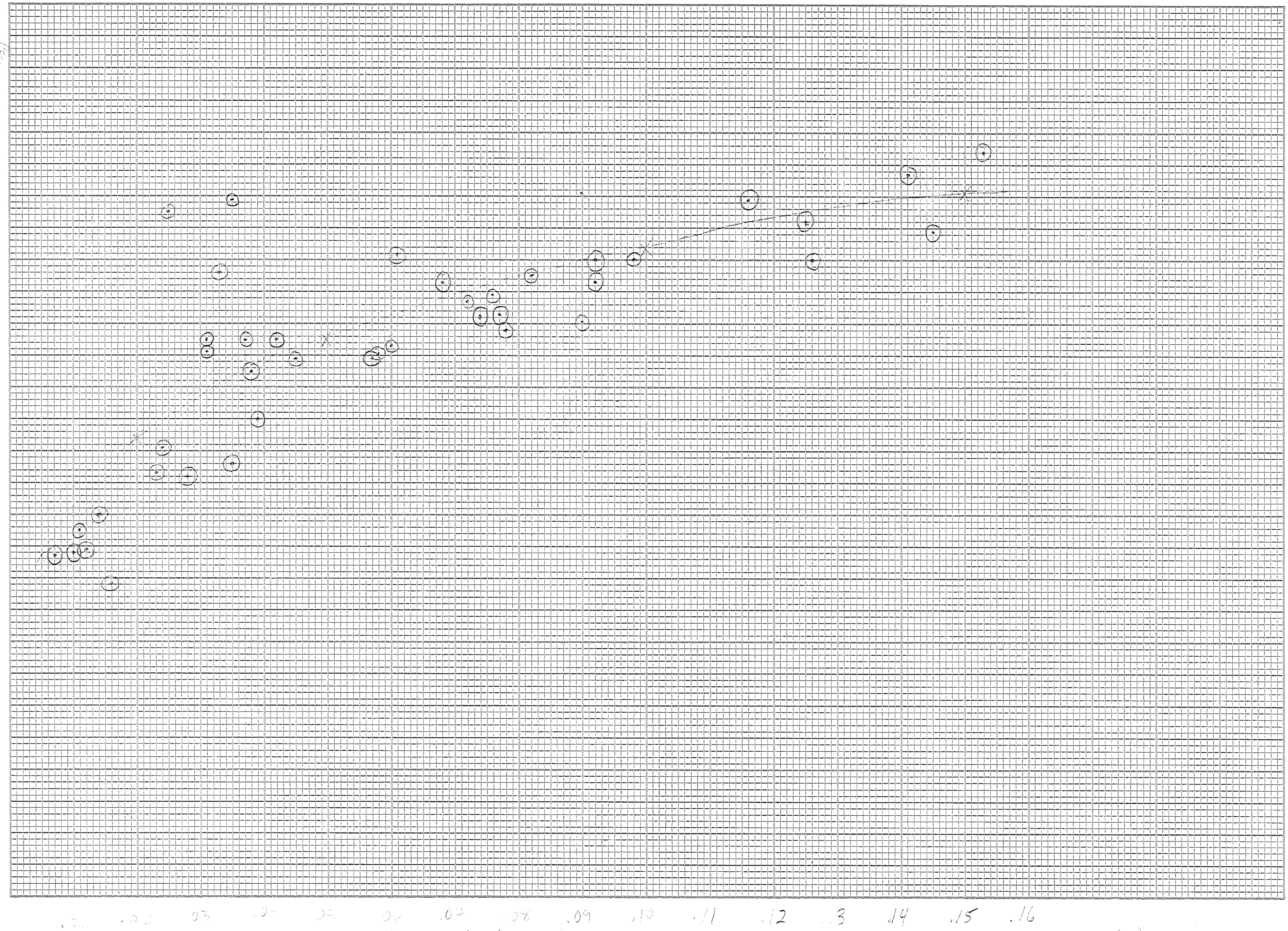


Fig. 7: Crab weight vs. Shell length outside of Aggregations

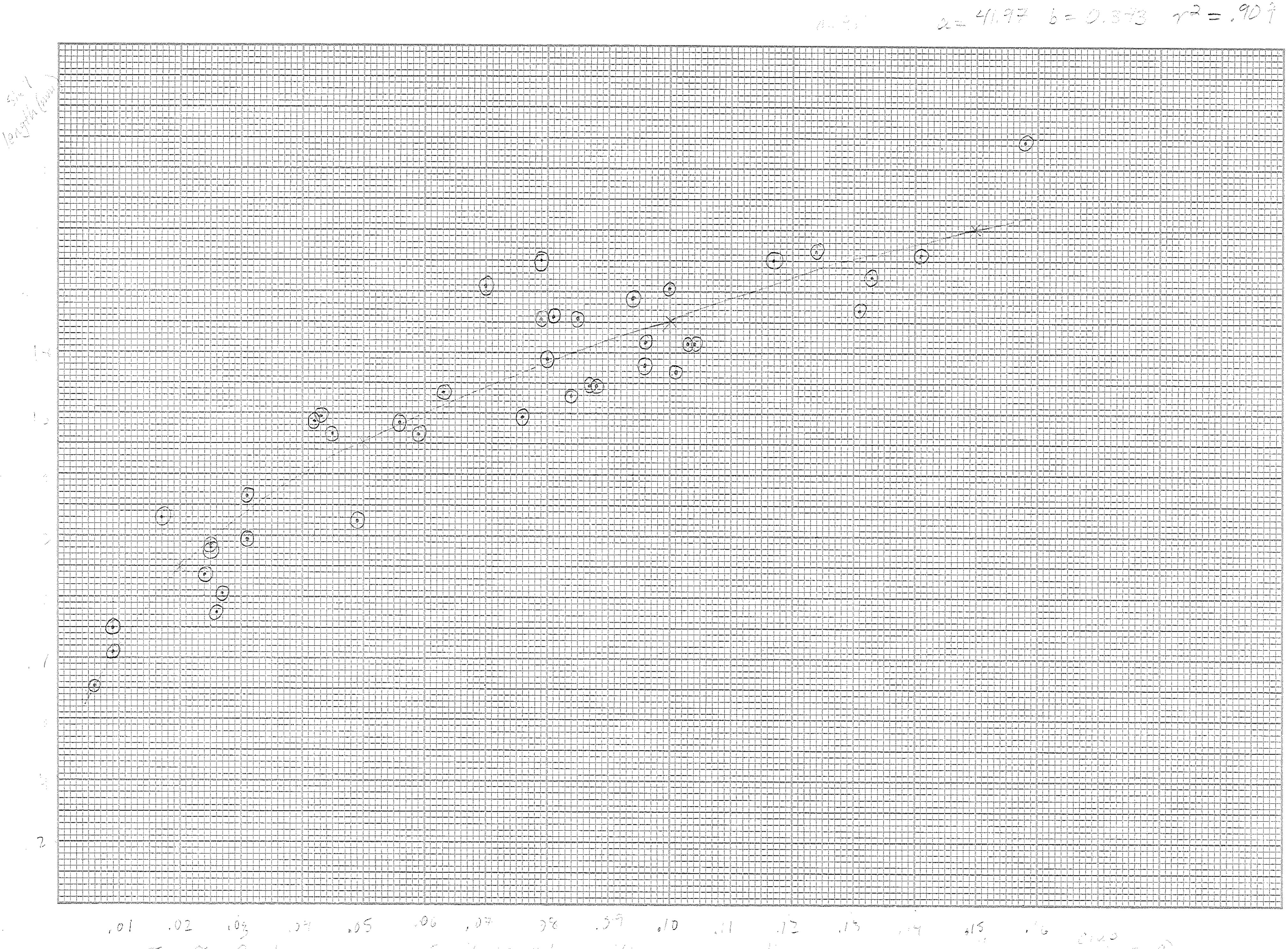


Fig 8: Crab weight vs Shell length within aggregations.

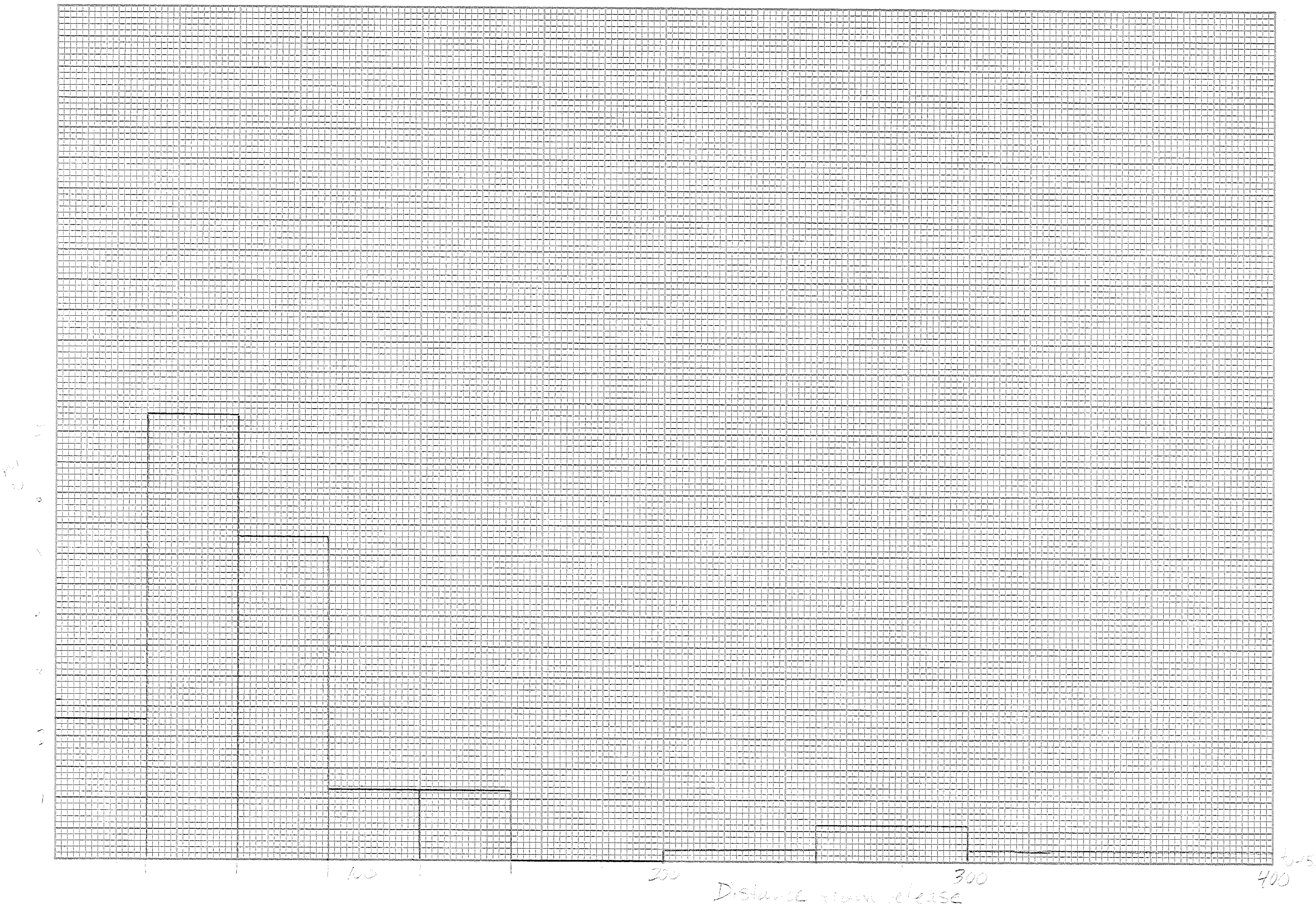


Fig 9: Frequency of individuals per distance from release site.

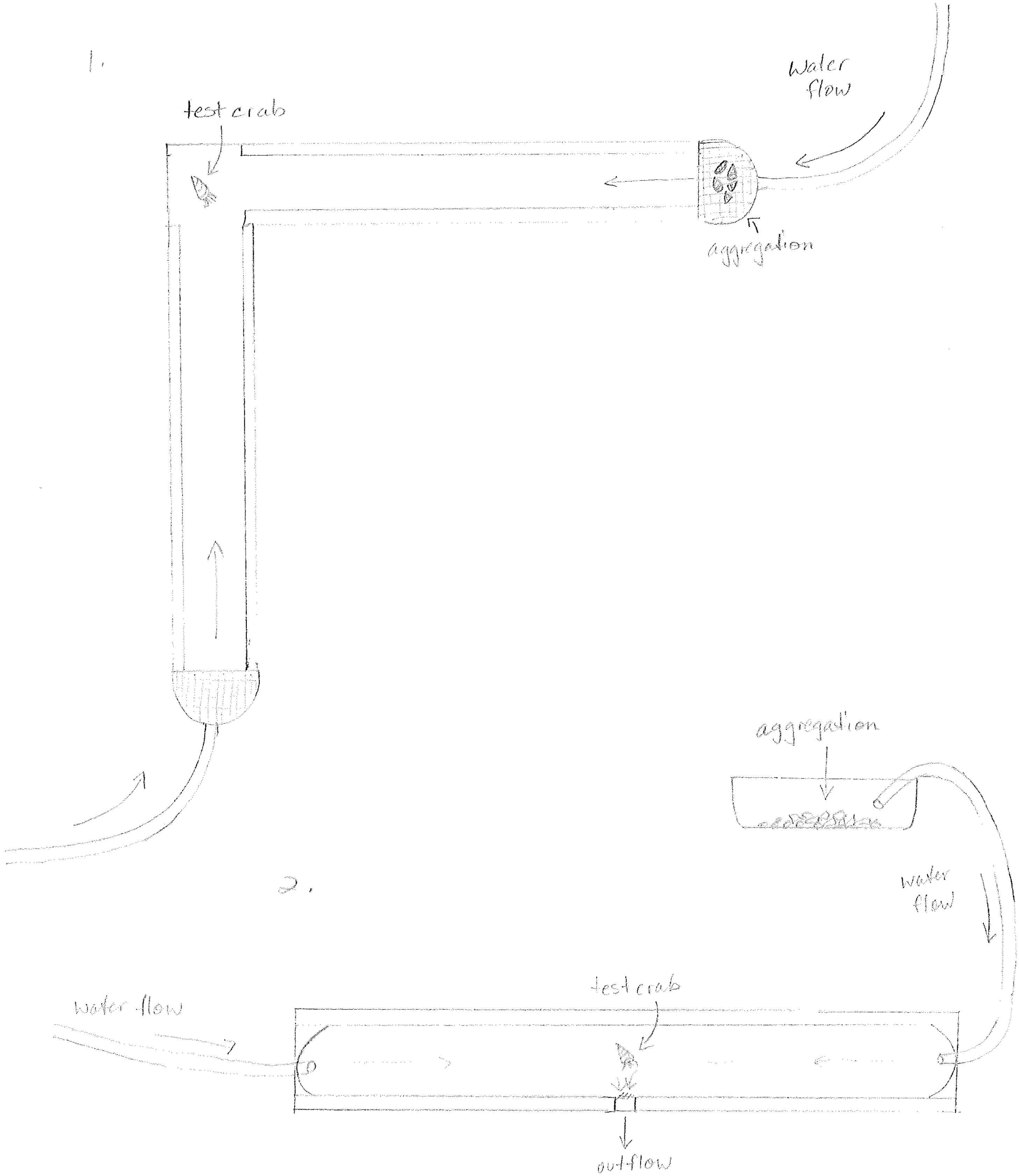
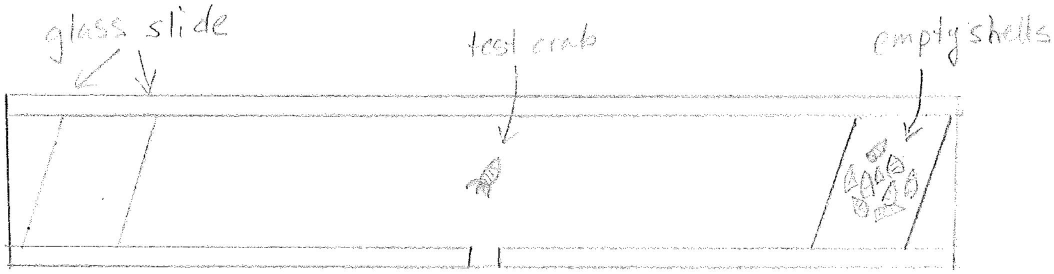
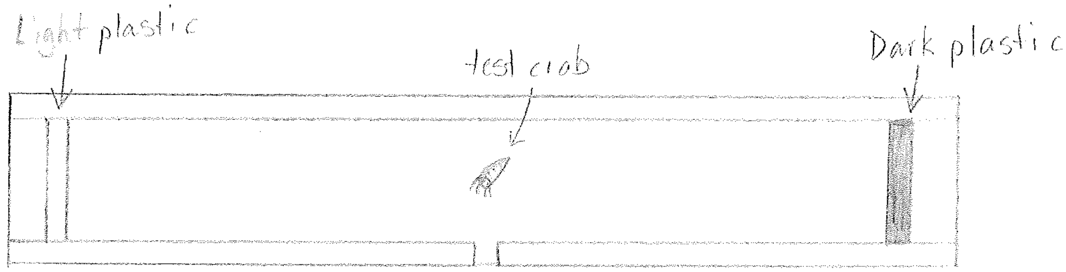


Fig. 10: Diagram of two setups for chemotactic response



1. visual Setup



2. Phototaxis setup

Fig. 11: Diagram of apparatus for visual and phototaxic responses

DISCUSSION

The aggregation dynamics results show several things. Firstly, aggregations are plastic. The crabs move in and out of aggregations daily. Secondly, the cues for aggregating appear to be the same for all crabs and are not aggregation specific. If aggregations do serve mainly as sources for better-fitting shells, it would be to a crab's advantage to visit many groups in order to increase the probability of finding a better fitting shell.

good point

Thirdly, in each of the aggregation sites there were certain areas in which aggregations usually occurred. The presence of these sites suggests that environmental factors are important in determining the locations of aggregations. Certain areas such as depressions or those spots overhung by coral may reduce water turbulence that could ~~affect~~ these small animals.

Empty gastropod shells in Discovery Bay are definitely a limiting resource. Many crabs occupied broken or decrepit shells. The empty shell introduction experiments showed that at least some of the crabs are seaching for another shell. Hermit crabs might be expected to be quite sensitive to the introduction of a usable shell into the envrionment. Because empty shells are rare they should be picked up immediately in order not to be lost from the

good

circulating shell "pool" – either to processes of sedimentation or to other competing hermit crab species. The greater the shell pool, the greater the chance for a better fit.

The results of the shell fit to crab measurements showed that crabs of a given size in both samples tend to choose the same size shells; although, some small crabs in the out ~~sample~~ had much larger shells than expected. However, variation of shell fit was shown to be greater within the scattered sample. It was not clear to us beforehand what results to expect from these samples, but an a posteriori explanation might be the following: At the time of the sample, crabs within an aggregation had already sought out and exchanged shells to improve their fits. [This can occur quite rapidly (Hazlett pers. comm.).]. Scattered crabs may be on their way to join aggregations, or may be travelling to a different aggregation to find a more desirable shell. [The results of the above experiment were analyzed for a fit to a power curve because of the presumed cubic relation of internal volume ~~to~~ and shell length. Power curves do fit the data well.]

Desiccation experiments did support the hypothesis that a cluster of crabs can better resist the detrimental effects of low tide exposure, as compared to lone crabs. In this ~~case~~ theory, crabs would be expected to aggregate only during the day, as nighttime low tides do not expose crabs to the sun. It is quite possible that the behavior observed on the reef flat is an adaptation retained from an ~~possible~~ evolution in the intertidal region.

The experiments regarding cues involved in the aggregation phenomenon indicated that several factors may control aggregation dynamics. Crabs were shown to orient positively toward light areas in the early morning. They also could distinguish piles of shells and moved toward them. Finally, crabs exhibited a positive taxis toward water flowing from a conspecific aggregation ~~over~~ when offered a choice between it and plain sea water and between it and water flowing from non-aggregating crabs.

These abilities could fit into a hypothetical morning reaggregation pattern: crabs moving out of the algal feeding grounds orient toward light areas of sediment pockets. Once on the sediment a combination of visual cues and chemical stimuli may enable an individual to pinpoint a cluster. Although no chemical analysis was performed, an "aggregation pheromone" could be involved in the process: groups of crabs may concentrate a substance attractive to other crabs, or, those involved in shell exchange might release a more specific pheromone, stimulating other crabs to initiate shell exchanges. In both instances, crabs benefit by the circulation of their shells within the population, increasing the probability of a better shell fit for those involved.

The pheromone experiments also indicated that some kind of chemical stress signal may be released by crabs when disturbed. Trials with P. marshi-water substituted for plain sea water showed that crabs did not orient toward a product of respiration. What cannot be determined from our experiments, however, is whether C. tricolor were actively avoiding P. marshi as sensed in the flow or truly homing on a C. tricolor pheromone.

In summary, it was found that on coral reef flats in Jamaica, C. tricolor forms large aggregations of various crab sizes. The aggregations are dynamic congregations, varying in individual numbers, members, and location from day to day. These hermit crabs may travel distances of at least two meters in 24 hours and are probably capable of much more. Aggregation behavior is probably under the control of a combination of cues, involving phototaxis, vision, thigmotaxis, and pheromones or other chemicals. The clustering behavior could be a relic from an evolution in the intertidal zone. More probably, however, it serves to bring individuals of the population to a common ground where mutual exchange of shells could circulate a limiting resource, increasing the probability of a good shell fit for each individual.

Many of our experiments would have been better performed with larger sample sizes. Several topics remain for further study:

1. More detailed behavioral observations and analysis of C. tricolor aggregations
2. The nature of the chemical cues used by aggregating hermit crabs
3. The role of substrate choice in morning reaggregation
4. The importance of these reaggregating cues at other times of the day.
5. Extensive shell labeling to observe individual crab movement especially at night.
6. The role of predators on aggregation behavior.

LITERATURE CITED

Vance, Ritchard R. 1972. Competition and Mechanism of Coexistence in three sympatric species of intertidal hermit crabs. Ecology 53 no. 6 pp. 1062-75.

We would also like to acknowledge Dr. Brian Hazlett for his valuable information on the subject of hermit crabs.