THE EARLY LIFE HISTORY AND REPRODUCTIVE BEHAVIOR OF THE MAOMAO, ABUDEFDUF ABDOMINALIS (QUOY AND GAIMARD)

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by

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SECTION I

INTRODUCTION

The family Pomacentridae (Damsel fishes) consists of a large group of marine fishes which are widely distributed in shallow waters of tropical and sub-tropical seas, and typified by their small size and close association to the substrate. Many of the pomacentrids exhibit bright coloration, and this fact, coupled with the unusual associations that some genera have with coelenterates, early attracted the attention of naturalists. Despite the appeal of these rather specialized groups (particularly the commensal anemone fishes), little attention has been directed toward the rest of the family, even though they are usually conspicuously represented in the fish fauna of reef areas in the tropics.

In Hawaii, the family is represented by eleven species, one of the best known and apparently most abundant being the endemic, Abudefduf abdominalis (Quoy and Gaimard), referred to locally by its Hawaiian name of "maomao". The maomao is a small, rather shy fish, distinctly marked with five vertical black bands on a brassy-green to yellow body. A gregarious species, it is often found in loose aggregations numbering several hundred fish. Maomao occupy a wide range of habitats, and reproduce by attaching their eggs to the substrate in a nest which is defended and cared for by one of the parents during incubation. Upon hatching, the young migrate into shallow water areas along the shore where they are abundant during certain seasons.

The maomao's abundance in a variety of habitats, its broadly omnivorous diet, mode of reproduction, and some of its behavioral characteristics suggest that it is a rather well adapted and successful component of the reef community. It is the aim of this investigation to point out some of the characteristics of this species that allow it to occupy its position of prominence.

The initial phase of this study includes observations on some of the characteristics of the adult maomao that contribute to its preservation and versatility in adapting to changes in the environment. Factors controlling the spawning cycle, fluctuations in abundance, and fecundity are then reviewed in order to determine how they might influence the reproductive potential of this species. Embryonic, larval, and juvenile stages are described and analyzed in respect to various elements in the environment that affect their survival, and estimates of the magnitude and cause of mortality are made. Finally, adult reproductive behavior is reviewed in order to ascertain the significance of its various components, and the part each contributes toward the successful propagation of the species. All aspects of this investigation contribute to our scanty knowledge of the general life history of this species and its interactions with other elements of the reef community.

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Methods and Materials

This investigation was conducted primarily at the Hawaii Marine Laboratory at Coconut Island, in Kaneohe Bay, Oahu, although the facilities of the Waikiki Laboratory of the Hawaii Marine Laboratory, and the Department of Zoology and Entomology of the University of Hawaii were utilized during certain phases of this study.

Most of the sexually mature maomao examined during this investigation were obtained from the commercial trap fishery which lands its catch at Kewalo Basin in Honolulu, and the fish sampled were almost exclusively from the catch of Mr. Sam Kaolulo, whose traps are laid in twenty to one hundred feet of water between Kewalo Basin and Koko Head, Oahu. This source of maomao was used primarily for gonad and morphometric analysis, while other mature specimens obtained by poisoning, spearing, and pole fishing were used for the examination of stomach contents, analysis of growth and migration, and various studies of this species in captivity.

The reproductive activities of maomao were observed in two shallow water spawning areas at Coconut Island, designated as the "Southwest Point" and the "Tuna Pond" spawning areas (see Figures 1 and 23 for the location of these and other facilities utilized on Coconut Island). Known spawning sites were indicated by symbols painted on the nearby retaining walls, and the frequency with which they were occupied by spawning fish was recorded over a four year period. Maomao were also induced to attach their eggs to concrete slabs placed in the water in these spawning areas. These spawning slabs were 12" x 14" and 1" to 1½" in thickness; the surfaces of some were marked off in 2" squares to facilitate estimating the area of clutches of eggs attached to them. Each slab was constructed with a wire handle which aided in its placement and removal from the water. These slabs, with their attached eggs, were removed from the spawning sites and placed in a specially designed rearing apparatus which allowed close observation and continued development of the eggs, and retained the larvae in an area that closely approximated conditions of the natural environment. Since considerable difficulty has been encountered in rearing marine fishes through certain larval stages, and this apparatus proved to be a successful incubator for maomao larvae, it was considered that a detailed description of its design might prove valuable to other workers. This description is presented in Appendix A.

Studies of maomao larvae were made primarily from individuals hatched and reared in this special apparatus, however, larvae were also obtained from plankton hauls and from other sources.

An extended program of juvenile maomao collecting was carried out at Diamond Head Park, and a detailed survey of this area is presented in the section on juvenile habitats. Additional juveniles were collected from various shallow water areas around all of the main Hawaiian Islands.

The following descriptive terminology is used throughout this presentation:

(a) Embryo - stages from fertilization to hatching

(b) Larva - stages from hatching to individuals with a fork length of 12 mm., at which time the vertical bands on the sides of the body are usually visible.

(c) Juvenile - stages at 12 mm. fork length, or about 10 mm. standard length, until sexual maturity is reached at about 120 mm. (standard length).

(d) Adults - individuals of 120 mm. standard length and over.

Unless otherwise specified, fork length is used throughout to specify the length of larvae. Standard length is used to specify the length of juveniles and adults, because frequent injury to the caudal fin makes the use of fork length impractical.

The following definitions of length are used:

(a) Total length - the distance from the tip of the snout to the most posterior projection of the spread caudal fin.

(b) Fork length - the distance from the tip of the snout to the fork of the tail.

(c) Standard length - the distance from the tip of the snout to the most posterior point on the hypural fan, which is usually beneath the most posterior scales on the caudal peduncle in mature maomao.

Measurements of larvae and juveniles were made under magnification; those of the larvae are considered accurate to within 0.1 mm., and those of the juveniles to within 0.5 mm.

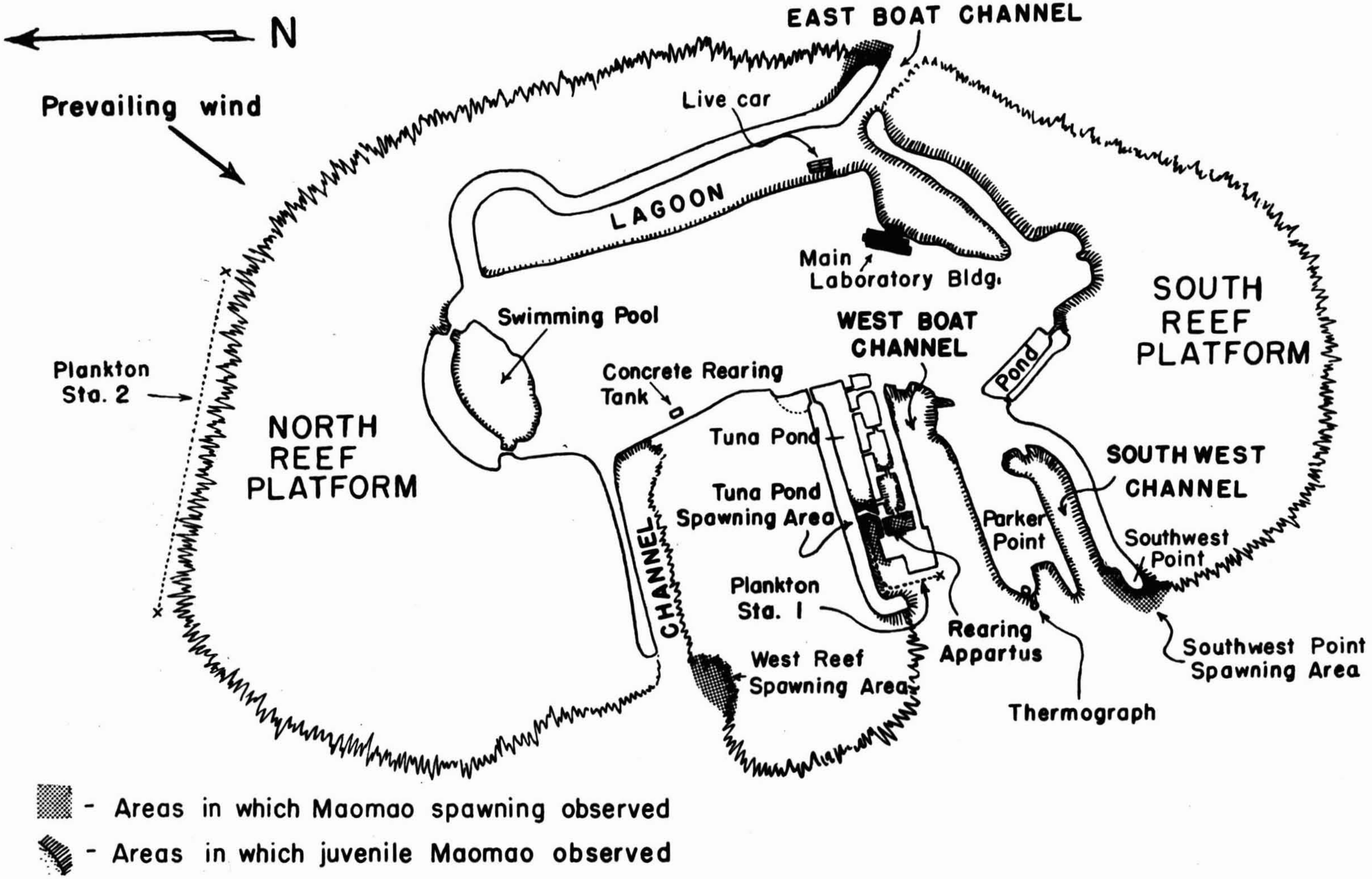


Figure 1. Map of Moku o Loe, or "Coconut Island," Kaneohe Bay, Oahu, showing installations and areas pertinent to this study of the reproductive behavior and early life history of the maomao.

SECTION II

LIFE HISTORY

Habitat

The habitat of the maomao has been observed to be quite varied, extending over a considerable range of substrate types and depths. Substrates with which the adult maomao are associated include living and dead coral, limestone, basalt, and combinations of the above. They are not found commonly in areas with muddy or extensive sandy bottoms, or in localities where the water is consistently brackish or turbid. Juvenile maomao inhabit relatively sheltered, shallow water areas such as reef platforms and tide pools (see section on Juvenile Habitat).

One of the basic requirements of a suitable habitat for adult maomao seems to be a readily accessible place of refuge; e.g. coral growth; cracks, holes, or caverns in the substrate; rock piles, ledges, or man made structures (such as sunken vessels) which serve as a sanctuary to which they retreat on the approach of danger. Maomao have been observed in depths from 120 feet to the surface and are often found in aggregations of a few to several hundred individuals, although such aggregations may only be evident during certain periods of group feeding. They avoid the very turbulent water of the breaker zone but are sometimes found in slightly deeper adjacent areas of moderate water movement; however, their usual habitat is relatively quiet water, in areas where algal growth is not excessive.

The maomao is one of the most abundant Hawaiian pomacentrids, and it appears to be the predominant form of reef fish in some areas.

Observations of this species in the field revealed four possible factors influencing its distribution. First, and probably of primary importance is the availability of a readily accessible refuge into which individuals can retreat on approaching danger. Allee, et. al.(1949) point out that one of the primary reasons that animals congregate is to be near or to occupy sheltered niches. This is evident to anyone who has observed the fauna in shallow water areas around the Hawaiian Islands, especially where wreckage of ships or airplanes has fallen into an otherwise barren and uncluttered area. A number of observations have been made of such refuges around the island of Oahu. A typical example is a sunken landing barge near the entrance to Pearl Harbor in about 30 feet of water. The bottom for a considerable distance around this wreck is smooth and barren of any visible animal or plant life, yet this wreck shelters a very large population of maomao and other species of reef fishes.

Such observations suggest that the size of maomao populations may be limited by the shelter available, and on the basis of these observations personnel of the local Division of Fish and Game have been prompted to place artificial shelters in certain barren areas to increase the standing crop of reef fishes. The results of this venture are thus far inconclusive; however, a similar practice has been successful in increasing the standing crop of some species of fresh water fishes by affording protection from predators for juveniles during a vulnerable period.

A second factor controlling the distribution of maomao is the availability of food. Since the maomao is omnivorous, feeding on a great variety of organisms, this factor is probably not as restrictive as with some species. Maomao have been observed in large, relatively stationary, feeding aggregations, which might indicate that the habitat was occupied to take advantage of the currents carrying planktonic organisms into the area. Planktonic copepods and other crustaceans are apparently a preferred item in the maomao diet (see section on food and feeding habits).

A third factor appears to influence the congregation of maomao in certain areas, although the exact associations are not yet clear. In some areas the distribution of reef fishes is quite spotty, with large aggregations clustered in a comparatively small area on the reef, separated by large areas practically devoid of fishes. Such distribution may be partially dependent on shelter available, as well as other factors in the physical environment. However, it has been observed that a number of fishes on the reef are attracted by the small labrid, <u>Labroides phthirophagus</u> Randall. Apparently this fish attracts a number of species to a given area on the reef where it picks external parasites from their bodies (Randall, in press). Although the maomao appears to be comparatively free of external parasites, it is also attracted to these areas, and on one occasion was observed undergoing inspection by a <u>L. phthirophagus</u>, although the labrid did not pick at the body of the pomacentrid. Repeated observations in the eastern end of Kaneohe Bay during the spring of 1957 always revealed that a majority of the maomao were in aggregations around pairs of this labrid. The first consideration was naturally that the labrid had attracted all of the other fishes due to its feeding habit; however, the association may not be that simple. The labrid may take advantage of a natural aggregation of fishes that was caused by other phenomena, or some species may be attracted by this labrid, and other species may follow, motivated by some social drive.

Being substrate spawners, a fourth factor that affects the distribution of maomao is the availability of suitable substrate on which to spawn. This factor may be more influential in certain areas, depending on the nature of the substrate. This is discussed in the section on the analysis of reproductive behavior.

The existence of aggregations of maomao is known to local trap fishermen who often use them to their advantage. One fisherman with an exceptionally large catch of maomao landed on October 7, 1955, attributed his success to the recent discovery of a new "maomao hole" or aggregation at a depth of about 100 feet. Such aggregations are probably caused by a combination of the above factors.

The distribution of adult maomao is actually dependent on the distribution and movements of the larvae and juveniles, together with migrations of the adults. The larvae possess only limited powers of locomotion during the early free-swimming stages and are at the mercy of prevailing currents, but as they mature they attempt to move inshore to shallow protected areas. Nothing is known of the re-entry of juveniles into deeper water. Only scanty information is available on adult maomao migration as it did not fall within the scope of this investigation; however, during a period in which trials of various fish tags were being carried out, some information was obtained on adult movements.

Adult maomao captured in the vicinity of the Tuna Pond spawning area on Coconut Island were tagged at various times throughout the year and returned to this same area. These same fish were observed to remain in this vicinity for a period of about four weeks, after which they either lost their tags and their identity to an observer, or they migrated to other areas. The former appears probable for maomao kept in captivity retained similar tags for only four to six weeks. Although a population of about 50 to 60 adult maomao seemed to remain in the vicinity of the Tuna Pond gates, the amount of interchange between members of various local populations or groups in adjacent areas is not known. Randall (1955) conducted a series of studies with tagged manini (Acanthurus sandvicensis), and concluded from release and recapture records that extensive migrations of this species probably do not occur under natural conditions. This same study revealed that three out of eleven fish displaced a considerable distance from the area from which they had been taken, returned to that area.

A homing instinct such as suggested by Randall for the manini may also be present to some extent in the maomao, although the data is insufficient to draw any conclusions. A maomao taken in a trap near "Sand Island", about one mile west of Coconut Island in Kaneohe Bay, was tagged and released, and it was recaptured by a fisherman at a point approximately one half the distance back to its original point of capture.

Regarding migrations in other pomacentrids, Bardach (1958) performed tagging experiments on a number of species of reef fishes in Bermuda, including Abudefduf saxatilis (Linnaeus). Five individuals of this species were tagged on a small reef (2.47 acres) located about 300 meters from the nearest adjacent reef. Two of the fish tagged were recaptured after 30 days and one was seen after 50 days on the same reef on which they had been tagged. From additional observations on Pomacentrus fuscus and P. leucostictus which were observed in the same locations over a period of 40 days, the author suggests that, "Pomacentrus live out their entire life spans in a small area of reef environment," although the data presented did not seem to warrant such a broad statement. Longley and Hildebrand (1941) and Beebe and Tee-Van (1933) both comment on the strong territorial tendencies in the pomacentrids, and the former authors observed a sergeant-major (Abudefduf saxatilis) (that was malformed and therefore could be easily identified) around the same coral head during two successive years. A similar behavior is suggested for the maomao locally, since aggregations can be found in reef areas which are isolated from other reefs by deep water and individuals or groups are seldom seen in the areas between. It therefore seems reasonable to assume that maomao seldom migrate any great distances; however, this aspect of the biology has not been thoroughly investigated.

Food and Feeding Habits

The food and feeding habits of the maomao were investigated in order to disclose some of the biotic interactions, and to relate these aspects of the life history to the apparent success of this species. Success of a species is interpreted to mean its ability to occupy a variety of ecological niches and maintain relatively stable populations without being greatly affected by modifications in the environment. The adult maomao is classed as being broadly omnivorous on the basis of stomach content analysis, and it appears to be well adapted to a great variety of dietary items, endowing it with considerable resilience to changes in the availability of any particular item of food.

The feeding habits of the maomao reflect the versatility of this species, and allow it to exploit efficiently available food under diverse conditions. Among the noteworthy aspects of the adult maomao feeding habits are the aggregations it forms under certain circumstances. These feeding aggregations are of two types termed the "curtain" and the "ball". The type of aggregation formed in feeding seems to depend on the location, depth of water, availability of certain food items, and perhaps other factors.

The "curtain" feeding aggregation has been observed a number of times around the island of Oahu, and is usually restricted to water of depths greater than 25 feet where a persistent current exists. This aggregation consists of a group of maomao in curtain-like formation, extending from the bottom to near the surface, all facing into the current, picking elements from the passing plankton. Individuals usually maintain the same relative position in the "curtain", although they may move short distances laterally and vertically to capture organisms. This type of feeding aggregation is only adaptable to certain situations in which the movement and the plankton supply are adequate. From personal observations, and those made by other trained observers, estimates of the number of maomao making up these aggregations vary from 200 to over one thousand. These "curtains" of feeding maomao may extend up from the bottom more than fifty feet, but when alarmed, as by the approach of a diver, the fish withdraw to substrate refuges. This feeding arrangement in the maomao appears to be a very efficient utilization of the planktonic food available, as a large volume of water is exploited with a minimum expenditure of energy, and without direct competition between individuals for food items.

The "ball" type of feeding aggregation observed is one which involves fewer individuals and is commonly seen in shallow water areas. These aggregations usually consist of from 30 to 100 individuals actively swimming together near the surface of the water. The maomao swim in tight circles in various planes to give the effect of a "ball" of fish rolling near the surface. Such aggregations were first described by Tester (1953), who suggested they might be associated with reproduction. Although such aggregations often serve as a point from which females are lured into preliminary spawning maneuvers (see section on reproductive behavior) observations thus far indicate that the primary activity of such groups is associated with feeding. This form of feeding aggregation is most frequently seen during the morning hours in shallow water, and prey are mainly crab zoea and other positively phototaxic crustaceans.

When not in one of the more specialized feeding aggregations described above, adult maomao are often seen swimming lazily about picking organisms out of the water or from the substrate.

The diet of the maomao is quite varied as illustrated by the stomach content analysis presented in Table 1. Specimens utilized for this analysis were obtained from various locations around the island of Oahu throughout the year. Copepods were clearly the major item in the maomao diet as indicated by this analysis. These crustaceans were the major organisms both from the percent stomachs containing the item, and the average bulk of organisms in the stomachs. Among the most common copepods recorded were the following: Calanoida; *Euchaeta marina*, *Scolothrix bradyi*, *Neocalanus gracilis*, *Undinula* sp., *Candacia pachydactyla*, *Candacia* sp.; Harpacticoida; *Sapphirina* sp., *Copilia* sp.,

TABLE 1

DIETARY ITEMS FOUND IN 103 MAOMAO STOMACHS FROM FISH RANGING IN SIZE FROM 2.5 TO 180 mm. STANDARD LENGTH

Item	Number of Fish Containing the Item			Percentage of Stomachs Containing Item	Average Percent Composition by volume (as percentage of total volume)	
	Standard Length (mm.)				Std. Len. (mm.)	
	2.5-10	10-30	30-180	All Fish	10-30	30-180
Detritus	--	9	4	13	10	5
Coarse Algae	--	6	11	18	20	33
Fine Algae	2	17	14	34	25	24
Chaetognaths	--	--	3	3	--	12
Ascidians	--	1	5	6	20	5
Polychaetes	--	1	1	2	2	2
Gastropods	--	2	--	2	6	--
Insects	--	6	1	7	23	1
Crab larval stages	2	5	9	17	18	17
Shrimps	--	2	10	12	2	10
Copepods	5	31	30	68	51	42
Amphipods	2	14	9	26	25	12
Misc. small crustaceans	--	2	3	5	7	5
Crustacean fragments	2	2	10	14	20	42
Eggs	2	5	21	29	9	15
Fish larvae	--	--	1	1	--	1
Unidentified remains	2	8	21	32	35	47
Empty	5	2	0	7	--	--
Total	13	34	56			

Oncaea sp. One or two copepod species usually greatly outnumbered all others in a given stomach; however, the dominant forms varied in specimens from different regions. The algae consumed by the maomao included species from the following genera: Hypnea, Ulva, Polysiphonia, Cladophora, Ectocarpus, and Lyngbya. Other crustaceans found in maomao stomachs included Amphipods (Gammaridae and Caprellidae), crab and shrimp larvae, and a few isopods. Crustacean fragments, apparently from larger crabs, formed an important part of the diet of those individuals with this item in their stomachs. Some of the fragments examined were identified as parts of a portunid crab; however, most of the fragments were from unidentified crustaceans.

Another important dietary item found in some adult maomao stomachs was fish eggs. Most of these were round (probably pelagic), measuring from 0.9 to 1.2 mm. in diameter, although a few elliptical pomacentrid-like eggs, and some smaller crustacean eggs were also seen.

The literature on food and feeding in the pomacentrids is restricted to a few notes in widely scattered works. Longley and Hildebrand (1941) examined three stomachs of Abudefduf saxatilis (Linnaeus) and found they contained mostly algae, with some copepods and a few fish eggs. Dawson, Aleem, and Halstead (1955) examined the stomach contents of Abudefduf sordidus (Forskal) and A. septemfasciatus (Cuvier) from Palmyra Island and found them both to be strictly herbivorous. Randall (1955), reporting on the food habits of the same two species from Onotoa Atoll in the Gilbert Islands was in agreement with the above findings. The present author, in a survey of the food of pomacentrids collected off of Waikiki, Oahu, found the following: Dascyllus albisella Gill, carnivorous (mostly copepods); *Abudefduf imparipennis* (Vaillant), omnivorous (mostly annelids); *Pomacentrus jenkinsi* Jordan and Evermann, strictly herbivorous; *Chromis vanderbilti*, carnivorous (copepods and eggs).

With the possible exception of *Abudefduf saxatilis*, the pomacentrids examined in this brief survey all appear to have a rather restricted and specialized diet, which, in general, reflects the more restricted range of habitats to which they are confined.

The morphology of the alimentary tract of the maomao revealed that it was well adapted to handle the wide range of items found in its diet. The mouth is small and protrusible; the jaws are equal, each containing a single row of close-set, strong, sharp-edged incisiform teeth (see Fig. 2). The teeth are basically truncate; however, the lateral teeth in the jaw usually have an accentuated medial cusp. The teeth in a 148 mm. specimen numbered 50 in the lower and 48 in the upper jaw. No teeth exist on the vomer, palatines or tongue. The pharyngeal teeth consist of a lower, triangular plate and two pairs of laterally situated upper plates all studded with areas of both sharp and bluntly rounded, closely set teeth. These teeth appear well suited to aid in the mastication of large pieces of algae and crustaceans, the remains of which are often found in maomao stomachs. A short esophagus extends posteriorly from the buccal cavity and enters the triangular, thick-walled stomach in its antero-dorsal region. Three finger-like gastric caeca branch laterally from the region of the pylorus on the ventral portion of the stomach. From this point, a thin-walled, convoluted intestine leads posteriorly to the anus.

Thus the adult maomao is well adapted to ingest, and probably depends largely on a diet of copepods, supplemented by other crustaceans

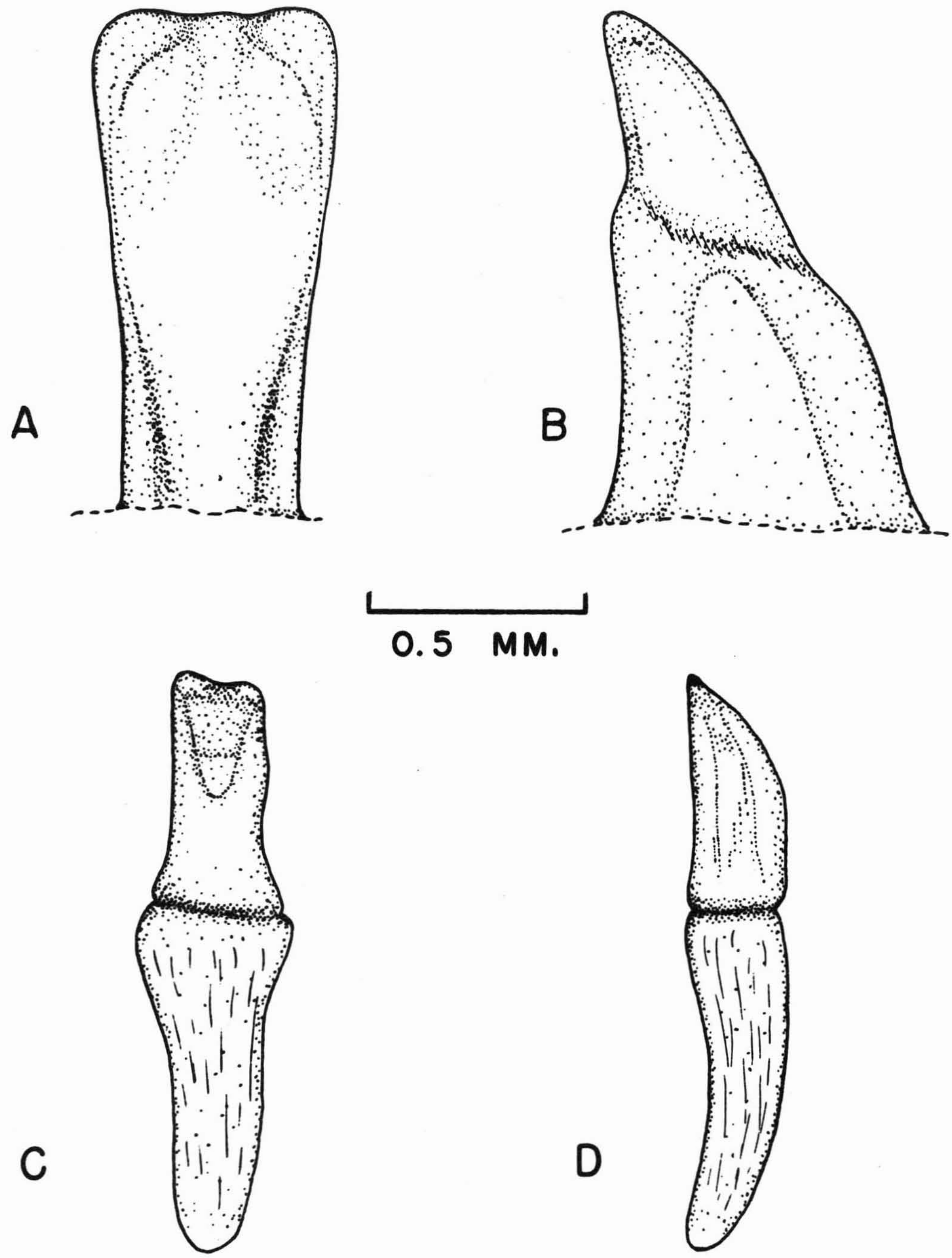


Figure 2. Teeth from the lower jaw of a 141 mm. maomao. A. Posterior aspect of a tooth adjacent to the midline. B. Right side of tooth shown in A. C. Posterior aspect of a lateral tooth (42nd from the midline). D. Right side of tooth shown in C. Comparable teeth of the upper jaw differ only slightly from these. Some specimens show a more accentuated medial cusp in the lateral teeth than is shown here.

and eggs in the plankton. Its sharp incisiform teeth also make it well adapted for feeding on attached algae, which it apparently does when other food is not abundant. This dentition, along with the protrusible mouth of the maomao, also serves to aid the parent fish in cleaning an area on the substrate for the attachment of eggs.

Various workers have attached importance to the length of the gut in relation to the body length when comparing species with different diets. Such dimensions merely reflect the ratio of the surface area of intestinal mucosa to the body size of the fish (Barrington in Brown, 1957). In examining 56 species of fishes from the Red Sea, Al-Hussaini (1947) found the following range of relative gut lengths associated with diets: plankton feeders, 0.5 - 0.7; carnivorous fishes, 0.5 - 2.4; omnivorous fishes, 1.3 - 4.2; herbivorous fishes, 3.7 - 6.0. The average relative gut length of adult maomao is about 2.4, which is in agreement with the above findings, and may reflect the ability of this species to exist on a strongly omnivorous diet.

Coloration

Coloration of the adult maomao falls into two general categories; sexual or nuptial coloration, and normal adaptive coloration. As the treatment of both categories will be primarily descriptive, the specialized nuptial coloration will be included in the description of reproductive behavior, and only the normal adaptive coloration will be discussed in this section.

Examples of adaptive coloration are numerous and generally well known in the fishes, as they are throughout the animal kingdom (Cott, 1940; Norman, 1951). Among the pomacentrids a tremendous variation in coloration exists as illustrated by examples of the two extremes. Very gaudy coloration is displayed by *Hypsypops rubicunda* (Girard) and most of the members of the subfamily Amphiprioninae, which apparently serves to advertise a territory and perhaps indirectly lure prey, as in some of the anemone fishes (Verwey, 1930b; Kritzler, Fox, Hubbs, and Crane, 1950). The other extreme includes species with extremely drab, inconspicuous coloration, which serves to be protective by reducing the fish's contrast with its normal background. *Abudefduf abdominalis* lies somewhere between the two extremes, but it is of especial interest because of the wide variation in coloration it displays.

Considerable attention has been directed toward variations in the color pattern of the sergeant-major, *Abudefduf saxatilis*, which is closely related to the maomao with almost identical markings and coloration. Townsend (1929) describes and illustrates two color phases in this species, a light and a dark phase. In the light phase, the ground color between the vertical black bands is yellow to silvery, while in the extreme dark phase the ground color darkens and the stripes disappear making the fish appear uniformly black. Longley and Hildebrand (1941) also observed these two color phases in *A. saxatilis*. They observed the light phase in fish feeding over a light sandy bottom, or when swimming among coral heads, while the dark phase was displayed by fish in crevices, and especially by fish in deep water. They report that some individuals observed in crevices at ten to twelve feet were so dark that the black vertical bands were scarcely distinguishable.

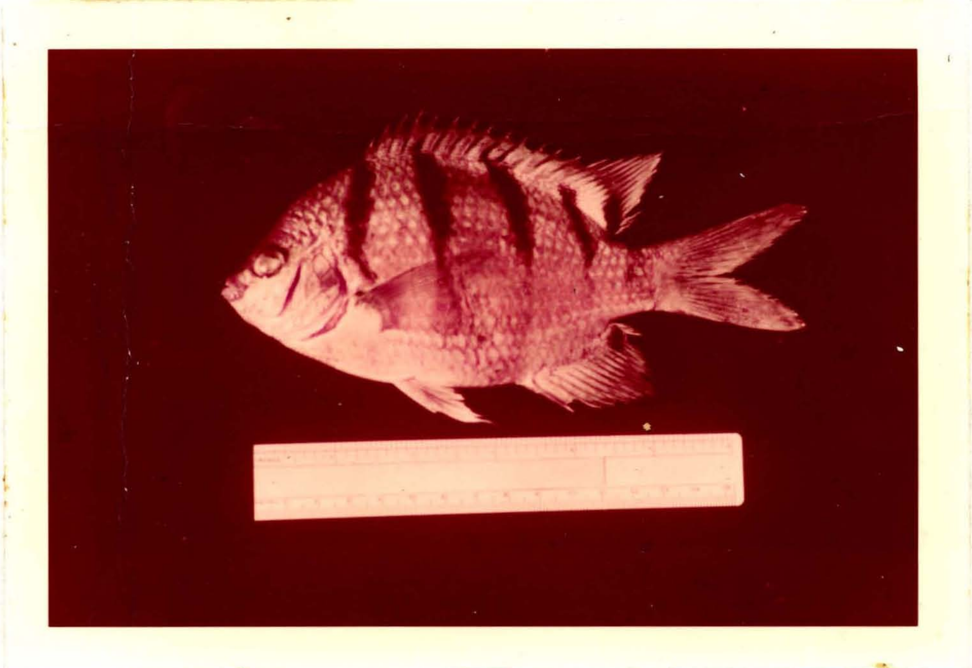
These findings are in remarkable agreement with those observed in *Abudefduf abdominalis*. Observations on the coloration of the maomao revealed the light and dark phases also; however, in the light phase the ground color had two distinct aspects, brassy-green and pure yellow. The brassy-green aspect of the light phase is illustrated in Plate I, which shows this coloration in the upper 1/3 to 1/2 of the body, with the lower portion of the body pale yellow to silvery. The fins are a dusky silver, and the vertical bands are a distinct black in the light phase. During the yellow aspect of the light phase, the brassy-green is replaced by pure yellow, and the fins appear less dusky. The dark phase is similar to that described for _A. saxatilis_, with duskiness of varying intensities covering the normal coloring, until at the extreme the entire fish appears black, and if the vertical bands are distinguishable at all they appear slightly more gray.

Observations of the maomao in nature showed that this species also assumes a coloration that allows it to present a minimum of contrast with its background. This was illustrated in an observation made in the vicinity of Coconut Island in February, 1954, of a large aggregation of maomao extending from the surface to a depth of about 25 feet. Those fish near the surface were all of the light phase, while the others were darker - the greater the depth, the duskier the coloration.

Color adaptation of fishes to blend with their background is well known and is carried out with striking control in some species of flat fishes. Odiorne in Brown (1957) reviews such processes, and points out that the stimuli required to initiate these color changes are primarily visual in nature.

The effect of dark surroundings on maomao was illustrated by placing three adults in each of two thirteen-gallon glass walled aquaria through which sea water was circulated. All six fish were of about equal hue, and of the brassy-green aspect of the light color phase. Both aquaria

PLATE I



A freshly killed specimen of <u>Abudefduf</u> <u>abdominalis</u> illustrating the brassy green aspect of the light color phase. This 147 mm. male was taken from the commercial trap catch on September 10, 1955. In this color reproduction the natural colors have been altered slightly; the normally yellow body is shown here as orange, and the greenish hue on the dorsal body is bluer in this photograph than seen in nature.

were located on the shaded porch of the main laboratory building of the Hawaii Marine Laboratory at Coconut Island. One aquarium was then covered with an opaque rubberized cloth which excluded all light, and light was only admitted for two to three minutes each day when these fish were fed. The other aquarium was left uncovered as a control. After a period of just one week, the fish in the covered aquarium had become extremely dark, so that the vertical bands were hardly visible, while the controls were only slightly duskier. In addition, maomao kept for some time in subdued light in tanks at the Steinhart Aquarium in San Francisco displayed an extremely dusky coloration. Odiorne, op. cit., points out that, in situations such as these, melanophores may increase in number as well as in size, presumably by the proliferation and differentiation of prospective pigment cells and possibly by the mitotic division of the melanophores themselves.

White backgrounds seem to be accompanied by the opposite effect, and maomao kept in such an environment soon become very pale. This was noted when several maomao were placed in a large, shallow wooden tank which was painted with a glossy white enamel, and was unprotected from the sun except for periods in the late afternoon. These fish were all about the same brassy-green color when placed in the tank during the first week in June. During the following two months they all became extremely pale; very silvery ventrally, with just a faint yellow hue on the dorsum of the body. The vertical bands also faded to a pale gray, and were much reduced in length. In other similar investigations it was found that this fading in color was the direct result of a decrease in the number of melanophores, apparently from their degeneration. In short term experiments with <u>Fundulus heteroclitus</u>, when individuals were confined to a white background the decrease in melanophores was at the rate of about 1 percent per day (Odiorne, op. cit.).

Longley and Hildebrand (1941) report that the color changes in Abudefduf saxatilis from the dark to the light phase can be very rapid when this species is suddenly excited. A similar rapid change in coloration, not directly associated with the background color, is also evident in the maomao and is believed to be under hormonal control. When maomao were placed in a thirteen gallon glass aquarium and allowed to assume the dark phase in subdued light, they could be made to transform to the light phase very rapidly by banging on the side of the aquarium or otherwise exciting them suddenly. A similar reaction has been observed in other species of fishes and is termed "excitement pallor" which results from the fishes being alarmed or frightened. This pallor is a result of a rapid and extensive aggregation of melanophores, such as is caused by adrenaline. However, the mechanism controlling this phenomenon was not investigated in the maomao.

Other than the nuptial coloration discussed in the section on reproductive behavior, no specific color phase is associated with any specific reproductive activities. Tester (1953) noted that a maomao observed guarding a clutch of eggs was a very bright yellow; however, numerous observations of maomao guarding clutches of eggs revealed a wide variety of coloration within the phases mentioned, most of them corresponding to the brightness of the background. In a few cases where a very light colored fish was seen in dark surroundings, it was considered to be the result of an alarm response similar to that discussed above.

REPRODUCTION

Structure of the Reproductive Systems

The structure of the reproductive systems in *Abudefduf abdominalis* is not unlike that usually found in teleost fishes that exhibit external fertilization. In the maomao, as in most teleosts, the passage of sexual products from the gonad to the genital pore is direct, without being released into the coelomic cavity.

In the male maomao the gonads are paired, laterally compressed structures suspended from the posterior dorsal portion of the coelom by paired mesenteries. These testes are opaque and white to pale yellowish-brown. They are usually asymmetrical, the left testis being larger than the right in most cases. A vas deferens leads posteriorly from each testis, and the ducts pass out through a single pore at the tip of the urogenital papilla, a conical structure located just posterior to the anus (Figure 3A). This conical papilla in the male arises from between two fleshy structures, and lies in an indentation in the ventral body wall pointing in a posterior direction. The urogenital structures are often partially covered by two lateral rows of scales, and apparently during reproduction these scales are withdrawn to permit the erection of the papilla and the direction of sperm onto the egg mass.

In the female maomao the same general structural organization exists. The primordial ova are embedded in the germinal epithelium of the ovary, and as these cells mature they are cast into the lumen which is continuous with a posterior oviduct. This condition is referred to as "cystovarian", and, as previously stated, is common to all but a few families of teleost

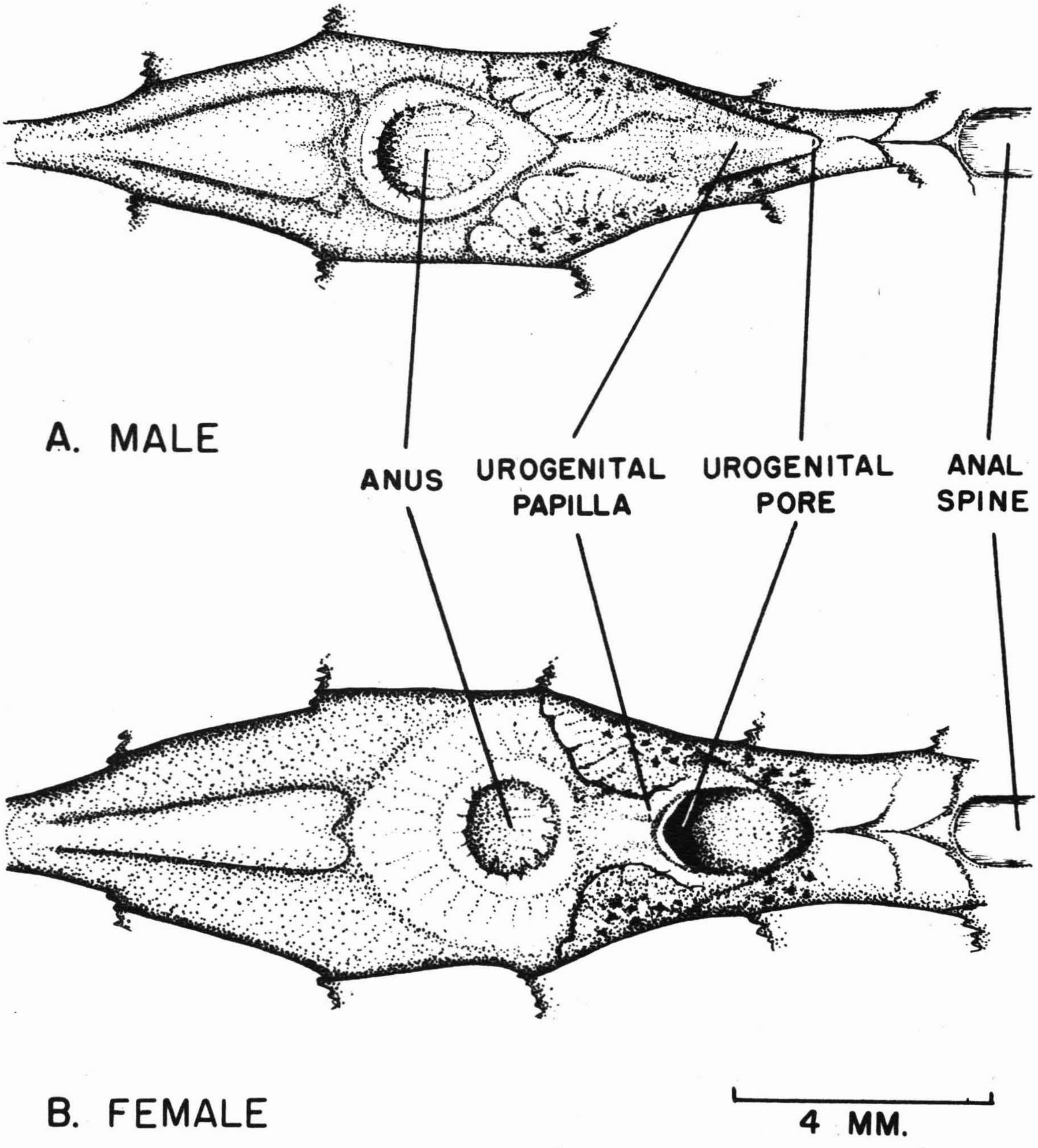


Figure 3. External genitalia of two sexually mature maomao. A. The genital region of a 151 mm. male. B. The genital region of a 139 mm. female.

fishes (Goodrich, 1930; Hoar in Brown, 1957).

The maomao ovaries are paired, rounded structures suspended from the posterior dorsal portion of the coelomic cavity by mesenteries. They are very pale pink to white in immature specimens, and gradually change in color and shape as the female becomes sexually mature. As in the male, the left gonad is usually much larger than the right. As the ovary increases in size, the posterior end becomes relatively larger than the anterior, and the color changes from pale pink to a deep cherry red or orange, depending on the color of the yolk material. During spawning, the ova are forced into the oviduct located at the posterior end of the ovary and out through a "v" shaped pore in the genital papilla. This papilla is more blunt and rounded than the comparative structure in the male, and the opening is not terminal, but slightly anterior to the apex. As in the male, this structure lies in a recess in the ventral surface of the body and is normally partially covered by the adjacent scales (Figure 3B).

The release of germ cells has not been observed at close range in the maomao, and therefore the position of the external genitalia during spawning is not known. These structures have been observed during spawning in a number of fishes, including some of the pomacentrids. Breder and Coates (1933) observed spawning in *Pomacentrus leucoris* Gilbert at close range, as did Garnaud (1951, 1957) for *Amphiprion percula* Lacepede, and *Dascyllus trimaculatus* (Rüppell). In all of these cases, erection of the genital papillae was noted.

Regarding the asymmetrical arrangement of gonads in this species, the relative position of the larger gonad was not always the same, and therefore some data is presented in support of a possible explanation of this phenomenon. During the examination of 2,385 maomao obtained from the local trap catch, it was noted that in a large percentage of both males and females the left gonad was significantly larger than the right. In some cases, however, the two gonads appeared to be approximately the same size, and in a very few cases the right gonad was much larger than the left. In addition, two males and two females examined possessed but a single gonad each. These data, obtained from visual examination of the gonads, are summarized in Table 2.

TABLE 2

RELATIVE SIZE OF PAIRED GONADS IN 2,385 MAOMAO EXAMINED FROM TRAP CATCH DURING 1954 - 55 - 56

	Males (1625 examined)	Females (760 examined)
Percent with left gonad larger	86.5	97.5
Percent with right gonad larger	0.4	0.1
Percent with gonads approximately the same size	13.0	2.1
Percent with one gonad only	0.1	0.3

The significance of such asymmetry is discussed by Kubo and Onoe (1951) who observed a similar situation in Sardinia melanosticta. They point out that the equilibrium of weight in the body cavity is important, and since the right lobe of the liver and the pylorus place more bulk on the right side of the body, the left gonad becomes unequal in size. No marked asymmetry in adjacent organs was observed in the maomao; however, such organs as the stomach may naturally fall to one side during development. It appears as though the allotment of space to allow certain organs such as the intestine to function properly is an important consideration and is perhaps a major reason why one gonad is restricted in growth. The mechanism by which one gonad is restricted is not immediately apparent. Mechanical pressure alone does not seem to be the determining factor as the size difference is noted in the gonads at a very early stage of development, before pressures are exerted by adjacent organs. An explanation for the control of this differential growth in the gonads must therefore be sought in the early developmental processes or perhaps in the genetic influence exerted.

Gonad Maturation Stages

In order to obtain further information on the nature of maomao spawning, a detailed examination of the gonads from trap caught samples was undertaken. Between 5 February 1954, and 28 May 1956, the gonads from 760 females, and 1,625 males were weighed, examined, designated as to the degree of maturity, and notes were taken on their size, shape, and color. The maturity of these gonads was initially designated according to a method suggested by Blackburn (1941), but it soon became apparent that maomao gonads did not lend themselves readily to such a refined classification which included seven distinct stages of maturity. The following modified classification suggested by Tester (1951) was therefore adopted:

Stage I. Immature: gonads small, stringy, and often difficult to classify as to sex. Ovaries slightly rounded, pale grayish-brown to pink. Eggs visible to the naked eye, and transparent under magnification. Testes white to pale yellowish-brown.

Stage II. Initially maturing or recovering spent: gonads occupying about one-quarter of the body cavity. Ovaries rounded, semi-transparent, pale pink or orange, and often mottled with darker red spots. Testes flattened, grayish or yellowish white.

Stage III. Ripening: gonads occupying about one-half of the body cavity. Ovaries rounded, more enlarged posteriorly, light red or orange with mottled darker areas, eggs visible through the ovary wall. Testes yellow to white.

Stage IV. Fully ripe or nearly so: gonads occupying three-quarters of the body cavity or more. Ovaries very deep red or orange, often mottled with lighter spots, eggs visible through the ovary wall, one ovary usually larger than the other (up to twice the volume), smaller ovary rounded throughout its length, larger ovary laterally compressed with enlarged posterior end. Testes white, compressed, often composed of two or three sections divided by fissures, one testis usually larger.

Stage V. Spent: gonads similar to Stage II. This stage seldom observed in the maomao, probably because all gametes are not released in a single spawning.

The assignment of stages to gonads in the maomao sampled was subject to some error due to the subjective influence of the maturity of other fish in the sample, the color of the gonads, and perhaps other factors; however, a constant effort was made to be objective and base judgements solely on the above criteria.

Although fully ripe maomao below 130 mm. were uncommon, a 119 mm. ripe female (ovaries Stage IV) and a 120 mm. ripe male were encountered during the adult sampling program. Data from growth trials conducted at Coconut Island indicate that maomao can attain a length of 120 mm. in one year, and therefore it is assumed that they are capable of reproduction at that age.

Only a few immature specimens (Stage I) were encountered in this sampling program, primarily because the trap fisherman from whom the sample was obtained generally discarded all maomao of 100 to 110 mm. or less.

A summary of the maturity stages of samples examined during 1955 is presented in Tables 3 and 4. These data reveal that the highest percentage of Stage IV specimens is found between January and September, with a maximum in May and June as indicated by the maturity stages of both the male and female gonads. The lowest percentage of ripe fish is encountered from October through December, the months in which the greatest number of Stage V (spent gonads) and Stage II (initially maturing or recovering spent gonads) are also found. The paucity of Stage V gonads found is attributed to the difficulty encountered in distinguishing such gonads from those of Stage II. Also, males

TABLE 3

STAGES OF OVARY DEVELOPMENT EXPRESSED IN PERCENTAGE OF TOTAL SAMPLE, FROM TRAP CAUGHT MAOMAO - 1955

Month	Sample Size	Stage*			
		II	III	IV	V
Jan.	28	39.3	25.0	35.7	0
Feb.	35	28.6	37.1	34.3	0
March	32	28.1	28.1	43.8	0
April	25	32.0	24.0	40.0	4.0
May	41	4.9	46.3	48.8	0
June	32	12.5	25.0	59.4	3.1
July	30	26.6	30.1	40.0	3.3
Aug.	23	26.1	47.8	21.7	4.4
Sept.	81	34.6	28.4	35.8	1.2
Oct.	66	47.0	33.3	12.1	7.6
Nov.	41	41.5	48.7	0	9.8
Dec.	22	68.2	22.7	9.1	0
Total	456				

*Stage I (Immature) females not included as they were rarely found in these samples.

TABLE 4

STAGES OF TESTIS DEVELOPMENT EXPRESSED IN PERCENTAGE OF TOTAL SAMPLE, FROM TRAP CAUGHT MAOMAO - 1955

Month	Sample Size	Stage*			
		II	III	IV	V
Jan.	63	19.0	46.1	34.9	0
Feb.	44	31.8	36.4	27.3	4.5
March	76	32.9	39.5	27.6	0
April	48	20.9	45.8	33.3	0
May	59	20.3	37.3	42.4	0
June	92	15.2	42.4	42.4	0
July	71	16.9	53.5	26.8	2.8
Aug.	77	19.5	57.1	23.4	0
Sept.	99	23.2	48.5	27.3	1.0
Oct.	104	52.9	36.5	5.8	4.8
Nov.	47	76.6	14.9	2.1	6.4
Dec.	56	71.4	19.6	3.6	5.4
Total	836				

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*Stage I (Immature) males not included as they were rarely found in these samples.

captured while guarding clutches of eggs, indicating they had recently released some of the contents of their testes, still had Stage III gonads. This suggests that multiple spawnings take place during a single season, and after each spawning sufficient partially developed gametes remain to cause the gonads to appear as Stage II, or possibly even Stage III.

Although the frequency of spawning of a single maomao was not determined, multiple spawnings in a single breeding season have been observed in other pomacentrids. Verwey (1930a) observed a single pair of Amphiprion percula spawn fourteen times between the middle of April and the end of November in the Onrust Aquarium, Batavia. During the period of most reproductive activity (June through August), nine spawnings were observed, with an average lapse of 10.5 days between broods. In one case spawnings were separated by only seven days. Garnaud (1951) observed similar frequent spawnings of A. percula. A single pair of Dascyllus trimaculatus also was observed to spawn frequently while in captivity. Seventeen spawnings were observed in a period of seven months, with a minimum time between spawnings of only six days (Garnaud, 1957).

In order to confirm the results obtained from visual analysis of gonad maturity stages and to shed further light on the overall picture of maomao spawning, another method of gonad analysis suggested by Tester (1951) was utilized. This method involves determining the relative gonad weight, or gonad weight as a percentage of the total weight of the fish, as a measure of its ripeness. When these relative weights are averaged on a monthly basis and plotted for a year, they form a graphic picture which shows the nature of the spawning cycle and the period of maximum spawning of the population sampled. This has been done in Figure 4 for female maomao sampled during 1955. The general shape of this curve, with a gradual increase in relative gonad weight to a peak in June, followed by a steady decline to a low in November, reflects the reproductive activity of the maomao in the area sampled and is in close agreement with the results obtained from the analysis of gonad maturity presented in Table 3. In both of these analyses, a peak of spawning is indicated for June, 1955. This time of maximum spawning is further confirmed in the number of juveniles observed entering the Diamond Head tide pools at about this time in 1955 (see Figure 20).

Sex Ratio

The sex ratio was determined by visual examination of the gonads of 2,313 maomao which were randomly sampled from the commercial trap catch between June, 1954 and June, 1956. These samples contained 1,587 males and 726 females, or 68.6 percent males and 31.4 percent females, and the number of males exceeded the number of females in almost every sample examined (Table 5).

The cause of such an unequal sex ratio in the maomao is purely a matter of speculation at this point; however, some factors that may contribute to it are discussed briefly. If an inequality does exist in the sex ratio of the adult maomao generally, it is probably due to unequal mortality caused by some behavioral difference of the sexes at some time during the life history. It is more probable that the unequal sex ratio obtained in this investigation is due to selective

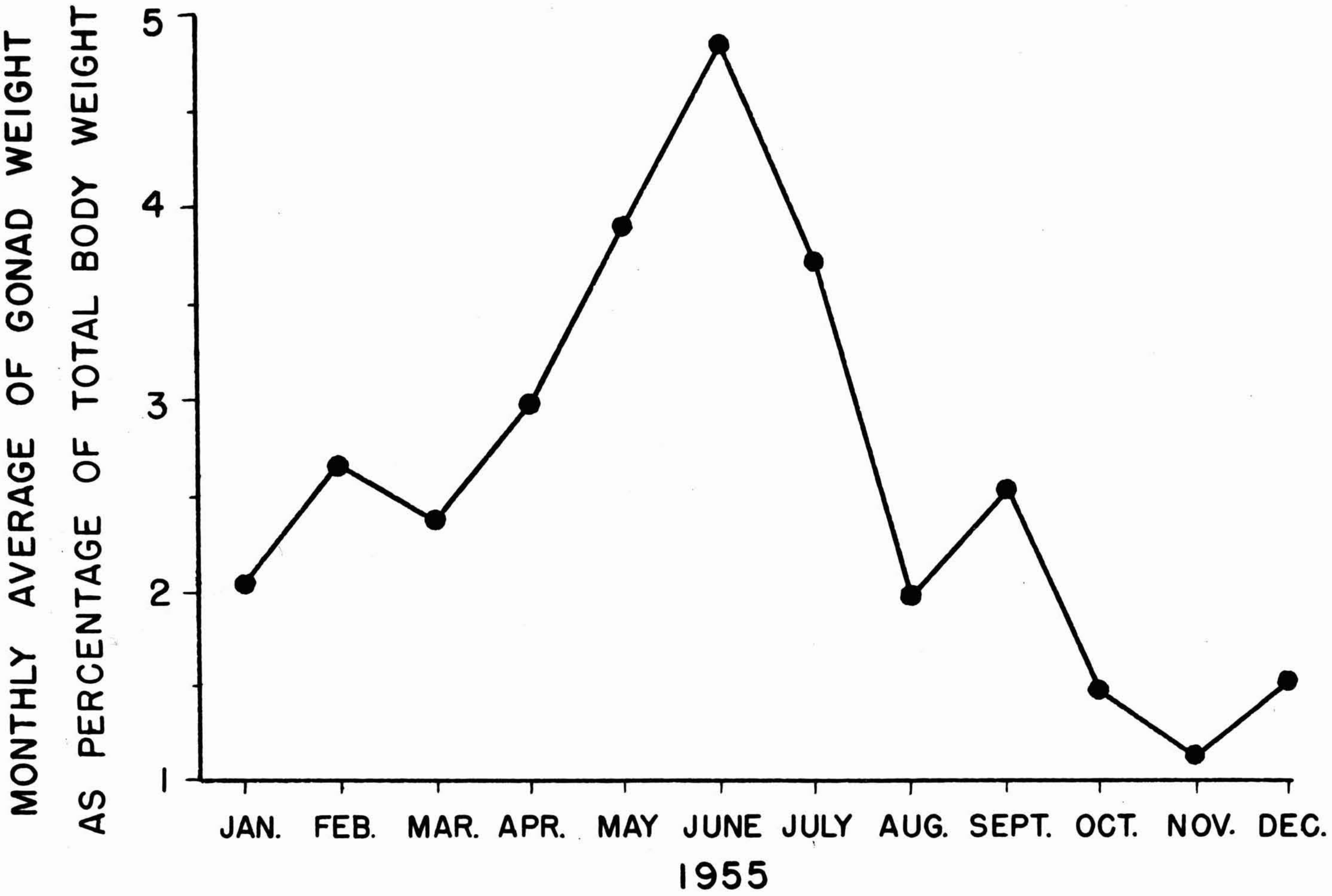


Figure 4. The monthly average of relative gonad weights (weight of gonad expressed as a percentage of total body weight) of 456 female maomao from random samples of trap caught fish during 1955. Immature specimens are not included.

TABLE 5

SEX RATIO OF TRAP CAUGHT MAOMAO FROM WEEKLY SAMPLES OVER A TWO YEAR PERIOD

Month	Total Sampled	Number of Males	Number of Females	Percent Males
(1954)				
June	58	49	9	84.5
July	80	44	36	55.0
Aug.	123	92	31	74.8
Sept.	76	54	22	71.1
Oct.	104	72	32	69.2
Nov.	70	53	17	75.7
Dec.	112	75	37	67.0
(1955)				
Jan.	94	66	28	70.2
Feb.	80	45	35	56.3
March	117	82	35	70.1
April	77	52	25	67.5
May	119	78	41	65.5
June	125	93	32	74.4
July	105	75	30	71.4
Aug.	100	76	24	76.0
Sept.	187	102	85	54.5
Oct.	174	108	66	62.1
Nov.	96	55	41	57.3
Dec.	82	60	22	73.2
(1956)				
Jan.	77	57	20	74.0
Feb.	110	81	29	76.3
March	41	33	8	80.5
April	69	58	11	84.1
May	37	27	10	73.0
Total	2313	1587	726	

sampling. Randall (MS.) relied on the same commercial trap catch from which to obtain samples of manini (Acanthurus sandvicensis). Although he did not determine the sex ratio of this species throughout the year, he found that in May, 1953, a sample of 291 manini consisted of 68 percent males. From samples of manini obtained by less selective methods such as poisoning and seining, however, he found that 60.7 percent of a sample of 221 manini were females. In both cases the samples are relatively small, but this does point out the selective nature of traps in regard to this species.

Since the percentages of male manini and maomao are about the same in the trap catch, a similar selective process could be operating in both cases. Such a process may be due to some behavioral differences, such as the males being more curious or aggressive than the females. The trap fishermen report that seldom are just a few maomao found in a trap; traps usually contain either a large number or none at all. This may indicate that the sexes aggregate separately and follow each other into the trap; however, there are no observations thus far to support such a statement. Thus, large scale, non-selective captures are necessary in order to obtain a more accurate picture of the sex ratio of the maomao in nature.

Although the number of males exceeded the number of females in almost every sample obtained, the sex ratios varied between individual samples and from month to month. (Table 5). In order to test the hypothesis that the sex ratio was consistent with time statistically, and thereby show that the selective process was relatively constant, the data were checked by the method of multiple chi-square suggested by

Snedecor (1946: 206). This hypothesis is tested using the formula:

$$\chi^2 = \frac{SpX - \bar{p}SX}{\bar{p}\bar{q}} \qquad (1)$$

in which $\bar{p}$ is the average probability of getting a male in a monthly sample, $\bar{q}$ is the average probability of getting a female in the same sample, X is equal to the number of males in an individual sample, and p is the probability of males occuring in that sample. From the maomao sample data presented in Table 5, $\bar{p} = 0.6861$, and $\bar{q} = 0.3139$. Application of these data from samples pooled on a monthly basis over a 24 month period results in a chi-square value of 69.52. With 23 degrees of freedom, the probability of having a consistent sex ratio in time is less than 0.01, and therefore the hypothesis is rejected. In addition, since no apparent correlation exists between the change of sex ratio and reproductive activity, it is assumed that sampling of the two sexes is unequal and with differing degrees of intensity at various times.

Sexual Dimorphism

No marked sexual dimorphism was apparent in the maomao other than the temporary nuptial coloration observed in the breeding males (see section on reproductive behavior for details). The sexes can be distinguished externally in mature specimens by close examination of the external genitalia. The most apparent difference was in the urogenital papillae as illustrated in Figure 3. In addition, adult maomao from the commercial trap catch revealed a consistent, minor size difference throughout all of the samples taken. Of a total of 2,385 maomao sampled, the average standard length of 1,625 males was 144.0 mm., and of 760 females was 137.8 mm. This difference was encountered regularly in samples and no doubt reflects a condition in natural populations. However, since selective sampling of the sexes is indicated, the magnitude of this size difference may not be considered reliable until further non-selective data are available.

Ova Development

The maomao ovary is a thin walled structure with branching clusters of germinal epithelium extending from the periphery into the lumen for a distance of 2 to 3 mm. The primordial ova are found in this peripheral germinal epithelium, and as they mature they are released into the lumen, a process that gradually distends the ovary.

The ovaries appear to be very uniform in regards to their internal structure and contents. This was demonstrated when ovaries from a 142 mm. and a 162 mm. specimen designated as Stage IV were removed from the fish and transverse slices made at four points along the longitudinal axis of each gonad, including points very near the extremities. From each slice the dimensions of the gonad wall, germinal epithelial structures, and the frequency of ova of various sizes was determined. No significant difference was observed in any of the measurements taken from one fish, either between slices within a single ovary, or between slices of paired ovaries. It was therefore concluded that a transverse slice at any point on either right or left ovary would yield a representative sample of the material contained in both ovaries of an individual maomao.

In order that the size and degrees of maturity of ovarian eggs might be used in determining the magnitude and possibly the time and frequency of spawning, it was necessary to place these ova into various categories. Following a modification of a method of classification suggested by Tester (1951), the ovarian eggs were grouped in four stages based on their size, appearance, and location in the gonad.

Stage A. Primordial ova (Figure 5A): These are immature, transparent ova which are embedded in the germinal epithelium and serve as a reservoir or stock pile of primitive eggs from which the later stages periodically mature. They range from 0.03 to 0.15 mm. in maximum diameter, and are completely transparent up to about 0.06 mm. when the nucleus takes on a coarse granular appearance. At about 0.15 mm. the cytoplasm begins to become granular at the end closest to the nucleus.

Stage B. Developing ova (Figure 5B & C): These developing ova gradually emerge from the ovarian tissue and are eventually expelled into the lumen of the ovary. They range in size from 0.15 mm. to about 0.8 mm. and consist of an irregular shaped mass of granular yolky material. Up to about 0.35 mm., these eggs display a characteristic banded nucleus and a chorion which gradually thickens and then loses its identity within the opaque yolk mass. This stage is embedded in ovarian tissue up to about 0.5 mm.

Stage C. Ripe or nearly ripe ova (Figure 5D): These ova are always free in the lumen of the ovary. They range from about 0.8 mm. to 1.1 mm. and are roughly elliptical, with granular red or yellow yolk

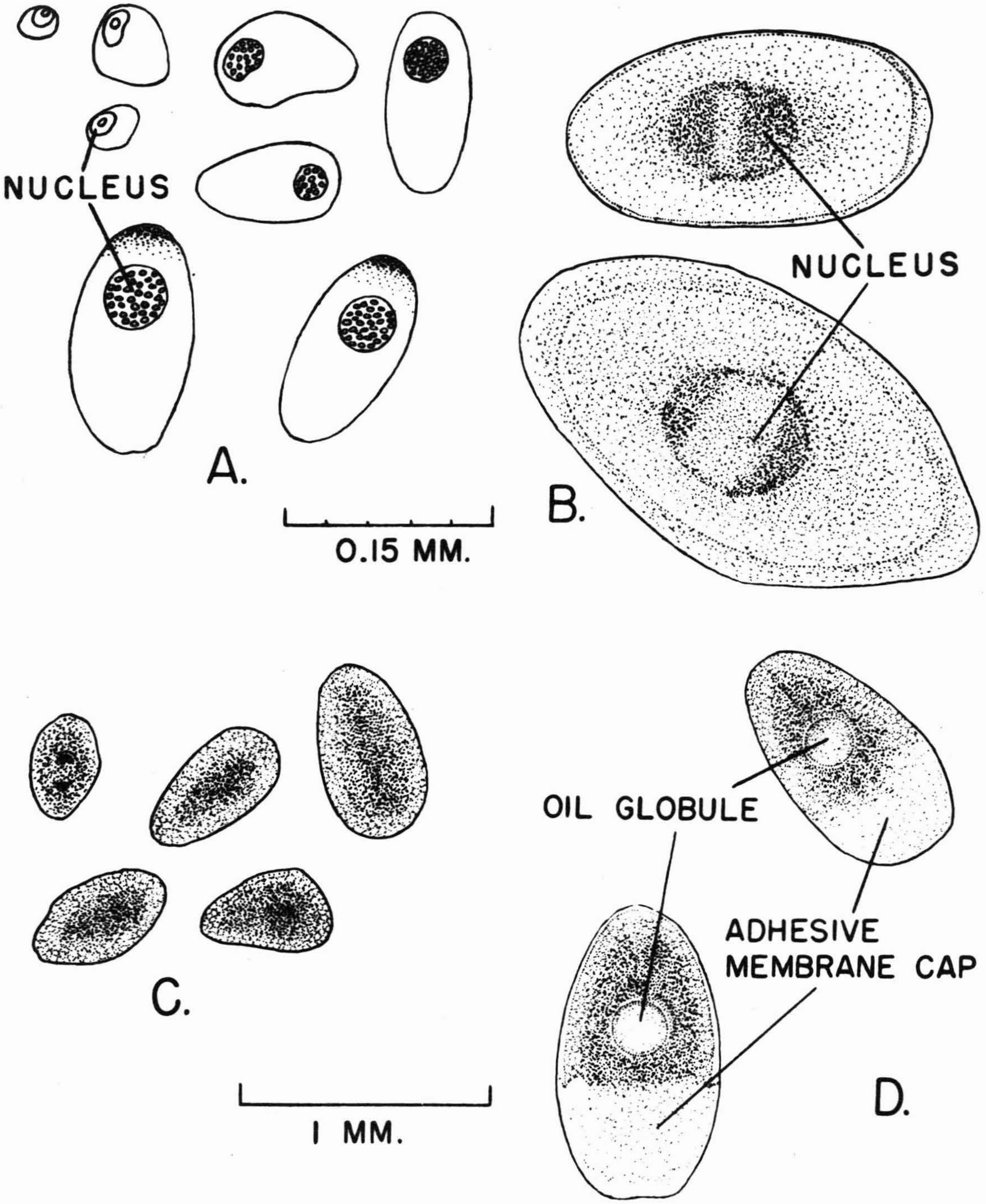


Figure 5. Stages of developing maomao eggs drawn from fresh material taken from the ovaries of several mature specimens. A. Primordial ova (Stage A). B. Developing ova (Early Stage B) with characteristic banded nucleus. C. Developing ova (Late Stage B). D. Ripe and nearly ripe ova (Stage C).

material. Two of the characteristics of ova in this stage are (1) an adhesive membrane cap covering the enlarged end of the ova, and (2) at least one large oil globule which moves rather freely in the semi-fluid yolk when the ova is rotated. As these ova reach maximum size, and probably just prior to spawning, a thin transparent zone forms, surrounding the yolk mass.

Stage D. Residual ova: These ova are similar to the ripest Stage C ova in size and appearance; however, they are in various stages of disintegration. The yolk appears more translucent and the ova have often lost their firmness and are ruptured and flattened. When observed, these ova were always in the lumen of the ovary and were few in number.

The egg diameter frequency distribution of Stage B and C ova has been used as a means of determining the number of times a fish spawns in a given season, and even the exact time of spawning within the season (Clark, 1925, 1934). In plotting the length frequency of ova from Stage 4 maomao ovaries a typical distribution with three modes such as illustrated by Tester and Takata (1953) for the aholehole (Kuhlia sandvicensis) was encountered. This distribution typically consisted of three pronounced modes, one of Stage B and one of Stage C ova. Only rarely were Stage D ova encountered in the maomao.

Clark (1925) was able to demonstrate that the grunion, Leuresthes tenuis, spawned on a two week cycle throughout the spawning season by following the progression of modes of egg diameters. She happened to encounter a very special situation in which all of the fish spawned within a day or two of the bimonthly spring tides. Examining the length frequency distribution of ova diameters of the maomao with a similar objective in mind, failed to produce any conclusive results. This was probably due to the small size of the samples, the irregularity of the sampling, and the fact that the maomao spawn almost continuously throughout the year, although they appear to favor certain seasons and certain periods during the lunar month.

Fecundity

The fecundity of a female fish is defined as the number of eggs spawned by that individual in one year. This figure is easily estimated in a species that spawns but once a year. However, in the maomao, multiple spawnings in one year are indicated by the modes of egg diameters, and therefore an estimate of fecundity is possible only if the number and magnitude of individual spawnings can be observed. This was never possible during the investigation of maomao reproduction, and the only estimate obtained was for the number of eggs released in a single spawning.

The method utilized for estimating the number of eggs in a single spawning was that of Tester (1951: 93). Following this method, ovaries were removed from the fish, blotted dry, and weighed to the nearest 0.002 grams. A small piece of the ovary, including the germinative tissue and ovarian wall, was removed and weighed, and the number of Stage C (ripe or nearly ripe) eggs were counted. This allowed the calculation of the number of Stage C eggs in the entire ovary by a simple ratio. The ovaries chosen for this analysis were those classified as

Stage 4 according to the classification previously described, and in addition they weighed more than 2 percent of the body weight of the fish from which they were removed.

The results of the analysis of eleven specimens is presented in Table 6, indicating that between 9,400 and 41,700 ova (with an average of 21,400 ova) are spawned at one time by the maomao.

In order to see if a relationship between fecundity and the size of the fish existed, fish were chosen with lengths ranging from 119 to 169 mm. A significant correlation did exist between the estimated number of eggs spawned at one time and the standard length of the fish, despite considerable variation ($r = 0.625$, P less than 0.05). The cause of this variability in the number of ripe ova is not evident at this time; however, fecundity often varies with age as well as food and other environmental conditions, which were unknown quantities in the specimens analyzed.

In regard to fecundity in fishes, it has been pointed out that a relationship exists between the mode of reproduction of different species and their fecundity. According to Hoar (in Brown, 1957), viviparous species and species exhibiting parental care produce fewer eggs than those which spawn pelagic eggs and leave them unattended. The fecundity of only a few local reef fishes has been estimated and in most cases it consists of the number of eggs in a single spawning. Among the pelagic spawners, Tester and Takata (1953) found that the aholehole (_Kuhlia sandvicensis_) varied considerably but averaged about 100,000 eggs per spawning, while Randall (MS.) from a single determination estimated that the number of eggs spawned at one time by the manini (_Acanthurus sandvicensis_) was about 40,000. Among the substrate spawners that guard their eggs, Strasburg (MS.) estimated that a

TABLE 6

ESTIMATED NUMBER OF RIPE OR NEARLY RIPE EGGS IN MAOMAO TAKEN FROM COMMERCIAL TRAP CATCH

Captured	Standard Length (mm.)	Est. No. of Eggs (Thousands)	Gonad Wgt. as Percentage of Body Weight
6/10/55	119	9.4	2.2
7/23/54	124	11.1	8.5
5/27/55	128	24.5	6.2
7/8/55	132	25.9	6.1
5/4/55	136	12.8	4.4
1/17/55	142	18.7	6.1
1/17/55	145	16.5	12.2
2/22/55	146	18.9	8.2
4/15/55	158	33.6	11.2
6/10/55	163	41.7	15.5
3/29/55	169	21.9	6.4
	Average	21.4	

blenny, *Istiblennius zebra*, produced a little over 10,000 eggs in a single spawning. If we consider, a priori, that the number of eggs in a single spawning reflects the total fecundity, these examples generally follow the originally stated relationship.

Among the pomacentrids, a number of observations have been made on individual spawnings, and a few determinations of actual fecundity are given. One of the most fecund of the pomacentrids appears to be *Dascyllus trimaculatus* (Rüppell). Garnaud (1957) counted 21,809 eggs in a nest and stated that the number varies between about 20,000 and 25,000 eggs per spawning. Between September 1956 and April 1957 a record of 17 spawnings was made, and although not mentioned in his paper, the author stated in personal correspondence that this was the continuous record of a single pair of fish. From this it might be concluded that the fecundity of *D. trimaculatus* is in the order of 350 - 400,000 eggs. Garnaud (1951) found that two female *Amphiprion percula* (Lacepede) averaged about 880 eggs per spawning; however, considerable variation existed in the number of eggs between spawnings. Each of these females was observed to spawn at least 10 times in one season in an aquarium. The number of eggs in a single spawning by one female ranged from 351 to 1,497, and by the second female from 283 to 1,432 eggs. The author states that these spawnings occurred from late February through August, and he implies that the summer spawnings produced more eggs than the earlier ones. Verwey (1930a) working with *A. percula* in Batavia was in disagreement with Garnaud (op. cit.) on the number of eggs spawned by this species in a single brood. Verwey states that the brood consisted of about 200 to 300 eggs, and since the interval between spawnings is from seven to fourteen days with a rest period during the shifts in the monsoons, he concludes that the fecundity of this species is about 5,000. Verwey (op. cit.) also observed three broods of eggs spawned by Amphiprion ephippium (Bloch), and found that the brood size was about the same as that of A. percula. Brinley (1939) states that another small pomacentrid, the beau gregory, (Pomacentrus leucostictus) deposits its eggs in old conch shells, "in closely packed clusters of several hundred." Observations on Pomacentrus leucoris Gilbert by Breder (1932), and Breder and Coates (1933) revealed that this species spawned an estimated 400 to 500 eggs per spawning while held in captivity in the New York Aquarium.

Although fragmentary, these reports suggest that the pomacentrids tend to spawn a relatively small number of eggs at frequent intervals throughout the spawning season, which may be quite lengthy. Since the number of eggs spawned varies with the size of the fish as well as environmental and physiological conditions, it seems futile to speculate further on the maomao fecundity until more information is available.

Nature of the Spawning Cycle

The nature of the maomao spawning cycle was investigated from a number of aspects, including the timing in the maturation of the gonads, the frequency with which new clutches of eggs were deposited, the length frequency distribution of juveniles migrating into tide pools, and the effects of various elements in the physical environment. Each of these aspects contributed information that was utilized to establish a general pattern of spawning throughout the year. Most of the observations made conformed closely to this pattern, even though the data were often derived from different areas and years.

Gonad maturity as an index of spawning has already been reviewed and illustrated in Figure 4, revealing continuous spawning throughout the year with a definite period of increased reproductive activity, or "breeding season" starting about mid-December or early January and continuing through July.

In an attempt to relate spawning activity with factors in the physical environment, temperature fluctuations during the breeding season were first investigated. Orton (1920) discusses the importance of temperature in the breeding of marine animals, and points out that under normal conditions animals initiate breeding at a definite temperature, which is a physiological constant for the species, or at a definite temperature change, which may be the maximum or minimum for the area in question. These phenomena may apply to the breeding season of the maomao as they do for a number of fishes. According to the data presented by Leipper and Anderson (1950) on surface water temperatures from the Hawaiian Island area for a six year period, the lowest maximum and minimum temperatures were recorded from January through May, which generally coincides with the most active period of reproduction in the maomao as indicated by the relative gonad weight, the number of new broods observed, and the number of juveniles entering the tide pools for the four year period covered by this investigation. Also the sharpest drop in the minimum temperature recorded throughout the year is between October and November, which coincides with the apparent low ebb in spawning activity of the maomao. Thus it appears as though maomao favor colder water for spawning, and that a marked drop in water temperature may initiate spawning in December or January. A similar trend toward spawning during the spring and early summer when water temperatures are lowest has been observed in other local reef fishes; i.e. Pomacentrus jenkinsi (Gosline, 1957), Acanthurus sandvicensis (Randall, MS.), Kuhlia sandvicensis (Tester and Takata, 1953), Istiblennius zebra, and Entromacrodus marmoratus (Strasburg, MS.).

Observations on the number of new clutches or broods of eggs were made throughout a four year period revealing a spawning cycle of the same general configuration as that determined from plotting relative gonad weights (Figure 4). These observations were carried out in the Tuna Pond and Southwest Point spawning areas at Coconut Island (see Figure 1), and although the number of clutches observed was relatively small, some revealing short term fluctuations were encountered during periods of peak spawning. These fluctuations indicated a lunar periodicity in spawning.

Numerous reports of lunar associated periodicity in reproduction of animals and plants are found in the literature, and reviews are presented by Fox (1923), Amirthalingam (1928), and Battle (1930). Twenty-five cases of organisms reported to have displayed lunar periodicity in reproduction are cited by Battle (ibid.); five cases in the algae, and twenty animals, including eleven polychaetes, five molluscans, and one species of fish. These fluctuations in spawning take very different forms as in three species of polychaetes which display bilunar periodicity in reproduction, spawning on the full and new moon, and in the case of the oyster, Enchelyopus cimbrius in which spawning goes on continuously during the breeding season, reaching a maximum during the spring tides at full and new moon. After investigating spawning in this oyster, Battle (ibid) concluded that the periodicity is not due to light, but to rhythmic effects of the alternating spring and neap tides which produce a similar rhythm in the spawning of this species. Other factors may act to assist in producing this rhythm, such as salinity at successive high and low tides, variation in the food available to the adult, and temperature variation. Amirthalingham (op. cit.) who investigated a lunar periodicity in the reproduction of Pecten opercularis did not attribute this phenomenon to tidal effects, food, or direct light of the moon individually, but thought that the cumulative effect of these factors might be responsible for the periodic spawning. He further suggests that in an animal there is a physiological rhythm that causes the development of the gonads to coincide with the full moon each month. Fox (op. cit.) investigated lunar periodicity in spawning of the sea urchin Centrechinus (Diadema) setosus at Suez and discounted hydrostatic pressure as a cause of spawning on the full moon, as the greatest tidal change at Suez is during the new moon and not the full moon. He concluded that periodicity is probably associated with the actual light of the moon, and perhaps changes in the chemical composition of the water which changes with the flushing accompanying spring tides.

One of the best known samples of spawning periodicity among the fishes is that reported for the grunion, Leuresthes tenuis by Thompson and Thompson (1919). They showed that these fish come in to spawn in the beach sand on high tides during the second, third, and fourth nights after the full moons of March to August. Clark (1925) pointed out that this spawning run takes place every two weeks instead of every four as as the Thompsons had concluded. This bilunar periodicity is associated with the spring tides that occur at the time of the full and new moon. According to both the Thompsons and Clark, the tides and not the phase of the moon, or moonlight per se, constitute the limiting factor on which the spawning fish depends, as spawning takes place even during periods of heavy overcast when moonlight is excluded.

Tester and Takata (1953) show a periodicity in the recruitment of the aholehole, *Kuhlia sandvicensis*, with an increased percentage of smaller fish occurring approximately every thirty days around the time of full moon. They suggest that this increase is probably either associated with periodic spawning, or that the migration of the young fish into shallow water is somehow controlled so as to occur mainly at this time. Randall (MS.) also presents evidence that an increase in the spawning probably takes place around the time of full moon as shown by the increase of mature gonads at that time, as well as some evidence of the periodic influx of transforming juveniles into the tide pools.

Lunar periodicity in maomao spawning was most apparent in the records of new nests made during periods of maximum reproductive activity, and best illustrated during the peak of the spawning season from April to August, 1957. Since increased spawning was most evident around the time of full moon, (see Figure 6), it was expected that a linear relationship would probably exist if the number of new nests were plotted against their proximity to the full moon. Plotting these data and fitting a line of best fit by the method of least squares resulted in a line with practically no slope, and therefore almost zero regression of spawning frequency on the full moon, ($\hat{Y} = 1.5 + 0.0035x$).

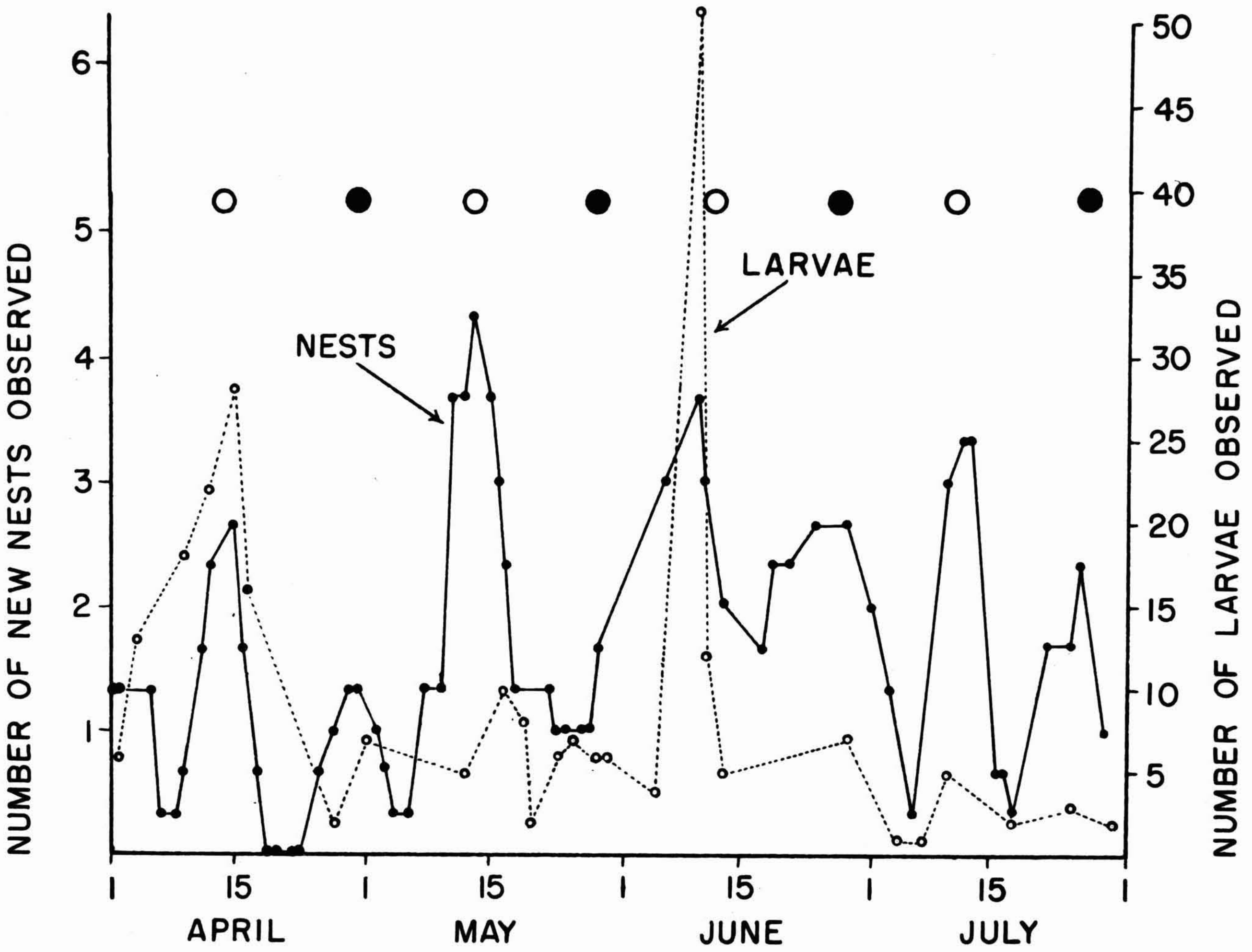


Figure 6. The frequency of new nests and larvae observed at Southwest Point, Coconut Island, in 1957. The solid line represents the number of new nests observed, and the broken line represents the number of larvae between 8 and 12 mm. (total length) observed in the same area. The curve for nests was smoothed by plotting a running average of three. The time of full moon is indicated by open circles, and the time of the new moon by darkened circles.

These unexpected results led to a re-examination of these data which revealed secondary peaks of spawning activity coincident with periods around the time of new moon in addition to those around the time of full moon (see Figure 6). An analysis of the data shown in Figure 6 is presented in Table 7 below, in order to further illustrate these relationships.

TABLE 7

THE FREQUENCY OF MAOMAO SPAWNING AS INDICATED BY THE NUMBER OF NEW BROODS OBSERVED IN THE SOUTHWEST POINT SPAWNING AREA DURING FOUR MONTHS OF 1957

Month	Major peak of spawning			Secondary peak of spawning		
	Date	Days to nearest full moon	Days from last major peak	Date	Days to nearest new moon	Days from last secondary peak
April	15	+ 1	-	29	0	-
May	14	+ 1	29	-*	-*	-*
June	10	- 2	27	26	- 1	58
July	12	+ 1	32	26	- 1	30
Average		+ 0.3	29.3		- 1	29.3**

* June secondary peak not distinct.

** Average of three months.

The total new broods observed (within three and one half days of a given moon phase) in each month for the new and full moon phases, and similar data for new broods in the first and last quarter were plotted and shown in Figure 7. This figure illustrates a marked increase of new

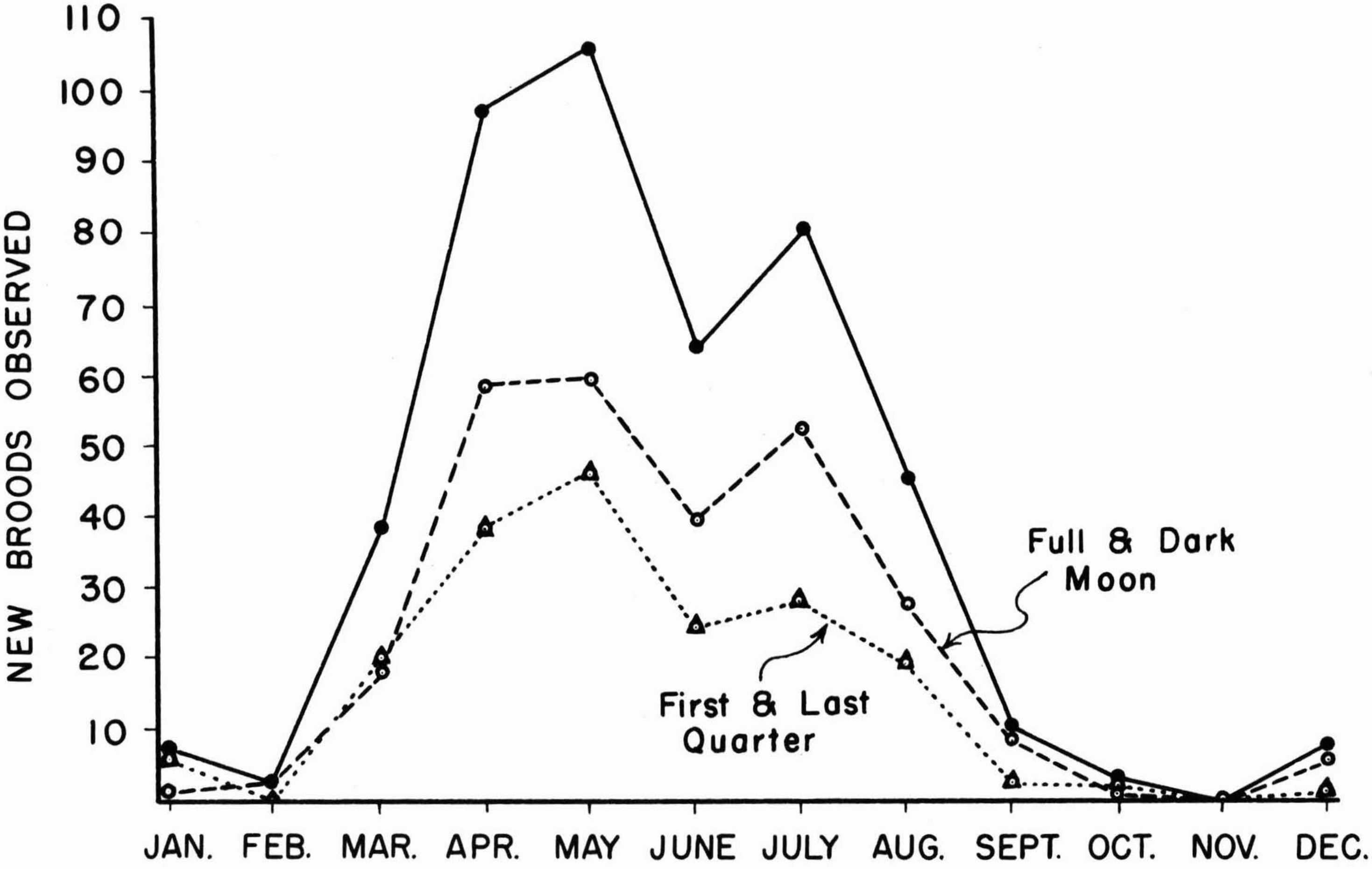


Figure 7. The number of new broods observed as an indication of the number of maomao spawning in spawning areas at Coconut Island during each month over a four year period. (1954 to 1957 inclusive) —●— indicates the total new broods observed during the four year period; --o-- indicates the number of new broods observed during periods around the full and dark of the moon; ····△···· indicates the number of new broods observed around the first and last quarter moon phases.

broods during the full and new moon phases except in months when spawnings were infrequent. A chi-square test revealed that the ratio of new broods observed during the pooled full and new moon phases to the pooled first and last quarter phases was significantly different from the 50:50 ratio (Chi-square value = 15.8, d.f. 1, $p = < 0.01$).

Lunar periodicity in maomao spawning did not become apparent until the data were carefully analyzed after most of the observations had been made in 1957, and therefore little was done to determine causal relationships. From the literature cited, it is apparent that in most animals that exhibit lunar periodicity in spawning the causes and mechanisms of these phenomena are not clear. However, most authors suggest that they are not simple, and are believed to be caused by multiple factors which may include light intensity, temperature, hydrostatic pressure, currents, changes in the chemical composition of the water, changes in the abundance of food, etc. Since maomao spawning continues throughout the lunar month and is only accentuated during periods of the full and new moon phases, it is suggested that the regular stimulus for initiating spawning is merely accentuated or augmented by some bilunar associated factor. It should be pointed out that these observations on the frequency of spawning were all made in shallow water, and such regular fluctuations may not occur among deep water spawners.

Further evidence of periodicity of reproductive activity is found in the length frequency distribution of juvenile maomao entering the tide pools, (see Figure 22). Although the relationship is erratic in smaller samples, during periods when large samples were regularly obtained, the smallest sized juveniles were most conspicuous about the time of full moon. Since the data indicate but one peak per month, this may be a phenomenon of juvenile migrations associated with a phase of the moon and therefore not directly a reflection of the periodic spawning.

Nests

The nests in which clutches or broods of maomao eggs are attached usually consist of prepared areas on hard substrates such as rock, coral, or concrete which is uncluttered by larger attached organisms. Other requirements of such an area are discussed in detail in the section on spawning behavior. The shape of the deposited egg mass depends largely on the shape of the available suitable area; however, if the chosen area is larger than required to accommodate the brood, the egg mass is usually circular. Since multiple spawnings take place on a single site, eggs added to an already existing circular clutch are deposited as a crescent shaped mass along 100 to 180 degrees of the periphery resulting in an elliptical clutch. Hatching of the initially spawned eggs therefore often leaves a crescent hollow circle of eggs.

The density of eggs deposited in the nests was determined by examining clutches that had been attached to concrete spawning slabs in the spawning areas at Coconut Island. These clutches were brought into the laboratory and examined with the aid of a binocular microscope, and the density of attached eggs was determined in a number of locations chosen at random on each slab. Thirteen such determinations from four separate clutches revealed an average density of 1.2 eggs per square millimeter, with a range from 0.96 to 1.60 eggs per square millimeter.

Estimates of the total number of eggs deposited in twenty-nine nests were made by measuring the dimensions of the egg mass, and using an average density of 1.2 eggs per square millimeter with the appropriate mathematical formulae for determining the area of the particular nest in question. In the case of irregular clutches, various measurements were taken and a scale drawing was made on a piece of grid paper. The area was determined by graphical integration of this drawing. Estimates of the areas and number of eggs are presented in Table 8. The average number of eggs in a single nest was 56,800, with a range from 10.1 to 116.9 thousand eggs.

Many of these nests had two distinct clutches of eggs at different stages of development, and as many as five well defined clutches have been observed in a single nest, each identified by a coloration characteristic of a different stage of development. It is unlikely that a single female spawns all of the eggs in nests containing multiple clutches, as these clutches may contain eggs with different colored yolk, whereas the yolk color of ovarian eggs is always homogeneous in a single female maomao.

OVA

Description of Ova

The ova of maomao are not unlike those of most marine teleost fishes in that they are mesolecithal and display teloblastic or incomplete cleavage. The animal pole, which is apparently always found at the larger, attached end of the ovum is identified prior to cleavage by a narrow white area on the surface of the yolk adjacent to the attachment structure.

When released, the larger half of the roughly elliptical ovum is enclosed in an opaque adhesive membrane cap utilized for its attachment

TABLE 8

SIZE AND CONTENTS OF TWENTY-NINE MAOMAO NESTS OBSERVED IN SPAWNING AREAS AT COCONUT ISLAND

Number	Date	Area (Sq. In.)	Area (Sq. Cm.)	Total Eggs (Thousands)
1	2/20/54	151	974	116.9
2	2/20/54	50	322	38.7
3	3/6/54	113	729	87.5
4	3/13/54	141	909	109.2
5	3/20/54	113	729	87.5
6	4/10/54	177	1141	137.0
7	4/12/54	42	271	32.5
8	4/17/54	49	316	37.9
9	4/24/54	75	484	58.1
10	6/18/54	13	84	10.1
11	7/7/54	77	497	59.6
12	7/20/54	23	148	17.8
13	9/1/54	31	200	24.0
14	5/6/55	44	284	34.1
15	5/6/55	113	729	87.5
16	6/9/55	94	606	72.7
17	8/3/55	72	467	56.0
18	4/28/56	113	729	87.5
19	4/30/57	67	433	52.0
20	5/2/57	47	300	36.0
21	5/14/57	65	419	50.3
22	5/20/57	28	181	21.7
23	5/21/57	90	581	69.7
24	5/21/57	31	200	24.0
25	5/21/57	63	407	48.8
26	5/25/57	69	445	53.4
27	5/25/57	48	310	37.1
28	7/13/57	40	258	30.9
29	8/1/57	88	567	68.1
	Average	73	473	56.8

to the substrate (see Figure 5). The adhesive properties of this membrane are specific in that it does not adhere to other maomao eggs, but adheres strongly to every other substance tested including glass, metal, coral, and even to the scales of the maomao itself. This adhesive membrane cap is attached to the egg at the animal pole, and its inner surface (surface in contact with the chorion) is non-adhesive, while the outer surface is highly adhesive. On release of the ovum into the water the adhesive membrane cap strongly adheres at the first point of contact with the substrate and subsequent turbulence of the water causes the ovum to sway to and fro in various planes resulting in the attachment of a large area of the adhesive surface of the cap. Eventually the cap is completely inverted and anchors the egg with a skirt-like attachment. When anchoring the egg in place, this membrane is 0.1 to 0.2 millimeters long and expands to cover a surface about 0.65 square millimeters. When viewed in an egg mass in nature, the attachment membranes of all of the eggs seem to be contiguous as was reported by Breder and Coates (1933) for the eggs of Pomacentrus leucoris; however, in the genus Amphiprion all membranes are distinct and separated from each other (Gohar, 1948). Garnaud (1957) reports that the female Dascyllus trimaculatus deposits an adhesive substance to form a basal network or foundation to which the attachment membrane of the ova stick. It appears as though this type of basal network is unnecessary in the case of the maomao, as the adhesive membrane alone anchors the egg with such tenacity that it is very difficult to remove it from the substrate. The specific nature of the adhesive on these membranes appears to have a definite value in insuring the proper distribution of maomao eggs in the nest. Since the eggs fail to stick to each other, the female is not required to place her genital papilla or ovipositor precisely in a vacant spot on the substrate when spawning but may express her eggs in the vicinity of open areas without danger of piling upon one another. This unique property of the adhesive membrane, plus possible tactile receptors located in the ovipositor, appears to be instrumental in insuring even distribution of the ova on the substrate and thus attaining proper spacing for efficient aeration and a maximum utilization of the prepared area.

The fertilized maomao egg is similar to other pomacentrid eggs that have been described. The yolk appears evenly distributed throughout the mature ovarian egg; however, upon spawning and fertilization the yolk contracts and becomes more dense, and a large fluid filled perivitelline space separates it from the chorion at the distal end or end opposite the point of attachment. The chorion is smooth, colorless, and transparent, and lacks any longitudinal striae such as those observed in the eggs of <u>Pomacentrus leucoris</u> by Breder and Coates (1933). The dimensions of 38 maomao eggs in various stages of development showed the average length was 1.29 millimeters, with the range between 1.17 and 1.40 millimeters. The maximum width was 0.67 mm. and the minimum was 0.62 mm. with an average of 0.66 mm. The egg size did not change noticeably during development. The yolk usually contains a single large oil globule about 0.2 mm. in diameter, two or three secondary oil droplets of 0.05 to 0.10 mm., and a variable number of fine droplets smaller than 0.05 mm. The proximal end of the yolk mass, or end nearest the attachment membrane, is capped with a thin, whitish layer of cytoplasm which appears to extend distally a short distance over the yolk mass. Actually a thin layer of cytoplasm covers the entire yolk mass but a heavier concentration at the animal pole makes it visible at that point. After fertilization a flow of this protoplasm toward the animal pole creates a more conspicuous telolecithal egg (Nelson, 1953: 249).

The color of the yolk usually is a light red or pink; however, in a few cases, maomao eggs with a yellow yolk have been observed. Orton (1955) has investigated variation in the color of marine fish eggs and suggests that diet may be an important factor in yolk coloration. Besides diet, Orton (ibid.) points out that background color of a species may affect the color of the yolk. She discusses the eggs of the cabezon, Scorpaenichthys marmoratus (Ayres) which occur in three color phases, pink, green, and colorless. This same species of fish occurs in three phases; red, green, and occasionally white. However, the exact relationship between the adult color phases and the yolk color of the eggs is not clear. The effect of diet on the carotenoid pigmentation of the pomacentrid fish Hypsypops rubicunda has been demonstrated; changes in the external pigmentation of this fish are closely associated with the carotene content of the food consumed (Kritzler, Fox, Hubbs, and Crane, 1950).

The yellow yolk in maomao eggs appears to be associated with only one of the areas observed and therefore some components of the food consumed in that area may cause this variation in yolk color. Yellow eggs were only observed in nests at Coconut Island and were never seen in the large number of ovaries examined from trap caught fish from other areas on Oahu. If constituents of the diet caused this color variation in the maomao eggs, their consumption appears to be infrequent as only a small percentage of the Coconut Island clutches observed were of the yellow color phase. Better understanding of this phenomenon requires isolation of the pigment responsible for this coloration and its possible relationship to metabolic processes and food consumed by maomao possessing ova of this color.

Stages of Development

The development of the maomao is very similar to that described for other pomacentrids, including *Amphiprion percula* (Lacepede) by Delsman (1930), *Chromis chromis* (Gunther) by De Gaetani (1932), *Pomacentrus leucostictus* Muller & Troschel by Brinley (1939), and *Abudefduf saxatilis* (Linnaeus) by Shaw (1955). Shaw (ibid.) found that the eggs of *A. saxatilis* hatch in about 6½ days after fertilization at a temperature of 24 degrees C. As the maomao is considered to be a close relative of *A. saxatilis*, it was not surprising to find that the development of these two species followed an almost identical pattern. The maomao hatches about six days after fertilization within the temperature range of 22.5° to 25.5° C. with the average temperature of 24.5° C.

The following description of embryonic development is based primarily on observations of maomao ova naturally spawned and fertilized in the vicinity of the Hawaii Marine Laboratory, Coconut Island. Although the details of various stages of development were recorded from a number of different clutches of eggs, the time sequence of development was not revealed until actual spawning and fertilization were observed and the subsequent development followed closely. Since spawning took place in shallow water, a sample of eggs was scraped from the clutch immediately after fertilization, placed in a jar of fresh sea water, and taken into the laboratory where they were observed with the aid of a binocular microscope until hatching.

First Day

Cell division proceeds rapidly after fertilization. The chorion lifts away from the yolk after fertilization, and the yolk constricts somewhat assuming a more spherical shape. An accentuated perivitelline space results at the vegetal pole (distal end); however, this space is small or absent at the animal pole during early stages of development. The blastodisc, located proximally, begins to cleave, and the first and second cleavages are along the longitudinal axis at right angles to each other. Two hours after fertilization the so-called four cell stage is completely formed, (Figure 8A). The eight and sixteen cell stages follow in rapid succession. However, because of the opacity of the blastodisc, definition of the blastomeres is more difficult beyond the eight cell stage. As cleavage continues, a knob-like blastula forms on the yolk mass, but epibolic growth makes the separation of the two areas less and less distinct except for their relative transparency. By 6½ hours the blastomeres have extended almost to the equator of the yolk mass (Figure 8B). Observations at 16½ hours reveal that the protoplasm has advanced over more than half of the yolk mass, and gastrulation is well under way. At one point along the division line between the yolk plug and the blastula a definite convergence and involution is evident. This causes uneven epibolic advancement of the blastula, and results in the formation of a yolk plug consisting of about one third of the surface of the yolk mass,

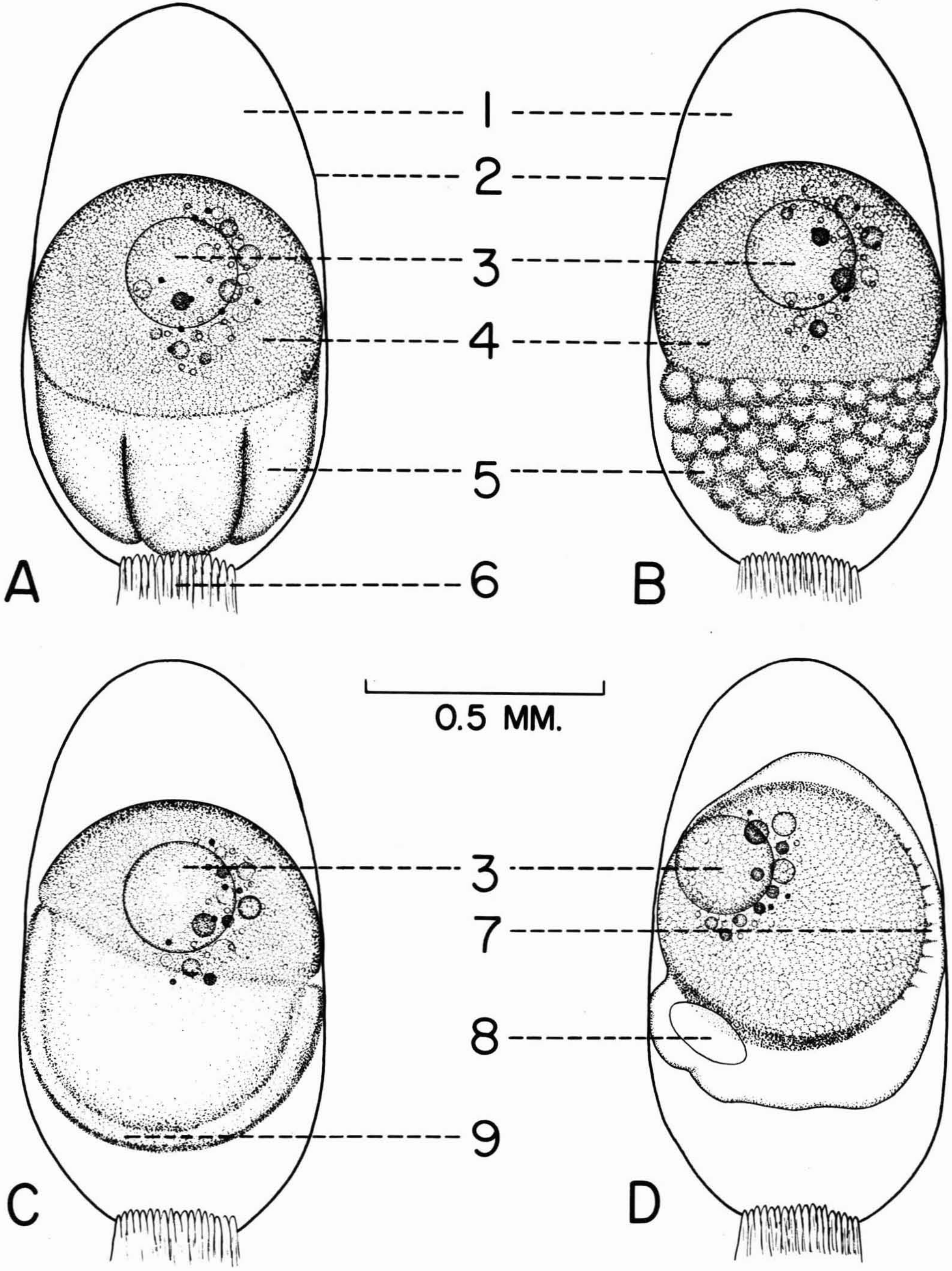


FIGURE 8. EARLY EMBRYOLOGICAL STAGES OF <u>ABUDEFDUF ABDOMINALIS</u>. A. 2 HOURS. B. 6.5 HOURS. C. 16 HOURS. D. 24 HOURS.

1. PERIVITALLINE SPACE. 2. CHORION. 3. OIL GLOBULE 4. YOLK. 5. BLASTOMERE. 6. ADHESIVE MEMBRANE. 7. SOMITE. 8. OPTIC VESICLE. 9. BLASTOCOEL.

(Figure 8C). About twenty hours after fertilization the advancing involuted shield has reached the original animal pole. A neural ridge develops from a thickening near the blastopore and advances distally. By twenty-four hours the yolk mass is completely covered by extra-embryonic membranes, the neural folds have joined, and the first signs of optic vesicles are visible in the cephalic region (Figure 8D).

Second Day

By twenty-eight hours the lens placodes of the eye have begun to form, twelve somites are present on the body, and the first signs of constrictions of the brain are noticeable. During the second day small stellate melanophores appear over the surface of the yolk sac, and along the ventral surface of the trunk and tail, which are now freed from the yolk sac. The optic cup and lens placode become clearly defined, and the choroid fissure gradually closes. The otic vesicle appears, and a marked constriction develops between the optic and otic vesicles separating the mesencephalon and rhombencephalon, while a lesser constriction forms to separate the prosencephalon anteriorly (Figure 9A). By the end of the second day the heart is seen beneath the head and feeble constrictions at the rate of about thirty-two per minute may be noted.

Third and Fourth Days

During this period the embryo continues to grow, primarily in length, and the size of the yolk continues to diminish.

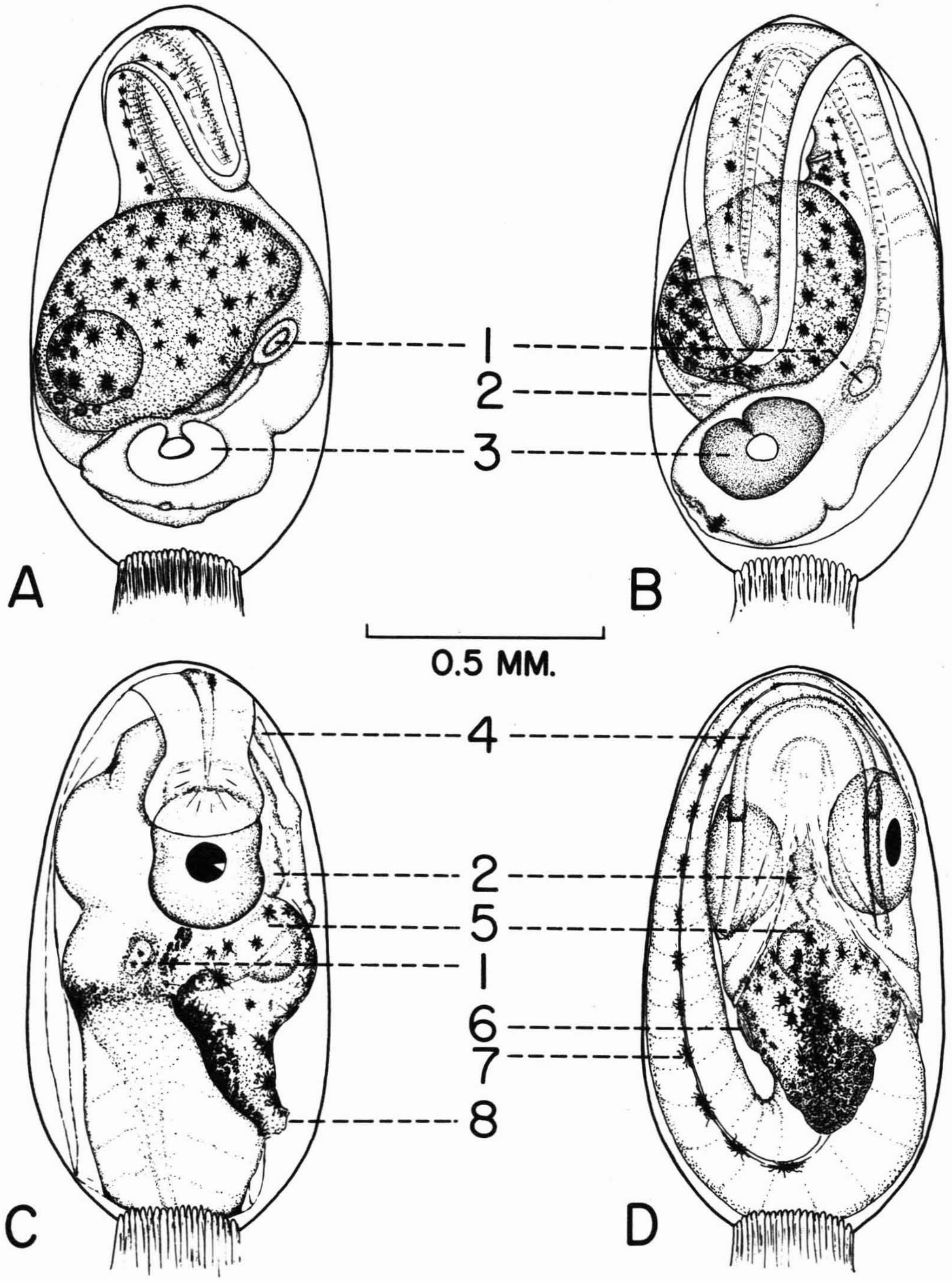


FIGURE 9. LATE EMBRYOLOGICAL STAGES OF ABUDEFDUF ABDOMINALIS. A. 40 HOURS. B. 65 HOURS. C. & D. 120 HOURS. 1. OTIC VESICLE. 2. HEART. 3. EYE. 4. LOWER JAW. 5. OIL GLOBULE. 6. PECTORAL FIN BUD. 7. TRUNK CHROMATOPHORE. 8. ANUS.

The tail becomes motile, doubles back on itself, and by the end of the fourth day lies along one side of the head. Retinal pigment begins to form in the eye by about sixty-five hours, and the choroid fissure is reduced to a small ventral indentation (Figure 9B). The heart enlarges and begins strong rhythmical contractions. The dorsal aorta, the vitelline artery, and other vessels of the vitelline plexus become visible and blood can be observed flowing through them. Most of the perivitelline space is filled with the rapidly growing embryo by the end of the fourth day.

Fifth Day

During the fifth day the embryo is capable of considerable movement within the chorion, and often rotates so that the head is at the distal end. A yellow pigmented area becomes visible during this period, dorsal and slightly anterior to the yolk sac in the area of the otic vesicle, and extending to the dorsal surface of the body. During the fifth day the embryo continues to grow, filling most of the remaining perivitelline space (Figure 9C & D). The tail, which had doubled back earlier, now reaches a point in the area of the snout, and doubles back again. The jaws have developed to a point where they display some motility, occasionally opening and closing slowly. The most noticeable change during the fifth day is in the eyes which have become solidly pigmented; the retina a jet black, and the iris has taken on a silvery iridescence.

In addition, the eyes have become mobile and are capable of slight twitching movements. The yolk sac has diminished to a fraction of its original size and a marked accumulation of chromatophores has taken place on its dorsal surface. The embryo still retains the ability to turn end to end within the crowded confines of the chorion, and usually does so when exposed to a bright light. At four days, twenty hours the heart has developed to a point where some convolution has taken place, and the rate is about 150 beats per minute. Blood is visible flowing through vessels in various parts of the vitelline plexus, and in the caudal artery and vein.

Sixth Day

Hatching takes place early on the sixth day with an average water temperature of 24.5° C.

Sources of Mortality

Excluding occasional cases of untimely invasions by large predators, mortality seems to be quite limited in these early stages of maomao development. Most clutches of eggs observed in the vicinity of Coconut Island passed through embryonic development with very little apparent mortality, resulting in the production of large numbers of larvae on hatching. Such was not the case with the clutches attached to concrete spawning slabs that were removed from parental care and brought into the laboratory for observation, or placed in the experimental rearing apparatus. In most of these cases the mortality was rapid and devastating.

The major sources of mortality in the developing ova determined during this investigation were:

(1) Predation

(2) Oxygen deficiency

(3) Invasion by microorganisms

(1) *Predation* - A large number of species have been observed devouring maomao eggs when the guardian maomao was frightened away, or otherwise removed from the vicinity of the clutch of eggs it had been protecting. These predators were primarily wrasses (Labridae), butterfly fish (Chaetodontidae), parrot fish (Scaridae), goat fish (Mullidae), and pomacentrids, including other maomao. Other groups were occasionally represented among these raiders. Among the most conspicuously present predators observed devouring maomao eggs in the Kaneohe Bay area were the labrid, *Thalassoma duperrey* (Quoy & Gaimard), and the butterfly fish, *Chaetodon miliaris* (Quoy & Gaimard).

Further evidence as to the source of predation on maomao eggs was gathered by personnel of the Division of Fish and Game, Board of Agriculture and Forestry, of the Territory of Hawaii, during ecological studies along the Waianae coast of Oahu. During the course of these investigations in the spring and summer of 1956 a number of species of fish were collected in the vicinity of extensive maomao nesting areas. Examination of the stomach contents of these fishes in some cases revealed that they had been feeding heavily on the nearby maomao eggs. Often the eggs were in the stomachs undamaged and could be identified without much difficulty. Of the fishes in the area sampled, those of the families Chaetodontidae and Mullidae contained maomao eggs in various quantities -- in some cases the stomachs were crammed with these eggs and little else. The chaetodons included *Hemitaurichthys zoster* (Bennett), *Chaetodon femblii* Bennett, *C. lunula* (Lacepede), *C. miliaris*

Quoy & Gaimard, *C. unimaculatus* Bloch, *Centropyge potteri* (Jordan & Metz), and *Heniochus acuminatus* (Linnaeus). The Mullidae included *Mulloidichthys auriflamma* (Forskal), and *Pseudupeneus pleurostigma* (Bennett).

In all observations of nests of maomao eggs in nature, a varying amount of harassment from potential predators is evident, often to the extent that the guardian fish is constantly rushing back and forth to drive off intruders. Just how some species are able to invade these guarded nests to feed extensively on the eggs, as their stomach contents indicate they do, is not well understood; however, certain activities of the guardian fish are such that the nest may be left unprotected for short periods of time, and thus vulnerable to invasion by predators. These activities are discussed in detail in the section on reproductive behavior. Regardless of how these eggs are obtained, it must be concluded from observations thus far that they are very attractive as a supplement to the normal diet of a large number of reef fishes.

(2) Oxygen deficiency - The oxygen requirements of the developing maomao embryo are such that circumstances resulting in a reduced supply, especially in the later stages of development, could contribute substantially to mortality.

The literature contains considerable evidence of the increasing oxygen requirements of developing embryos of fishes. Brachet (1950: 184, 268) discusses the respiratory metabolism of developing embryos and concludes that variations in oxygen consumption during early cleavage and later morphogenesis of the embryo are subject to various interpretations and controversy, although he admits, "Development is undoubtedly accompanied by a progressive increase in metabolism." Other workers, including Boyd (1928), and Philips (1940), have shown a progressive increase of oxygen uptake in fishes during embryonic development. Utilizing a Warburg Constant Volume Respirometer, Alender (unpublished notes) determined the rate of oxygen consumption for groups of developing maomao eggs between what he estimated to be the 10 and 120 hour stages based on the work of Shaw (1955) with <u>Abudefduf</u> <u>saxatilis</u>. His results showed an increasing rate of oxygen consumption with development, the 120 hour stage showing more than twice the consumption of the 10 hour stage.

As previously mentioned, clutches of eggs in advanced stages of development that were removed from the care of a guardian maomao to a nearby rearing apparatus where physical conditions were almost identical usually experienced high mortality within a short period of time. It was noted, however, that if these clutches were in an early stage of development and subjected to such a transfer, they survived for a much longer period of time. In the light of increasing oxygen requirements with development discussed above, it seemed likely that oxygen might be limiting in the case of the more mature embryos, although other factors such as an increased concentration of metabolites around the egg mass may have also contributed to the increased mortality.

In an initial attempt to determine some of the factors contributing to the mortality of developing maomao eggs, an experiment was set up in which various numbers of developing eggs at two stages of maturity were incubated in one gallon jars containing filtered sea water. This preliminary experiment involved twelve groups of eggs all incubated under the same conditions; eight groups at the ten hour stage, and four groups at the 80 hour stage of development. A marked difference was observed between the mortality of the 80 hour groups and the 10 hour groups, although there was little difference in the mortality between groups of the same age. During the first two days of incubation, an average mortality of 69 percent was encountered in the 80 hour groups, while the comparable mortality in the 10 hour groups was only 1 percent; however, the mortality in the 10 hour groups increased rapidly after the second day. Unfortunately oxygen determinations were not made during these trials, and further incubation experiments were all carried out in a specially constructed rearing apparatus which more closely approximated natural conditions. These results do indicate, however, that some factor associated with advanced stages of development causes increased mortality, and in the light of previous observations, including the work of Alender, op. cit., this limiting factor is very probably oxygen.

Further evidence of the increasing oxygen requirements of developing maomao embryos was observed indirectly in the behavior of the guardian maomao in the process of caring for broods in nature. During observations on the three-spined Stickleback, *Gasterosteus aculeatus*, Tinbergen (1953) found that increased oxygen requirements of the developing eggs were accompanied by increased ventilation of the clutch by the guardian male fish, and if eggs in an advanced stage of development were replaced by those in an early stage of development, the transfer was accompanied by a decrease in the guardian's fanning time. Such a behavioral reaction to oxygen requirements of developing maomao eggs by the parent guardian was investigated by means of field observations.

The process of fanning of the egg mass was a deliberate and distinct activity by the guardian male maomao, and its duration could be easily timed and distinguished from periods of other activity such as picking at the nest, feeding, chasing, etc. Some variation existed in the rate of movement of the fins during fanning depending on the state of excitement of the fish; however, it was usually relatively constant for a given fish throughout a period of observation. Therefore the hypothesis was tested that the length of time a guardian maomao spent fanning as a percentage of the total time observed, was correlated with the stage of development of the embryo.

Between April 30, and July 25, 1957, observations on fanning were made in the spawning areas at Coconut Island, and only in cases where there was no indication that the observer was seen by the fish during the period of observation was the data used, as the guardian's behavior pattern was greatly altered when the observer was seen. Also, only those guardian fish relatively free from harassment by invading predators were observed. The imposition of the above restrictions limited the number of valid observations considerably; however, the data, although limited in value due to its paucity, indicates a constant relationship (see Table 9). Estimates of the age of various clutches were based on daily records and accumulated data on color changes of nests at various stages of development, and except for observations on clutches the age of which was known exactly, the estimates of age are within twelve hours. Only those nests that contained single broods or broods of stages less than twelve hours apart were considered. The data as presented in Table 9 show an increase in fanning time with the age of the embryos, and when plotted with the oxygen requirements of maomao eggs (Figure 10), a close relationship is evident. Thus, the data indicate that the oxygen requirements of maomao eggs in

TABLE 9

RELATIVE TIME SPENT BY GUARDIAN MAOMAO

FANNING EGGS AT VARIOUS STAGES OF DEVELOPMENT

Date (1957)	Color of egg mass	Est. Age	Aver. time fanning (sec.)	No. of obs.	Aver. time other activities (sec.)	No. of obs.	Percentage of total time spent fanning
2 VII	Dk. Pink* Lt. Pink	10 hrs. 22 hrs.	8.8	6	24.8	4	26.2
6 V	Dk. Pink	-1 day	7.6	5	14.0	3	35.2
28 VI	Lt. Pink	1 day	9.4	7	10.8	6	46.5
13 VII	Lt. Pink	1 day	10.1	7	56.6	6	15.2
30 IV	Lt. Brown	3 days	17.4	7	22.6	7	43.5
17 V	Dk. Gray	3 days	5.2	6	13.2	5	28.3
20 V	Lt. Gray	4.5 days	16.8	6	10.0	5	62.7
25 VII	Lt. Gray	5 days	117.0	3	2.3	3	98.0

* A single nest containing two clutches of eggs with stages of development twelve hours apart.

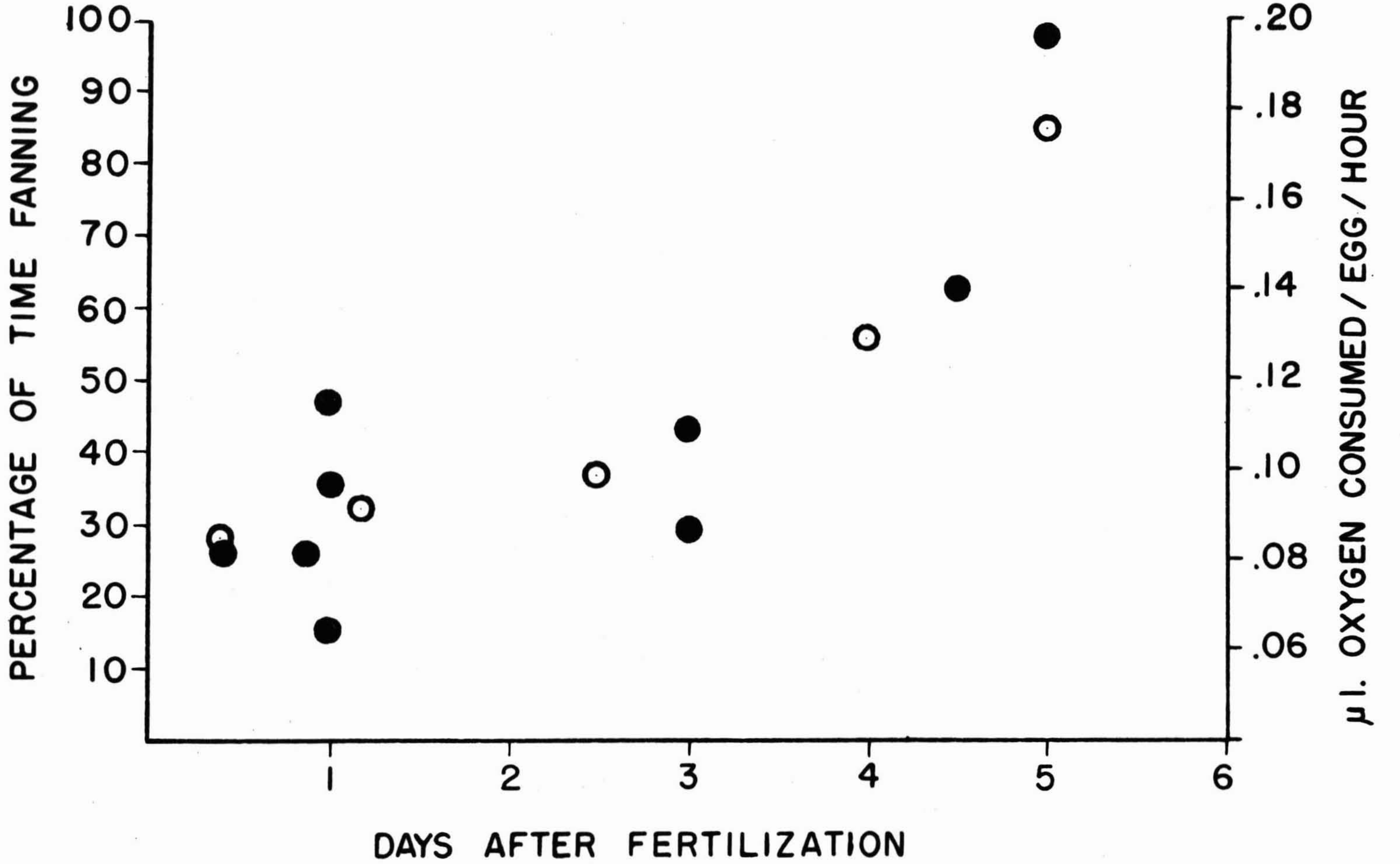


Figure 10. The percentage of time spent by guarding male maomao in fanning clutches of eggs at various stages of development, and the oxygen consumed per egg, per hour by maomao eggs during various stages of development. The darkened circles represent the average time spent fanning as a percentage of the total time observed, and the open circles represent oxygen consumed in microliters per egg, per hour. (After the unpublished work of Alender, 1956).

advanced stages of development are relatively high, and heavy mortality may result if the oxygen supply is interrupted at that time. Such interruptions may occur in cases where the guardian fish is so harassed by intruders in his territory that he has little time to ventilate his clutch of eggs, but it is not known if such interruptions are significant as sources of mortality in nature.

(3) Invasion of microorganisms - Both bacteria and protozoans rapidly invaded clutches of developing maomao eggs when they were removed from parental care, and often whole clutches would be killed within 48 hours after separation from their guardian. Even when concrete spawning slabs containing attached egg masses were brought into the laboratory and placed in a tank of circulating sea water, thus insuring an adequate oxygen supply, most of the eggs would be infected in a relatively short time. Thus, invasion by microorganisms may be a more important source of mortality than oxygen depletion, although interaction between these two sources probably exists.

ZoBell (1946: 61) cites a number of workers that point out the increased numbers of bacteria that occur close to shore in marine environments. ZoBell (ibid: 83-85, 193) further reports a tremendous increase in bacteria close to and on solid surfaces that he attributes to the concentration of nutrient material, the provision of surfaces for attachment for sessile bacteria, and a retarding of the diffusion of exoenzymes and partially digested food away from such areas. Oppenheimer (1955) investigating the effect of bacteria on developing fish eggs, reports that eggs incubated in running sea water accumulated large numbers of bacteria on their surfaces, and that numerous bacteria were found on later-stage fish eggs taken at sea. When first infected by microorganisms, developing maomao eggs viewed under magnification are characterized by an abundance of motile protozoans swarming over the surface of the egg; penetration of the chorion by microorganisms is evident. Soon penetration of the chorion takes place, the embryo dies, and the entire egg becomes opaque. The mechanism by which the chorion is initially penetrated is unknown, although the fact that 65 percent of all described marine bacteria are proteolytic (Zobell, op. cit.) suggests that it is probably due to bacterial action.

Viewed microscopically, infections begin at one or two loci on maomao egg mass and spread rapidly in all directions. In the center of infected areas a greyish slime covering, sometimes containing bright red blotches, forms about 48 hours after the first signs of infection. This slime, which is often associated with certain types of bacteria, and is characteristic of later stages of these infections, contains only a small fraction of the protozoans observed in earlier stages of infection. Such slime areas were sampled in four infected clutches of maomao eggs that had been moved into the laboratory at Coconut Island, and these samples were viewed with the aid of a phase contrast microscope. The dominant organisms seen were thin rods and spirogella; some motile cocci were also observed. No estimates of the abundance of these bacteria at various stages of infection of the egg mass was made.

Protozoans found to be more abundant in early stages of infection were also found in limited numbers in all clutches of maomao eggs examined, even those under parental care and displaying no signs of infection. Protozoans are found in the sea in great abundance as is evident from the remains of those which possess calcareous tests such as species of Foraminifera, and therefore they might be expected to be attracted to a rich source of organic matter such as a fish egg. Not a great deal of attention has been directed toward marine protozoans not possessing tests; however, Lackey (1936), in a survey of the Woods Hole area, found from 27,000 to 135,000 protozoans per liter of sea water. A general survey of the marine protozoans of Kaneohe Bay was not attempted, but samples of eggs were scraped from recently infected maomao nests around Coconut Island, and the protozoan population observed. The eggs in these samples were broken up and the contents of the perivitelline space of several eggs heavily infected with protozoans were pipetted off. Part of the contents of ten randomly chosen infected eggs was sampled from each of three clutches, and all of the material drawn off was combined and thoroughly mixed. A few drops of this combined sample was placed on a clean glass slide in a ring of methocel, and a cover slip placed over the preparation. Four such preparations were viewed with the aid of a compound microscope by being moved back and forth in a regular pattern on the stage, and the dominant organisms were counted, sketched, and an attempt was made at identification. The four most frequently observed protozoans are shown in Figure 11. Attempts to make permanent preparations of these organisms were not successful, and therefore exact identification by specialists with these groups was not possible. With the aid of the keys of Kudo (1954) identification was carried as far as possible.

Three ciliates and three flagellates were observed, as well as a seventh protozoan, thought to be a flagellate because its swimming motion was characteristic of this group. Following the classification of Kudo (op. cit.), and illustrated in Figure 11, A and B fit into the class Mastigophora, and since they seem to lack chromatophores they should be

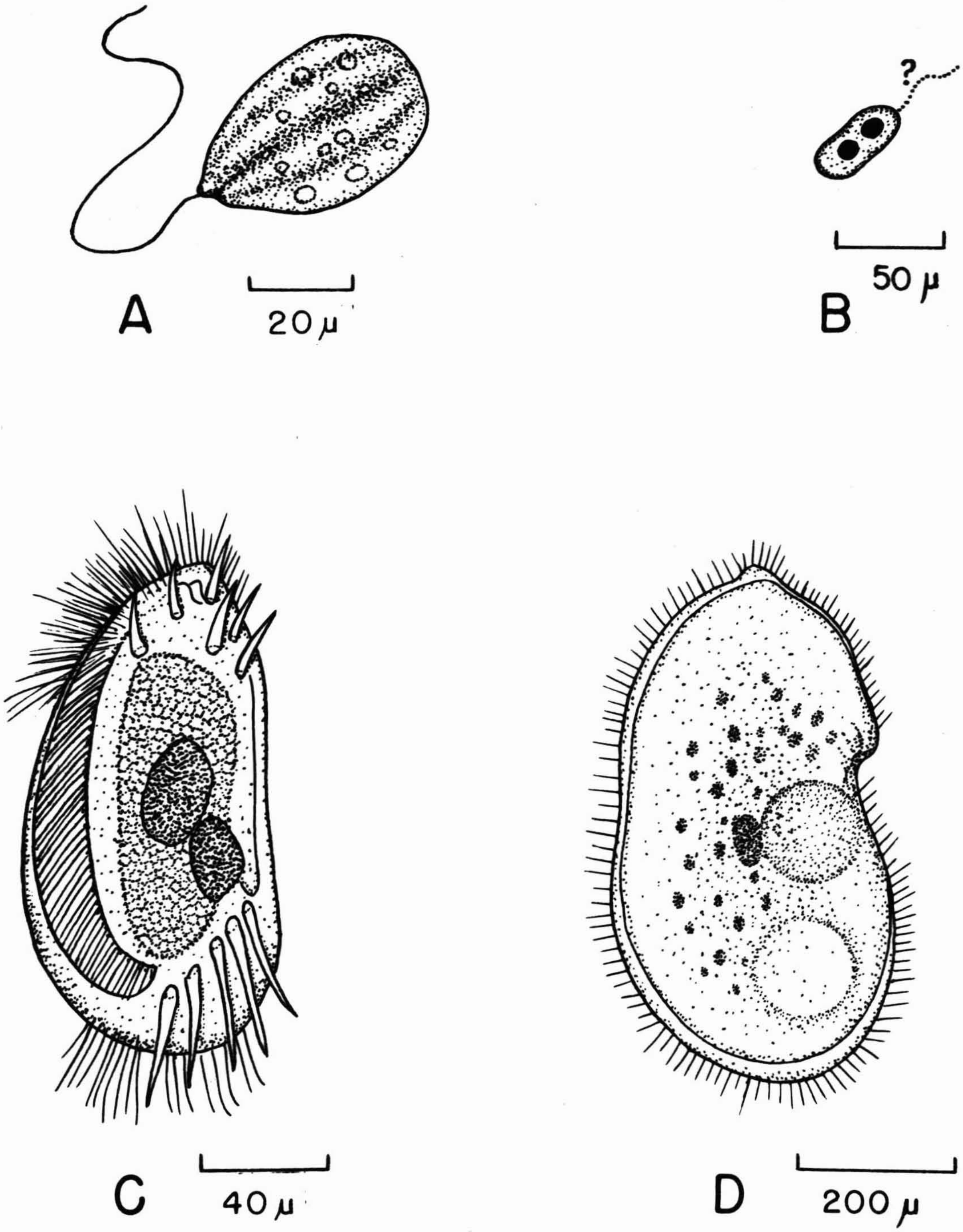


Figure 11. The four most frequently observed protozoans found in random samples taken from clutches of developing maomao eggs. A and B are Zoomastigina of the class Mastigophora, C is in the family Oxytrichidae of the class Ciliata, and D is an unidentified ciliate.

placed in the subclass Zoomastigina. A is slightly pointed at the anterior end, has a single flagellum of greater length than the body, and the pellicle forms six longitudinal ridges. Although B was common in the samples, it could not be satisfactorily examined under high magnification because of a failure to check its rapid swimming. The two nearly identical nuclei in B might lead one to believe that it was in the process of fission; however, this is improbable since all of the individuals seen had identical structures. The flagellum in B was never seen clearly, and therefore its length was not accurately determined. C and D represent the class Ciliata, which were not as common in these samples as the flagellates. C is dorso-ventrally flattened with six oral and five anal cirri, placing it in the order Spirotricha, and family Oxytrichidae. D is a blunt ciliate containing large vacuoles and a single nucleus, and the swimming motion is similar to that of the common *Paramecium caudatum*.

In the four preparations observed, representing a random sample of individuals taken from three clutches, A made up 27 percent of the total, B 23 percent, C 21 percent, and D 14 percent. Each of the three remaining species made up about 5 percent of the sample observed.

In summary, predation on developing maomao eggs takes place, and in some cases whole clutches may be devastated; however, this is believed to be an uncommon occurrence. Normally, the guardian maomao allows very little intrusion by predators into its territory, and only when its position becomes untenable, due to the invasion of such large intruders as sharks or humans, has one been observed to abandon its clutch, allowing more brazen species a brief period in which to consume the eggs.

Other sources of mortality appear to be due to oxygen deficiency and invasion of the developing eggs by microorganisms, especially during later stages of development. An interaction may exist between these latter sources of mortality, since both the oxygen requirements of the embryos and the number of microorganisms increase with time, and the greatly increased populations of bacteria and protozoa on the surface of the eggs may consume enough of the available oxygen to cause suffocation of the embryos. In an attempt to counteract this, the guardian maomao increases ventilation of the clutch during its later stages of development.

Estimate of Mortality

Estimates of mortality of the maomao prior to hatching were made indirectly by observing naturally spawned clutches of eggs at periods throughout incubation. It was noted that the guardian maomao, while caring for clutches of eggs in their natural habitat, would periodically inspect the egg mass at close range and occasionally pick off eggs, which were assumed to be dead or unfertilized. Since dead eggs appear to be the centers from which adjacent eggs are infected, their prompt removal helps to control the spread of infection. This picking of other than healthy eggs from the nest has been observed in other pomacentrids. Breder and Coates (1933) point out that with Pomacentrus leucoris both parents may care for the brood, and the fish in attendance will occasionally pick defective eggs from the clutch. Garnaud (1957) also describes this activity for Dascyllus trimaculatus, and he concludes that such care is essential for the survival of the brood.

In estimating the mortality of developing maomao eggs in nature, the irregular bare areas which formerly contained eggs were considered to have contained eggs which were defective and picked off by the guardian fish, or consumed by predators. Therefore, the ratio of bare area with the original limits of the egg mass to the total area of the clutch represents mortality prior to hatching. On the basis of observations of over fifty clutches it can be stated that the average mortality prior to hatching is very low (somewhat less than 10 percent) and never exceeded 30 percent.

LARVAE

Terminology

In this discussion of larval forms of the maomao the terminology of Hubbs (1943) is used throughout. Although the newly hatched form in the maomao is quite unlike the adult, no distinct larval form can be said to exist, as no abrupt transformation to the adult takes place. Rather there is merely a gradual change in appearance from the newly hatched, nearly transparent larva of about 2.7 mm. in length to the juvenile of about 12 mm. (fork length) which has all of the characteristics of the adult. Therefore, the term "larvae" will be used to define all developmental stages between the time of hatching until the vertical bands are clearly visible on the body. Hubbs (ibid.) refers to the terms "prolarva" and "postlarva" as divisions of the term "larva" before and after complete yolk absorption. Since it is difficult to determine exactly when the yolk is completely absorbed in this species, these divisions will not be utilized in this discussion.

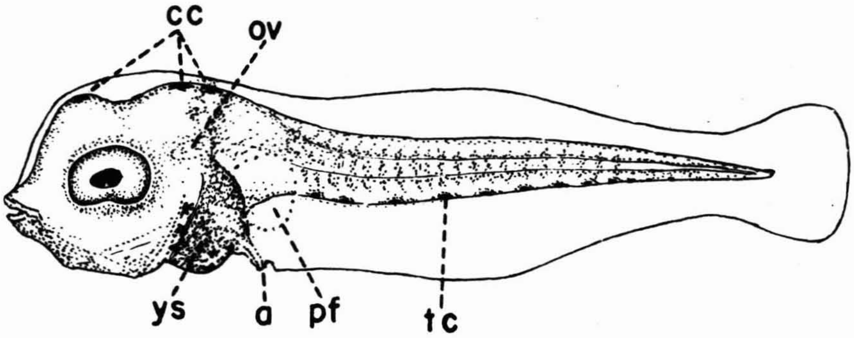
Description of Larval Stages

(1) Newly hatched larva (Figure 12A) - The newly hatched maomao has a blunt, opaque head, and a long transparent body surrounded by a continuous

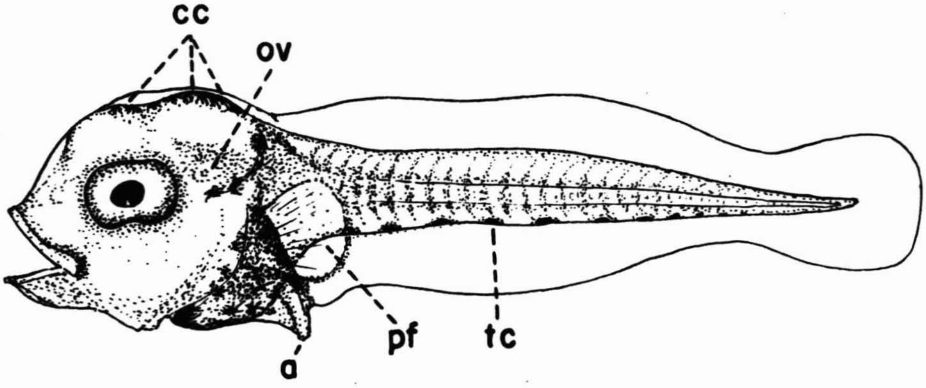
fin fold. A dorsal constriction dividing the prosencephalon and mesencephalon is quite pronounced. At least one and sometimes two stellate chromatophores are found on the dorsal surface of the forebrain in a region above the anterior border of the eye, and a group of three or more are found on the dorsal surface of the mesencephalon above the yolk sac. This arrangement of chromatophores is very similar to that described for Heliastes chromis (= Chromis chromis) by De Gaetani (1932), which is the only other descriptive work on pomacentrid larval forms in sufficient detail to allow such comparisons.

In this stage, the maomao eye is still irregular with a ventral indentation marking the old choroid fissure. The otic vesicle is still visible posterior and dorsal to the eye, and contains two round otoliths. The yolk sac and visceral organs occupy an opaque, triangular area which has its apex just ventral to the posterior border of the otic vesicle. Most of the surface of the coelom is covered by a silvery, iridescent membrane, and its postero-dorsal portion is heavily pigmented with chromatophores, with a few stellate chromatophores scattered over the anterior and ventral regions. Between 11 and 15 well defined chromatophores are found regularly spaced along the ventral profile of the trunk, extending posteriorly to the region of the fin fold constriction. This row of chromatophores proved of value in the identification of early larval stages of the maomao (up through the age of 5 days) obtained from plankton hauls. The average total length of the newly hatched larvae is 2.7 mm.

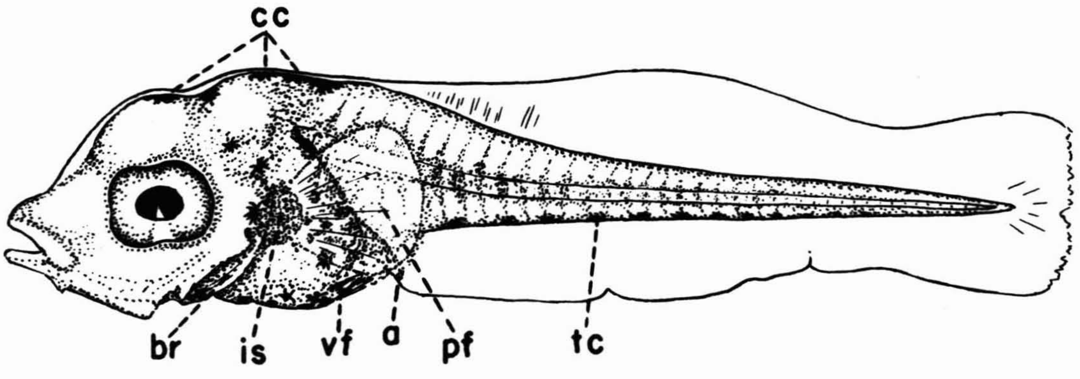
(2) Three days after hatching (Figure 12B) - In three days the larva has increased in length to an average of 3.1 mm., and the cephalic



A. NEWLY HATCHED LARVA



B. THREE DAY STAGE



C. FIVE DAY STAGE

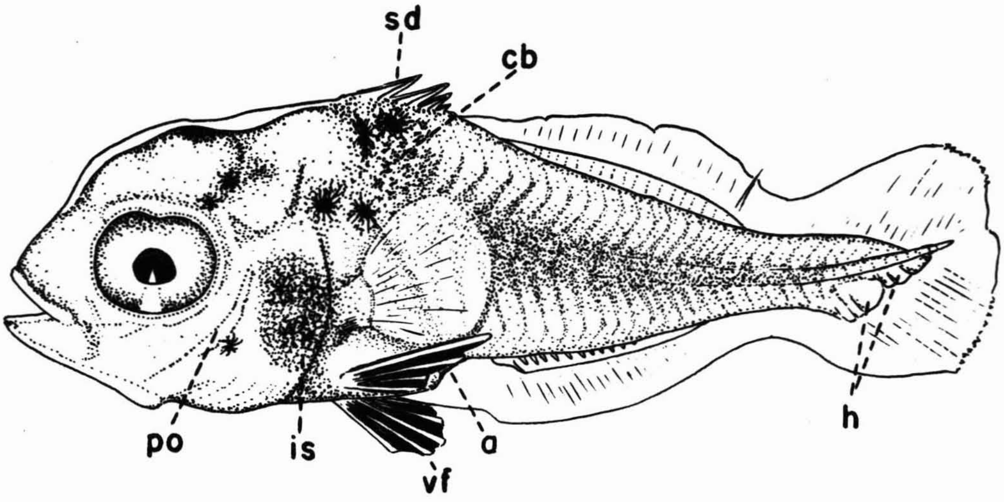
Figure 12. Early larval stages of Abudefduf abdominalis. A. Newly hatched larva. B. Three days after hatching. C. Five days after hatching.

a, anus; br, branchiostegals; cc, cephalic chromatophores; is, iridescent spot; ov, otic vesicle; pf, pectoral fin; tc, trunk chromatophores; vf, ventral fins; ys, yolk sac.

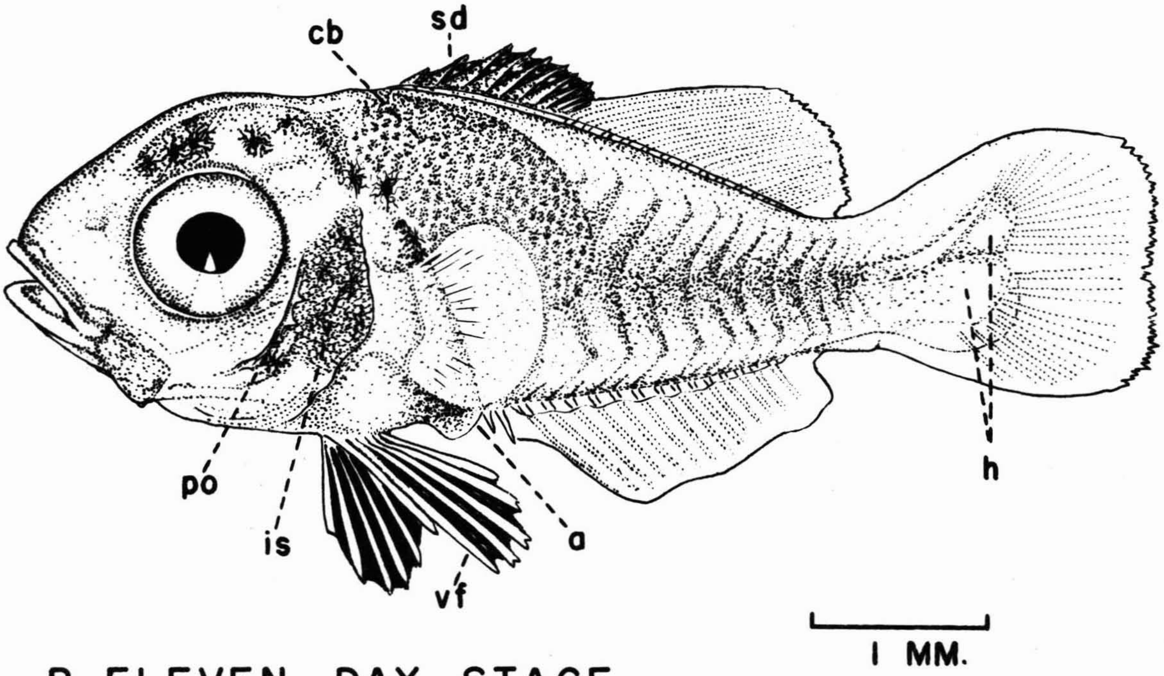
region has deepened considerably. The concentration of chromatophores has increased on the dorsal mesencephalon, and some have appeared above the apex of the triangular coelomic area in the region of the otic vesicle. Other details have not greatly changed.

(3) Five days after hatching (Figure 12C) - On the fifth day the average length is 3.5 mm. The general appearance of the larva is about the same, except that the cephalic region has become more elongate. First indications of ray formation in the region of the spinous dorsal and caudal fins are seen, and the caudal fin has become more truncate and jagged. The operculum is more clearly defined, beneath which the ends of the branchiostegals are visible. The primordial ventral fins are first visible at this time. Although the posterior coelomic cavity is still surrounded by a silvery membrane, the overgrowth of body musculature and surface pigmentation gradually conceals it. A more superficial silvery-iridescent spot becomes perceptible on the surface of the operculum just anterior to the base of the pectoral fin. This spot persists throughout the remaining larval stages.

(4) Eight days after hatching (Figure 13A) - Probably the greatest change in the general appearance of maomao larvae takes place between the five and eight day stages. The average length has only increased to 4.8 mm.; however, there is a marked increase in depth, and the fin regions become more clearly defined. Four elements of the spinous dorsal fin are visible, and the faint outline of rays are seen in the soft dorsal, caudal, and anal fin regions. The most striking development in this stage is that of the ventral fins which are bright yellow with scattered black blotches. These bright structures make this larval stage visible



A. EIGHT DAY STAGE



B. ELEVEN DAY STAGE

Figure 13. Intermediate larval stages of <u>Abudefduf abdominalis</u>.
A. Eight days after hatching. B. Eleven days after hatching.

a, anus; cb, superficial chromatic bodies; h, elements of the hypural; is, iridescent spot; po, preopercle; sd, spinous dorsal; vf, ventral fins.

macroscopically, whereas it was only seen previously with some difficulty and primarily because of the pigmented eyes. The formation of groups of diffuse chromatic bodies has begun just ventral of the spinous dorsal fin, and this area eventually expands to cover the entire surface of the trunk. The still transparent trunk shows the outlines of its characteristic musculature. In the caudal region, the extremity of the vertebral column shows a slight upturn, and the first elements of the hypural have begun to differentiate. The iridescent spot on the operculum has increased in size and now contains some stellate chromatophores.

(5) Eleventh day after hatching (Figure 13B) - Growth in depth and length has continued and at this time the average length is 6.5 mm. The fins have become completely separate and defined, and the full number of spines and rays have formed. The spinous dorsal fin has taken on the bright yellow coloration noted in the ventral fins, and is covered with irregular black blotches. The ventral fins have continued to grow, becoming greatly out of proportion to the rest of the body as compared to their relative size in the adult maomao. The area of superficial chromatic bodies has extended posteriorly and ventrally from the region of the hindbrain, and now covers about one-third of the surface of the trunk. The eye has enlarged and become more rounded. Serrations on the preopercle have become evident, and the iridescent spot on the operculum has become relatively larger.

(6) Thirteen days after hatching (Figure 14) - By this time the larva averages about 8 mm. in length and has taken on the general shape and proportions of the adult maomao with the exception of the enlarged ventral fins. The body is covered with superficial chromatic bodies except for the snout, lower jaw, and region of the caudal peduncle,

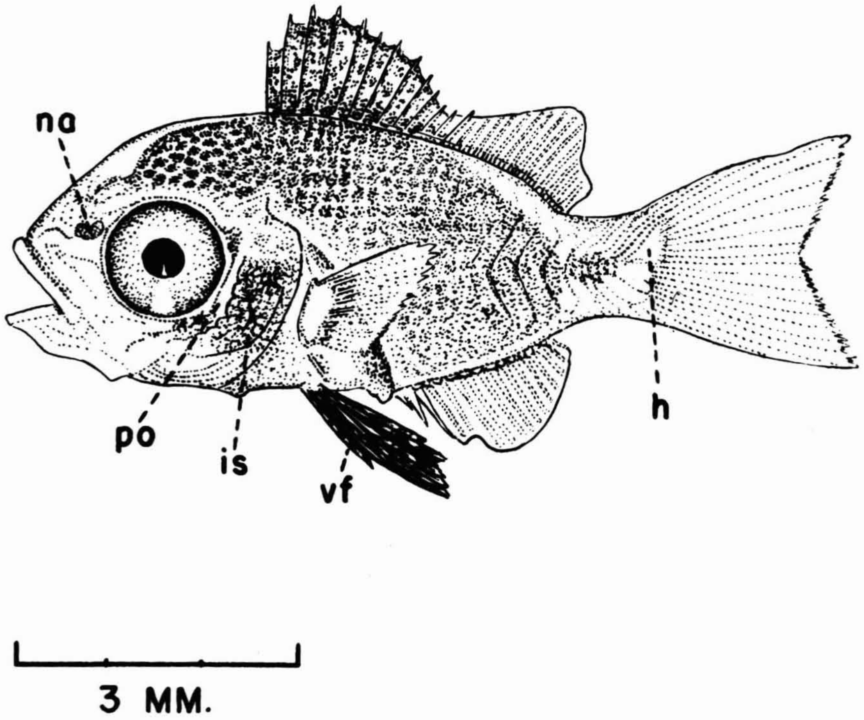


Figure 14. An advanced larval stage of *Abudefduf abdominalis*, thirteen days after hatching.

h, hypural; is, iridescent spot; na, nasal aperture; po, preopercle; vf, ventral fins.

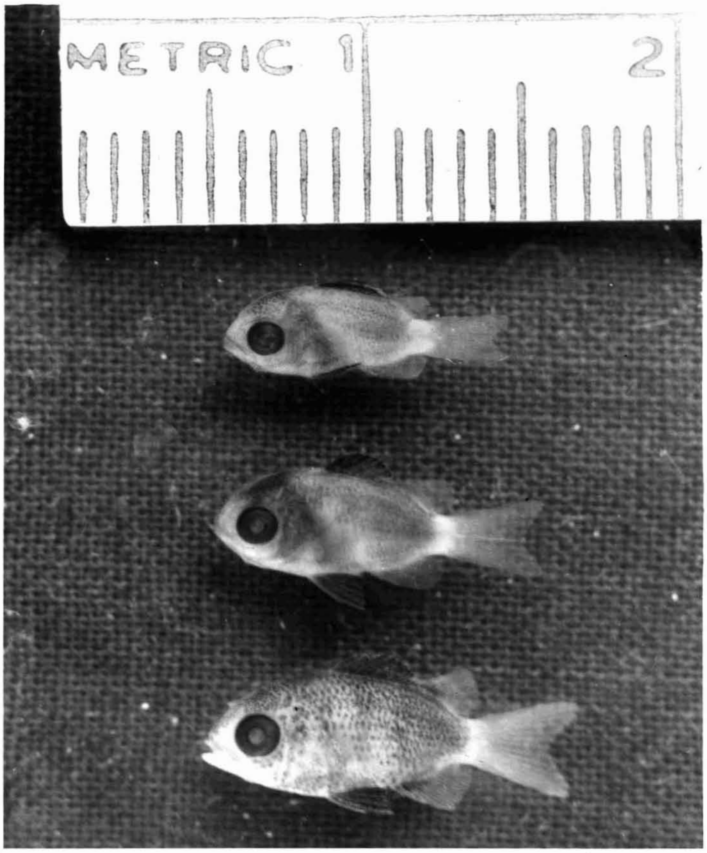


Figure 15. Advanced larval and early juvenile stages of *Abudefduf abdominalis* collected at Southwest Point, Coconut Island, and photographed under magnification.

although no vertical bands are yet seen. The hypural fan is clearly visible as the dominant bony structure in the caudal region, and the caudal fin has assumed a distinct forked outline. In the cephalic region the nasal apertures are visible with proper lighting, as are structures in the jaws. The iridescent area on the operculum has taken on a reddish hue and is less conspicuous.

At approximately 12 mm. fork length (at an age of about 20 days) the maomao larvae begin to display the vertical bands of the adult, and are considered in the category of juveniles.

Growth

Estimates of the growth rate of maomao larvae are based entirely on measurements of samples taken from the rearing apparatus at Coconut Island, in which conditions were very close to those found in nature. These data are presented in Figure 16, showing a growth from about 2.7 mm. at hatching to an average total length of 10 mm. in 17 days. Since a primary concern of the rearing experiments was to obtain an estimate of survival, only a few specimens were utilized for the purpose of measurement and description. Naturally the later stages of development (beyond eight days) were sampled less frequently than the younger stages, since the later stages had fewer numbers, and therefore their loss would be more critical to estimates of survival. From the twenty-four individuals measured between one and seventeen days after hatching, an average growth rate of 0.43 mm. per day was obtained, which is in close agreement with the average growth rate obtained for reared juvenile maomao (0.44 mm. per day).

Behavior

Knowledge of the behavior of larval maomao was obtained primarily

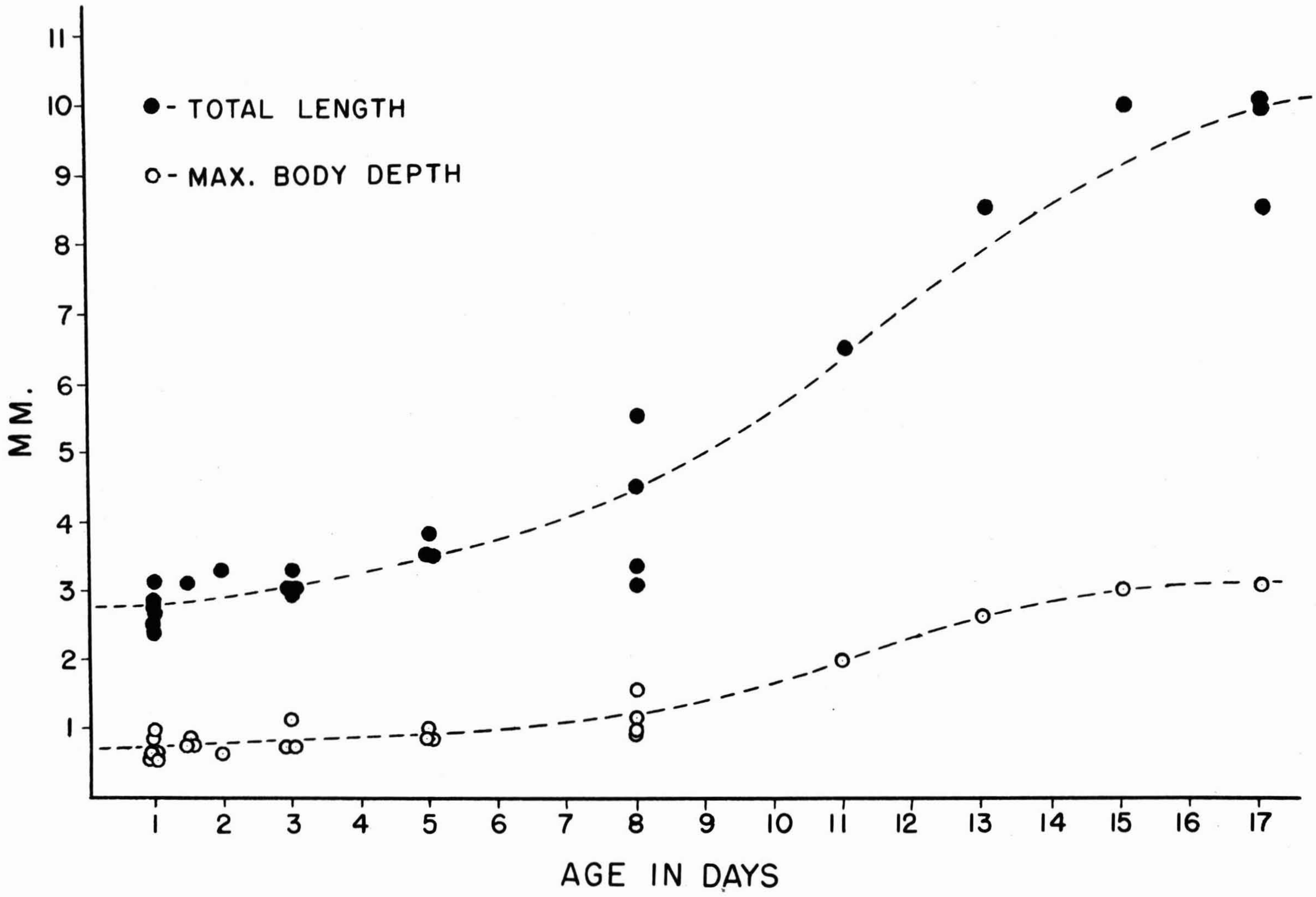


Figure 16. Growth curves for maomao larvae reared at Coconut Island. Broken lines represent the lines of best fit, fitted by eye. The maximum body depth is exclusive of fins.

from observations of broods hatched and confined to the rearing apparatus and aquaria at Coconut Island. On the 16th day of May, 1957, observations were made on approximately 1,000 recently hatched larvae (less than 24 hours old) held in the rearing apparatus which was located in the Tuna Pond spawning area (see Figure 1). During this observation period of about thirty minutes, the sun was obscured by the clouds, and the water was comparatively clear. The larvae were distributed more or less evenly in the inner net of the apparatus, and seemed to be rather inactive. Only occasionally would individual larvae swim in short darting movements of about two or three mm. by means of a rapid fluttering of the caudal fin. No distinct vertical or horizontal migrations were noted. The larvae remained at least 6 to 8 mm. away from the net at all times, and no attempts were observed to feed on particles on the net or to escape through mesh openings.

Further observations were made on day old larvae on August 7, 1957, when the sun shone brightly throughout the period of observation. Larvae were distributed throughout the enclosure; however, the concentration in the upper half was visibly greater than that in the lower half, indicating a possible phototaxic response. The swimming action of these larvae was rather slow, and in one general direction by a given larva, but the group showed no concerted movement in any one direction. Individuals would swim by means of a rapid fluttering of the tail, changing direction slightly about every second. They would approach the net, but would turn when a few millimeters away from it. Occasionally a larva would make a rapid dart of about 10 mm. as though it received a definite stimulus from an object nearby; however, no direct evidence of feeding was observed.

Three day old maomao larvae were observed in a 13.5 gallon, glass-sided aquarium located in the main laboratory building. This aquarium was situated so that one side was against the wall and all of the light entered from the opposite end and from the top. In this case a positive phototaxis was quite evident, as practically all of the forty to fifty fish in the aquarium were congregated against the glass side facing the light and on the surface.

Maomao larvae eight days old, observed in the rearing net, differed from the younger larvae in that they were much more active in their swimming, and swam in one direction for a longer period of time, rather than in short, jerky movements. The primary visible mode of propulsion was still by fluttering of the caudal fin.

In addition to these observations on captive fish, an attempt was also made to obtain some information on the behavior of maomao larvae in their natural habitat. In this regard, an investigation was undertaken aimed at determining the whereabouts of the larvae from the time they hatched until they appeared in sheltered, inshore locations such as tide pools and lagoons. As a preliminary step to check on the possible migration of larvae, a series of weekly plankton hauls was inaugurated on the first of February 1954, at two locations near Coconut Island (see Figure 1). These stations were originally designed to measure the amount of larval migration away from the reef into deeper water; however, at that time too little was known of the maomao spawning areas and current patterns, resulting in a poor choice of locations for these stations. Station #1 was located between the gate of the Tuna Pond, and a point directly off of the nearby wooden dock, a distance of about 40 yards through a known maomao nesting area, primarily subject to tidal currents only. Station #2 was parallel to, and about 30 yards north of the windward North Reef Platform on Coconut Island, and extended over an estimated distance of 200 yards. Tows were made with a one-quarter meter, #6 silk plankton net (74 meshes to the inch), towed from three to five feet beneath the surface at a speed of approximately two knots. The number of fish larvae taken throughout the year in these plankton hauls is summarized in Table 10.

The largest maomao larva taken in these hauls was four millimeters in lenth, and therefore estimated to be about seven days old (see Figure 16). From previous observations on the behavior of larvae of this age and younger it might be concluded that they have very limited powers of locomotion and are probably largely at the mercy of prevailing currents. Therefore, larvae taken at Station #2 may well have been spawned to the north-east (windward) of Coconut Island, and thus not associated in any way with Coconut Island spawnings. Since the smallest larva found in a protected inshore area (Southwest Point, Coconut Island) was 6.5 mm., it might be concluded that larvae between the lengths of 4 to 6.5 mm. (age about 7 to 11 days) acquire sufficient powers of locomotion to elude the plankton nets used in these hauls, and possibly also undertake a purposeful migration into shallow water.

Thus the data presented in Table 10 is primarily of value in demonstrating that a general increase in abundance of maomao larvae (as well as all other fish larvae) occurs during April, May, June, and July in Kaneohe Bay. This is in general agreement with the nature of maomao spawning cycle as determined from other sources discussed in

TABLE 10

FISH LARVAE FROM PLANKTON HAULS AT COCONUT ISLAND

Month	No. of Hauls Sta. 1	Total Fish Larvae Sta. 1*	No. of Hauls Sta. 2	Total Fish Larvae Sta. 2*	Total Fish Larvae Sta. 1&2	Total Maomao Larvae Sta. 1&2
(1954)						
February	3	11 (0)	3	6 (1)	17	1
March	4	7 (0)	3	4 (0)	11	0
April	2	10 (2)	3	30 (0)	40	2
May	5	31 (0)	5	43 (4)	74	4
June	4	17 (0)	4	16 (2)	33	2
July	3	6 (0)	5	25 (3)	31	3
August	3	0	3	16 (0)	16	0
September	4	1 (0)	4	16 (0)	17	0
October	6	1 (0)	2	9 (1)	10	1
November	3	2 (0)	3	7 (0)	9	0
December	5	2 (0)	5	8 (0)	10	0
(1955)						
January	4	15 (0)	4	26 (0)	41	0

*Number of maomao larvae in brackets.

the section on reproduction.

The only observations on the behavior of maomao larvae in nature are from those seen along the concrete retaining wall at Southwest Point, Coconut Island. A record of the number of larvae observed in this area between April 1, and August 1, 1957, is presented in Figure 6, along with observations of spawnings in the same area; however, relationships between the number of larvae, the spawnings, and/or the phases of the moon appear inconclusive from these data.

All of the larvae seen along the concrete retaining wall of Southwest Point were motionless, or nearly so, and all were within twelve inches of the wall, and a few inches of the water's surface. These larvae seemed to derive some natural protection from their small size and their drab coloration which was very similar to the nearby substrate. In addition, their still transparent snout and caudal area presented a visible profile quite unlike a fish, and very similar to fragments of algae and terrestrial debris commonly seen in the water close to shore. Maomao larvae were never observed within the branches of the coral _Porites compressa_ that is abundant in the area and commonly shelters the young of the pomacentrid _Dascyllus albisella_.

Thus, a positive phototaxis is indicated in maomao larvae up to three days after hatching when a strong light differential exists. The larvae are apparently planktonic and incapable of extensive migrations until seven to eleven days after hatching, at which time they move into shallow water along the shore.

Larval Survival

A number of laboratory experiments have been carried out with groups of insects, protozoans, and other animals in order to gather information on the characteristics of populations under various conditions in regards to early mortality. Andrewartha and Birch (1954), and Alee, et. al. (1949) have summarized much of this work. The findings presented are valuable in that they tell us what we might expect under certain conditions in nature; however, it is extremely difficult to actually confirm such findings with an entire population in nature, and usually we must be satisfied with inferences about natural populations from small random samples obtained under variable conditions. During this investigation the unique opportunity presented itself of directly observing an entire brood of larval maomao that had hatched from a single clutch of eggs placed in the rearing apparatus described in Appendix A. Although the environment was altered slightly by the confining net of the apparatus (at least by its exclusion of large predators), it was considered that most of the conditions within the apparatus were identical to those in the surrounding water from which the broods had been taken. Therefore, at least two important characteristics could be determined for such broods that are seldom known directly for natural populations; namely (a) their age, and (b) survival at various ages.

In order to determine the survival of larvae at various ages a method of counting the individual larvae was devised and proved reliable when the brood size did not exceed three hundred. Counts were made by an observer wearing a diving mask while leaning over the side of the rearing net, with his face beneath the surface of the water in the net containing the larvae. The net was visually divided into sections and all of the larvae of each section were counted. This was facilitated by the fact that the younger stages (which were the most numerous) did not move a great deal during the short period necessary for the count. Three counts were made during each observation period, and an average for that period was determined. Every effort was made to be objective in this counting procedure. Each count was recorded separately, and no reference was made to any previous counts until the entire experiment was completed. As a check on this counting method, an explanation of the procedure was given to a fellow worker at the laboratory, and he proceeded to count the larvae, resulting in a corroboration of the results previously obtained. When numbers of three hundred or more were encountered, it was not possible to count individuals as accurately and therefore another method of estimating brood size was utilized. As the density of larvae was fairly uniform over large portions of the container, the area occupied by twenty-five individuals was estimated and this was divided into the entire area with the same larval density. This method gave fairly uniform results on repeated trials, and the accuracy of these large counts is estimated to be plus or minus ten percent.

In the period from May 5, to the end of September 1957, eight clutches of maomao eggs were placed in the rearing apparatus at Coconut Island. Of these, five broods were successfully hatched and reared, at least for a few days, during which time they were counted at intervals, and the number of larvae surviving each day was recorded. These data are presented in Table 11. In order to better visualize the mortality of the individual maomao broods, the log of the number of survivors from each of the five broods was plotted separately against their age in days in Figure 17.

TABLE 11

SURVIVAL OF LARVAL MAOMAO FROM REARING TRIALS IN APPARATUS AT COCONUT ISLAND

Date	Brood No.	Age In Days	Ave. No. Survivors	Percentage of Survivors at Beginning of Previous Day Now Remaining	Remarks
5 V 57	1	At Hatching	45	-	From slab at U-2
10 V 57	1	5	7	15.5	
13 V 57	1	8	3	42.9	
14 V 57	1	9	2	66.7	
16 V 57	1	11	1(2)	100.0	1 removed
23 V 57	1	18	1(2)	100.0	
15 V 57	2	At Hatching	1000+(?)	-	From slab at M-1. Data not used due to uncertainty of initial count.
23 V 57	2	8	2	-	
11 VI 57	3	At Hatching	(?)	-	From slab at N
18 VI 57	3	7	6	-	
19 VI 57	3	8	6	100.0	
20 VI 57	3	9	6	100.0	
21 VI 57	3	10	6	100.0	
24 VI 57	3	13	5(6)	100.0	One removed
29 VI 57	3	18	5(6)	100.0	
20 VI 57	5	At Hatching	300*	-	*± 10%
21 VI 57	5	1	300*	100.0	From slab at C
24 VI 57	5	4	30	10.0	
28 VI 57	5	8	4	13.3	
18 VII 57	7	1	110	-	From slab at P
20 VII 57	7	3	51	46.4	
22 VII 57	7	5	31	60.8	
24 VII 57	7	7	0	0	
6 VIII 57	8	At Hatching	400*	-	*± 10%
7 VIII 57	8	1	375*	93.8	From slab at W-2
8 VIII 57	8	2	350*	93.3	
9 VIII 57	8	3	325*	92.9	
10 VIII 57	8	4	43	13.2	
11 VIII 57	8	5	10	23.3	
12 VIII 57	8	6	8	80.0	
13 VIII 57	8	7	8	100.0	
14 VIII 57	8	8	5	62.5	
15 VIII 57	8	9	5	100.0	
16 VIII 57	8	10	4	80.0	
17 VIII 57	8	11	0	0	

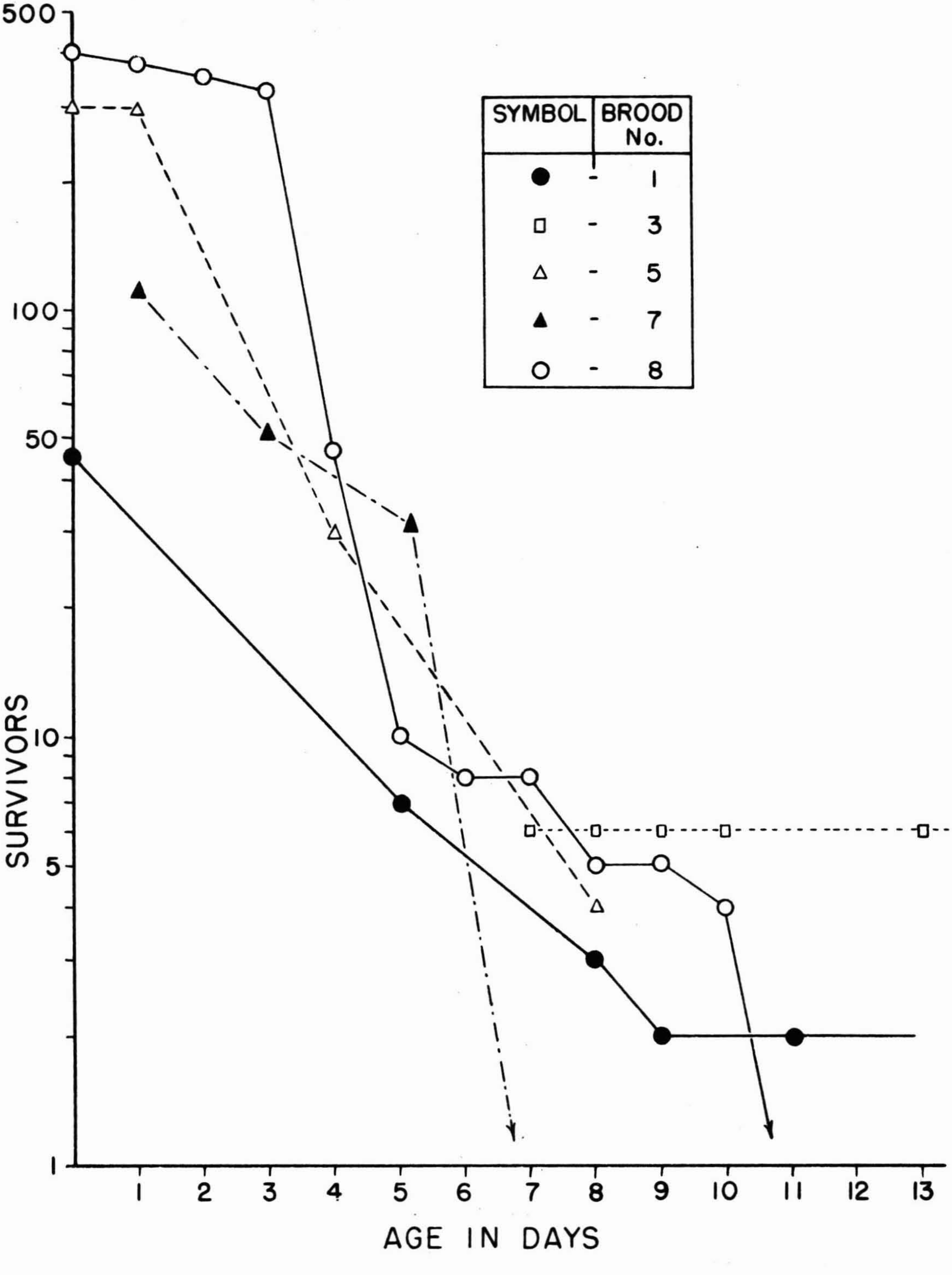


Figure 17. The log of the number of survivors from five broods of maomao larvae plotted against their age in days. Brood No. 7 had no survivors on the 7th day, and brood No. 8 had no survivors on the 11th day.

It became apparent that these data on the survival of larval maomao could be adapted for representation in a "Life Table" as described by Deevey (1947) (see also Dublin and Lotka, 1936; Pearl, 1940; and Allee, Emerson, et. al., 1949). Such a table describes something of the mortality relationships within a population when the age of individuals or components are taken into consideration. These maomao data appear to fit into the second category of Deevey (op. cit., p. 288), i.e., "cases where the survival (1_x) of a large cohort (born more or less simultaneously) is followed at fairly close intervals throughout its existence."

The combined data collected during the larval rearing trials were not immediately applicable to a life table because of the irregularity with which many of the observations were made. Therefore certain calculations were carried out in order to construct an average curve of survival for the five broods observed. First, the number of survivors at the beginning of each day was expressed as a percentage of the previous day's total (Column 3, Table 12). These percentages were averaged separately for each day after hatching, and then applied to a hypothetical population of 100, resulting in an average curve of survival, represented by the solid line in Figure 18 as the average percentage of larvae surviving. These data, when applied to an initial population of one thousand, result in an estimate of the number of individuals living at the beginning of an age interval, or 1_x in the "Life Table" (Table 13). In this table, d_x, or the number of larvae dying within a given age interval is determined directly from the number of individuals living at the beginning of the age interval since no recruitment takes place. Finally, the rate of mortality, or q_x in Table 13, is equal to the

TABLE 12

AVERAGE NUMBER OF MAOMAO LARVAE SURVIVING AS A PERCENTAGE OF TOTAL SURVIVORS OF PREVIOUS DAY

Age In Days	Number of Broods Averaged	Average Percentage of Previous Day's Survivors Surviving	Aver. Percentage of Initial Population Surviving at Beginning of Each Day
Hatching	-	100.0	100.0
1	2	96.9	96.9
2	1	93.3	90.4
3	2	69.7	63.0
4	2	11.6	7.3
5	3	33.2	2.4
6	1	80.0	1.9
7	3	83.3	1.6
8	4	54.7	0.9
9	3	88.9	0.8
10	2	90.0	0.7
11	1	75.0	0.5

TABLE 13

LIFE TABLE COMPILED FROM AVERAGE PERCENTAGE MAOMAO LARVAE SURVIVING OF FIVE BROODS FOR AN INITIAL POPULATION OF ONE THOUSAND

Age in Days x	No. Living at Beginning of Age Interval l_x	No. Dying In Interval of 1000 Born d_x	Mortality Rate Per 1000 at Beginning of Age Interval 1000 q_x*
0 - 1	1000	31	31
1 - 2	969	65	67
2 - 3	904	274	303
3 - 4	630	557	884
4 - 5	73	49	671
5 - 6	24	5	208
6 - 7	19	3	158
7 - 8	16	7	438
8 - 9	9	1	111
9 - 10	8	1	125
10 - 11	7	2	285

$$^{*}q_x = \frac{d_x}{l_x}$$

number of larvae dying in an age interval divided by the number of survivors at the beginning of that interval. This average mortality rate for the five broods of maomao larvae up to the age of eleven days is represented by the broken line in Figure 18.

Because of the limitations imposed on these rearing trials by the shortage of apparatus, it was necessary to limit their duration to less than two weeks. However, these trials were of sufficient time to show the period of high initial mortality, with a relatively constant mortality for the few survivors.

Discussion

It is evident from these data that heavy mortality takes place in this species during the second and third day after hatching, indicating a "critical period" at this stage of development in the maomao. Since the nature and even the very existence of such a "critical period" in the life history of fishes has been the subject of considerable discussion recently, this phase of the investigation was the object of particular attention and appears to warrant a more detailed discussion.

Fabre-Domergue and Bietrix (1897) observed high mortality at about the time the yolk sac was absorbed in attempting to rear marine fish, and they were the first to apply the term "critical period" to this particular phenomenon. Hjort (1914) considered the success of an early stage of development to be of sufficient importance to actually determine the success of a year class, although he did not have a great deal of evidence on which to base this hypothesis. He later expanded this hypothesis (Hjort, 1926) and stated that those larvae which did not find the special food they required at the very moment of hatching would die

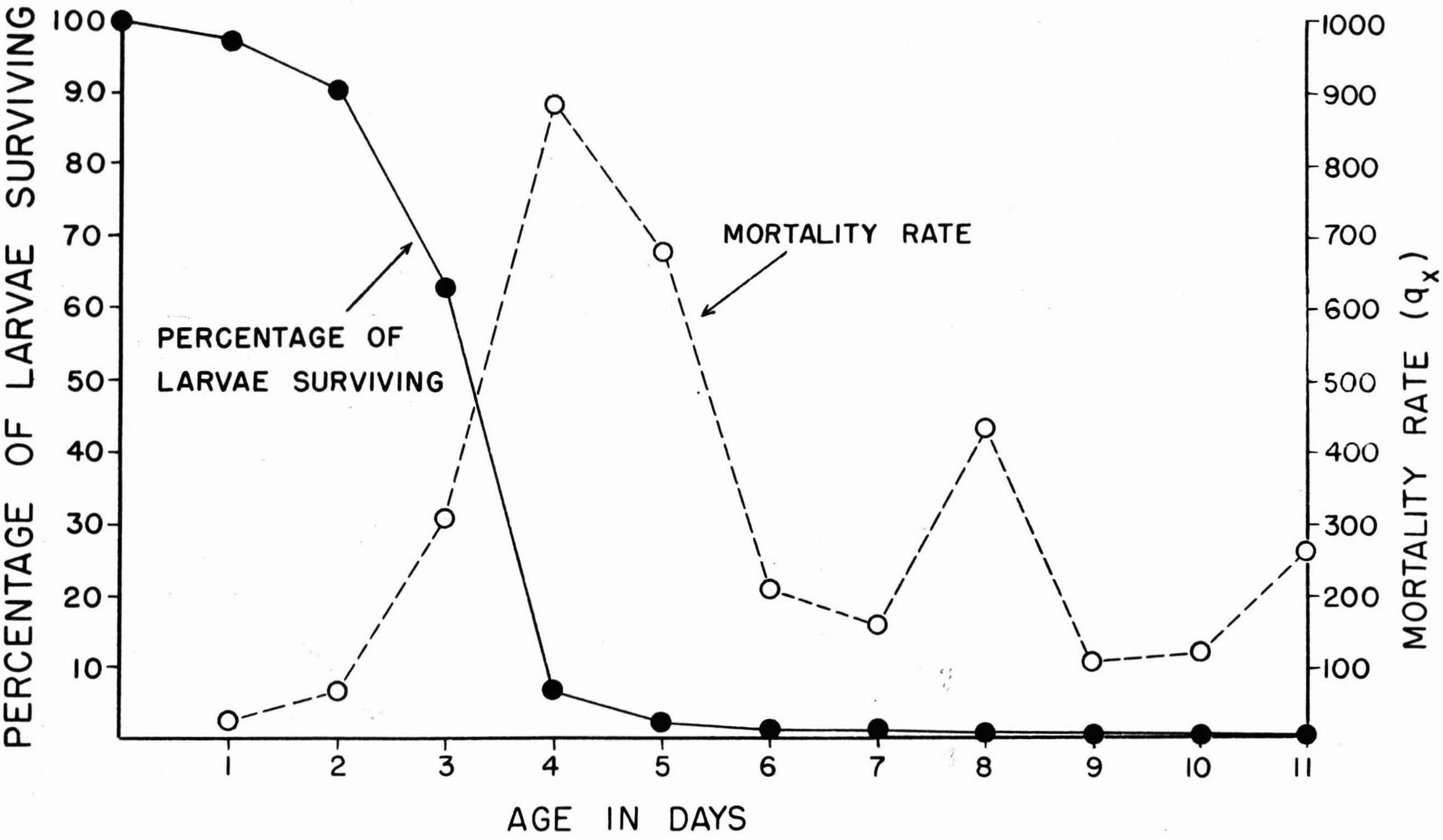


Figure 18. The percentage surviving and mortality rate of maomao larvae from rearing trials at Coconut Island. The solid line represents the average percentage of larvae surviving during the first eleven days of life. The broken line represents the average mortality rate (q_x) per 1,000 larvae alive at the beginning of the age interval.

of hunger. Therefore a successful year class depended on the proper food supply being coincident in both space and time with the hatching of the larvae. This concept has been generally accepted by many biologists since its proposal, but recently it has been subject to a critical review by Marr (1956) who points out that only two workers have presented any evidence in its support. Marr (ibid.) reviews the work of Sette (1943) on the Atlantic mackerel (Scomber scombrus) of North America, and the work dealing with the Pacific sardine (Sardinops caerulea) by Sette and Ahlstrom (1948), and Ahlstrom (1954). Sette (op. cit., Figure 17)shows a marked increase in the rate of mortality at about forty days for the Atlantic mackerel, although a recent re-examination of his data indicates that this may be closer to thirty days. The work on Sardinops caerulea is the only one examined by Marr that shows a critical stage in the early larval life; a sharp drop in the number of survivors occurs in the first five days, or until the larvae are about 3.25 mm. long. However, on re-examination of these data, an artifact was indicated, since many of the smallest larvae are lost through the meshes of the plankton net. Therefore neither case examined shows conclusive evidence of a critical period during larval development, and Marr (op. cit.) concludes that the question, "Is there a critical period in nature in the early life history of marine fishes?" cannot be answered categorically. The weight of the little evidence that exists points to survival at a constant rate or constantly increasing rate rather than toward a period of high mortality at some period in the early life history. He does propose, however, that if mortality is severely restricted in time, the chances that it would be observed would be greatly reduced, and conversely, a mortality rate without marked fluctuations in time would be more readily observed. Apparently Marr's discussion is aimed not so much toward the acceptance of a particular alternate hypothesis as it is toward conjecture regarding the validity of the present "critical period" hypothesis, in the hope this will lead to further study of the question.

Another discussion of this concept of the critical period is presented by Morris (1956) in which he examines the problem as encountered in the rearing of marine fishes in the laboratory. He points out that it is the rather sudden exhaustion of the yolk supply and dependence of the larvae on its surrounding environment for food that has led many workers to conclude that it is the absence or presence of the proper food available to the larvae that is the deciding factor for survival during this "critical period". But during the period of transition from complete yolk sac absorption to external feeding, a marked organogenesis also takes place involving the circulatory, nervous, respiratory, digestive, and excretory systems. Therefore the critical period is an interval of time differing according to species, in which the adequacy of a number of different organs must be demonstrated if the individual is to survive. This organogenesis must have progressed to a point such that the larvae can carry on an independent existence by the time the yolk is exhausted.

The data thus far presented point to a critical period in the early larval life of the maomao, occurring during the second and third day after hatching. This period is the same in all broods observed, and is relatively restricted in time, which conforms to one of the alternate suggestions of Marr (op. cit.). Although the exact time of yolk absorption and the various stages of organogenesis were not determined for these maomao larvae, the yolk sac was no longer visible on the second day after hatching; its exhaustion coinciding with this period of maximum mortality. The question therefore arises as to whether this critical period demonstrated in the maomao rearing trials is a valid reflection of what takes place in the unaltered natural environment, and, if so, what factors contribute to it.

In order to answer this question satisfactorily, environmental factors encountered within the rearing apparatus will be examined in detail, and the significance of their deviations from those in the surrounding natural environment discussed in regard to the effect they have on larval mortality. These factors are discussed separately, although they are probably subject to considerable interaction, and various factors no doubt combine to affect the well-being of the larvae under certain circumstances.

(a) Temperature - After numerous observations on larval marine fishes, Morris (1956) concludes that temperature proved to be the most influential of the physical factors upon the rates and modes of development of fishes he reared in the laboratory, and he attributes much of the inexplicable mortality encountered to temperature fluctuations. Although records were not kept of the water temperature within the apparatus during these maomao rearing trials, a free circulation of water took place through the nets in both a horizontal and vertical manner, and there is no reason to believe that the temperature within the nets differed significantly from that of the surrounding water. A continuously recording thermograph is located within about 150 yards of the rearing apparatus (see Figure 1) and records during the rearing trials revealed that surface temperatures ranged between 22.2° and 27.0° C. with a mean of approximately 25° C. No rapid temperature changes (more than 1° C. in 12 hours) were noted during this period, and no unusual fluctuations were coincident with periods of high larval mortality. Thus unnatural temperatures were not imposed on larvae by the apparatus and high mortality could not be attributed directly to temperature variations.

(b) Light - During rearing of the first three broods of maomao larvae natural light entering the inner rearing net of the apparatus was not greatly altered, except at certain periods during the day when the shadows of a nearby bridge fell across the apparatus. Another source of light not experienced in nature was the reflection of light from the brownish-yellow net making up the inner wall of the rearing apparatus.

During the time that the third brood was being reared, trouble was experienced from two species of fish from the surrounding water because of their jumping into the outer net of the rearing apparatus. These fishes were the small "Iao" (Pranesus insularum (Jordan & Evermann)), which would leap into the air when being pursued by predators, and the needle fish, Strongylura indica (Le Sueur), which would occasionally leap into the net. For this reason it was necessary to construct a fiber-glass screen cover over the entire apparatus, which reduced the light entering the center net considerably. This reduction of light in the rearing chamber may have affected the feeding efficiency of the larvae, as well as the distribution and abundance of food therein. It has been noted that positively phototaxic crab zoea, which are known to be fed on by maomao larvae, are abundant at certain times in plankton hauls taken in this area, and during periods when the proper angle of incidence of sunlight was encountered on the surface of the water within the rearing apparatus, these organisms could be seen swarming near the surface. A reduction of light would probably affect the distribution of these forms within the net, and might reduce their total number. The data do not indicate any marked change in the comparative success of broods reared before and after the cover was placed on the apparatus, and the critical period of maximum mortality in question took the same general form in all of the broods. Therefore, neither the quantity nor the quality of light was considered a significant factor in early larval mortality, although some unnatural conditions were imposed on the larvae in this regard.

(c) Salinity - The data from two previous investigations in the Tuna Pond area at Coconut Island show that variations in the chlorinity of surface waters was not great during the summer months. Tseu (1953, Fig. 10) has plotted the chlorinity and rainfall from this area from February, 1949, to February, 1951, and Tester et. al. (1955, Figure 1) has recorded chlorinities from September, 1952 to June, 1953. In both cases the chlorinity records for the months of low rainfall (May through August) show less than 0.5 $^{\circ}/oo$ variation. Rainfall appears to be the major cause of fluctuations in chlorinity in this area, and the average monthly rainfall for the months during the rearing trials (May through August, 1957) was 1.48 inches at Coconut Island. In May and June over half of the monthly total fell on one day, and in neither case did heavy rainfall coincide with the time of maximum larval mortality. Since circulation through the rearing nets was relatively unhindered, there is no reason to expect that larvae would be restricted to a salinity different from that found in their adjacent natural environment. Thus the slight variations in salinity encountered (based on rainfall and previous studies) did not appear to affect larval mortality significantly.

(d) Oxygen - Since the metabolic requirements of the maomao larvae are not known, it was not possible to determine if the oxygen supply in the surface waters in this area was adequate. A diurnal variation in the oxygen content of shallow waters does occur, and it can attain considerable magnitude under certain conditions, e.g., around coral reefs containing large numbers of living organisms (Tseu, op. cit.; Kohn and Helfrich, 1957). The nets of the rearing apparatus also supply surfaces on which marine organisms of many types, including numerous bacteria, settle, producing additional competition for existing oxygen. If a restricted supply of oxygen should coincide with a critical period in the development of the respiratory and circulatory systems, as suggested by Morris (op. cit., p. 51, et. seq.), as when larvae are transforming from dependence on vitelline and caudal circulation to branchial circulation, serious mortality could result. Thus, a critical stage in the maomao larval development may be associated with a limited oxygen supply occurring simultaneously with a critical stage in organogenesis, and the resulting mortality may be accentuated by oxygen consuming organisms which have settled on the surface of the rearing apparatus. This is all conjectural thus far, and determinations of the oxygen requirements of larval maomao are necessary before an adequate evaluation of the part played by this factor can be made.

(e) Currents and turbulence - Experience in handling maomao larvae showed that they are extremely frail and easily injured, and it was assumed that strong currents or turbulence might carry them into the sides of the apparatus and injure them. The area in which the rearing apparatus is anchored is well protected, being surrounded by walls and docks, and not directly exposed to the open water of the bay, (see Figure 1). The tidal exchange in this area causes a flow of water to and from the nearby ponds; however, the rearing apparatus is not located in direct line with any of the spillways to these ponds, and is not subject to noticeable currents. Considerable turbulence from surface waves caused by boats passing in the nearby West Boat Channel was noted from time to time; however, when observations of the larvae were made during these periods, they did not seem to be greatly affected, as the two nets of the apparatus effectively dampened most of the water action. The only noticeable movement of water within the inner net was a slight vertical movement, which conceivably could have affected larvae close to the bottom of the net. Surface turbulence caused by wind was never great due to the sheltered location of the apparatus, and it was all but eliminated from the inner net by the frames of the apparatus.

Thus the effects of currents and turbulence on larval maomao mortality are considered negligible within the rearing apparatus; however, these factors are probably responsible for considerable larval mortality of individuals in nature, especially with those which are carried or migrate into shallow areas where they are subjected to the violent action of shore waves. In this regard, it was noted that a tremendous increase in the number of maomao larvae observed at Southwest Point, Coconut Island, in June, 1957 (see Figure 6) was preceded by more than a week of very calm weather. This type of mortality would also account for the complete absence of individuals under 10 mm. (standard length) in all tide pool collections, and suggests that prior to this size they lack sufficient control to keep from being injured by the turbulence encountered in shallow water.

(f) Food - Since planktonic organisms are largely at the mercy of water currents, their distribution within the nets of the rearing apparatus is probably similar to that in the surrounding waters, with the possible exception of those too large to pass through the inner net, and those phototaxic organisms discussed in the section under light. The rearing apparatus may actually act as a concentrating apparatus for planktonic organisms, as grazing by larger predators is all but eliminated, and the planktonic larval forms shed by many of the invertebrates that attached themselves to the outer net of the apparatus during the course of these trials have ready access to this relatively protected area. The stomachs of maomao larvae less than 6 mm. in length were examined from both the rearing apparatus and plankton hauls made at stations #1 and #2 at Coconut Island. Qualitatively they appeared about the same, each containing but a few copepods and amphipods; however, it was difficult to determine if a quantitative difference existed, since all of the stomachs contained such a small amount of food. According to Crawford (1923), fish larvae only consume foods that they are physiologically capable of handling, regardless of what is available. Thus, it appears as though larval maomao require small copepods and amphipods for their initial feeding and to sustain them during the first few weeks after hatching. If contact between larvae and food is primarily a chance occurrence, as Hjort (op.cit.) and others have suggested, then the environment in the rearing net initially may be slightly advantageous to the larvae over the natural environment, as it eliminates competition from other plankton feeding organisms.

The existence of intraspecific competition for food among the larvae depends on whether there is sufficient food for the entire population within the apparatus, or whether they must compete for food to a point where some individuals fail to survive. In other words, is food in this case a density-dependent or density-independent factor? Although the data is not conclusive, the curves of survival (Figure 17) fail to show a great difference in the mortality rate between broods with an initial size of 45, and those with an initial size of 400. Thus, the initial high mortality is probably not dependent on competition for food within the population size range investigated; however, this aspect of the problem requires further study.

Therefore it is concluded that the rearing apparatus is probably not detrimental to the feeding of larval maomao, and may be advantageous over some conditions found in nature. This study has shed little light on the important question of the nature of initial feeding and its role in early survival.

From this review of the factors affecting larval mortality it seems reasonable to assume that the critical period, as well as the whole pattern of survival as determined from rearing trials, is a valid approximation of what usually occurs in natural populations of maomao. If we consider the assumptions of Morris (op. cit.) as valid (i.e., that the critical period is a time during larval development when the adequacy of a number of organ systems must be proven, in addition to a chance contact of the larva with the proper food), then the chances of conditions being optimum in favor of survival at this critical time seem extremely poor. However, on rare occasions, apparently all conditions are optimum for survival at the proper time, and a tremendous increase in the number of individuals surviving the critical period results. Although other factors probably tend to limit the population size at some later stage in such cases, the resulting standing crop is usually strikingly evident as a dominant year class. The classical example of such dominance is illustrated in the 1904 year class of Norwegian herring reported by Hjort (1926). A similar phenomenon apparently occurred with the 1956 year class of the Hawaiian Aweoweo (Priacanthus cruentatus) which appeared in tremendous numbers in some locations during 1957. The maomao appears to have experienced a substantially increased recruitment during 1956-1957, for surveys of the 1957 standing crop indicate that it is much larger than it has been for the preceding five years.

To cite an example of how a slight increase in early survival might affect a population, twelve new broods of maomao eggs were observed at Southwest Point, Coconut Island, between the first and the fifteenth of April, 1957. It has been calculated that the average brood contains about 57,000 eggs. With the application of 10 percent mortality estimated for the developmental stages prior to hatching, these broods would produce close to one half million larvae on hatching. It can be seen readily that only a slight increase in survival during the critical period of larval development would produce a tremendous increase in the number of juveniles, which would certainly be noticeable when they migrated into shallow water.

The example of broods observed between the first and fifteenth of April, 1957, (cited above) may be explored further in order to arrive at an estimate of larval survival. If we assume that the surviving larvae remained in the vicinity of Southwest Point, or at least that emigration equalled immigration, then the number of larvae observed along the wall in this vicinity might be utilized to estimate mortality during the first ten days after hatching. The number of larvae observed along the wall in this area between the tenth and the twenty-fifth of April was 68, or about 0.01 percent of the estimated number that hatched. Another estimate of larval survival obtained from five broods observed in the rearing apparatus for eight days resulted in an average survival of 1.9 percent of those that hatched. The difference between these two estimates may be attributed to factors not encountered in the rearing apparatus such as predation and injury due to turbulence.

JUVENILES

Habitats

Juvenile maomao are conspicuous inhabitants of tide pools and other relatively quiet, shallow water areas throughout the islands during certain periods of the year. This afforded an excellent opportunity to observe and sample them. Randall (1955) reports a seasonal occupancy of tide pools in Hawaii by juvenile manini (Acanthurus sandvicensis), as does Breder (1948) for juvenile Abudefduf saxatilis and three other pomacentrids in the Bahamas. During this investigation, extensive observations and samplings were carried out throughout the year to obtain information on the habitat, abundance, food, and other relationships of the juvenile maomao. Because of the rather specialized nature of the juvenile habitats, discussion of the tide pools, and other shallow water areas will be presented separately.

1. Tide Pools - Information on the tide pool habitat of juvenile maomao is based primarily on observations made over a four year period on a series of pools located at Diamond Head Park in Honolulu. A sampling program was inaugurated in this area which ultimately included observations on twenty tide pools at weekly intervals. These pools were designated as pools #1 through #19, and extended along a rocky section of shoreline for approximately three hundred yards. The substrate in the area containing these pools is composed of two general types of material described by Wentworth (1938) as detrital limestone and basalt. Pools 1 through 10 lie in a detrital limestone solution bench, while 11 through 17 lie among low basaltic outcroppings. Pool 18 is bordered on the inshore side by two patches of coarse sand separated by a knob of detrital limestone, and on the seaward side by a broad flat detrital limestone solution bench. Pool 19 is located at the east end of this bench. This entire shoreline is fronted by a broad reef (about 300 yards wide) of coral, coral rubble, detrital limestone and sand. Along the seaward edge of this reef is a buttress zone which, except for occasional channels, is exposed at mean lower low water. The prevailing northeasterly winds usually cause a moderate to heavy surf action along this buttress zone, which in turn causes a greatly reduced wave action along the intertidal zone containing the pools under discussion.

The pools occupied by juvenile maomao are all in the lower to middle intertidal zone, and partially to completely isolated at mean lower low water. Maomao were never observed to occupy supra-tidal pools of the type described by Strasburg (MS.) as the habitat for _Istiblennius zebra_.

In order to determine the general type of habitat preferred by juvenile maomao, and some of its specific characteristics, a survey of certain physical and biological aspects of these pools was carried out. An attempt was then made to associate factors in the habitat with the relative abundance of juvenile maomao found there. The pools surveyed were within the range of vertical zonation usually inhabited by juvenile maomao, but some of the pools seldom contained them. After preliminary observations had suggested that certain constituents of tide pools were of importance to maomao inhabitancy, the survey was begun. For each pool estimates were made of; (1) the approximate area when the tidal height was -0.1 ft. below mean sea level, (2) the maximum and average depth of water, (3) the amount of shelter for juvenile maomao (holes, cracks, ledges, large rocks, etc.), (4) the quantity of sand, (5)the amount of algal growth, and (6) the nature of the access to deeper water. The results of this survey, which included seventy-five observations of each pool, are presented in Table 14. In addition, estimates were made for each pool of the percentage of times maomao were found in that particular pool on collecting trips during which some maomao were observed. Items 3, 4, and 5 (above) were recorded in Table 14 according to the approximate percent of the total area of the pool they occupied, using a number scale of one to four, (1 = 25 percent or less of the area occupied, 2 = 26 percent to 50 percent, etc.).

In analyzing the data in Table 14 to ascertain what characteristics of a pool make it desirable as a habitat for the juvenile maomao, the pools were placed in two groups: (1) those which contained juveniles in 40 percent or more of the times that juveniles were successfully collected

TABLE 14

AN ANALYSIS OF CERTAIN PHYSICAL AND BIOLOGICAL FACTORS OF TWENTY TIDE POOLS AT DIAMOND HEAD PARK, OAHU, AND THEIR POSSIBLE INFLUENCE ON THE CHOICE OF HABITATS BY JUVENILE MAOMAO.

Pool No.	Approx. area (sq. yds.)	Depth in inches		Shelter (1-4)*	Sand (1-4)*	Algal growth (1-4)*	Opening to deep water	Relative occurrence of juveniles in total coll. (percent)
		Aver.	Max.					
1	20	8	(12)	3	1	3	Yes (shelt.)	50
1-A	60	12	(24)	2	1	2	" "	80
2	12	3	(6)	1	1	1	No	-5**
3	60	6	(12)	3	1	2	No	35
4	6	12	(14)	3	1	1	No	20
5	28	9	(12)	2	1	4	Yes (direct)	-5**
6	5	6	(12)	1	1	2	" "	-5**
7	3	5	(9)	2	1	3	No	50
8	12	12	(15)	3	1	3	No	60
9	3	12	(24)	4	1	4	Yes (shelt.)	70
10	.5	6	(6)	4	1	4	No	60
11	24	4	(6)	3	1	2	No	85
12	10	6	(8)	3	1	2	Yes (direct)	40
13	24	4	(12)	2	1	1	Yes (shelt.)	85
14	7	12	(18)	4	1	1	Yes (direct)	20
15	12	9	(12)	2	1	1	No	40
16	6	9	(12)	3	1	2	No	10
17	2	24	(30)	1	1	1	No	0
18	720	15	(36)	3	2	2	Yes (shelt.)	95
19	15	6	(8)	2	1	3	Yes (direct)	-5**

* Scale of 1 to 4 used to estimate the approximate percent of the total area of the pool occupied by that item; i.e., 1 = 25 percent or less, 2 = 26 percent to 50 percent, etc.

** -5 percent indicates less than 5 percent.

in this area, and (2) those which contained juveniles less than 40 percent of the time under the same circumstances. This revealed that the existence and relative position of a pool's access to deeper water seemed to be important as indicated by juvenile occupancy. Under category 1, 60 percent of these pools had openings to deeper water during lower low water, and all but two of these openings were sheltered from the direct surge, (the openings were parallel to the shore). In pools of category 2, 75 percent had openings into deeper water at mean lower low water, but in every case these openings were subject to the action of direct surge, suggesting that juveniles shun regions of continuous turbulence. No striking correlation is noted indicating a preferred depth; however, in the case of pool #2, the slight depth coupled with the scarcity of shelter and small inconspicuous opening probably contributed to its non-desirability as a juvenile habitat. Little variation exists between these pools in regard to the presence of sand; however, during observations on pool #18, as well as in other areas, juvenile maomao have never been observed in the vicinity of a sandy bottom. The shelter requirements depend largely on the size of the juvenile occupants. The younger maomao (up to about 18 mm.) seldom seek shelter, but usually remain at about mid-depth in a deeper portion of the pool when not feeding, whereas the older juveniles generally prefer deeper pools which afford cracks, holes, and overhanging ledges which they utilize as hiding places. The quantities of algae encountered in these pools do not seem to be important to the juvenile maomao. However, certain species of algae may discourage occupancy by most species of fishes (see Helfrich and Kohn, 1956, p. 27).

From the above comments, the following conclusions have been arrived at regarding the desirable characteristics of a tide pool as a habitat for juvenile maomao between 10 and 20 mm. (which is the size range most abundant in this habitat).

(1) Juvenile maomao seem to be most abundant (and apparently successful) in pools in the lower and middle intertidal zone, of moderate depth (12" to 36"), which are sheltered from the direct surge by ridges, outcroppings of rock, or solution benches. Such pools often have their long axis parallel, or nearly so, to the shoreline, and those which have openings to deeper water during lower low water, have such openings protected from direct surge of waves.

(2) The size of the pool per se seems to have little to do with the occurrence of juvenile maomao in it. The depth and amount of shelter offered by a pool have a varying effect on the occurrence of juveniles, depending on their size. It was noted that the larger juveniles prefer deeper pools, with more elaborate hiding places, than the smaller individuals. Apparently it is desirable to have an overhanging ledge or other concealment on the seaward side of a pool, under which the juveniles may take refuge and feed on organisms that are swept into the pool during the rising tide.

(3) Sandy areas are shunned by juvenile maomao. Algae of certain types is tolerated in moderate quantities. It is possible that some species of algae harbor small crustaceans utilized as food by these juveniles, and it may also afford some degree of cover and concealment.

Apparently one of the important advantages of a pool with these desirable characteristics is that it usually satisfies at least two of the basic requirements of the juvenile maomao; protection from large predators, and a fairly steady supply of food. It should be emphasized that these relationships were worked out for pools at Diamond Head Park, but the preferences exhibited here were also displayed in a number of other localities in which the juveniles were found.

2. Other than tide pools - Juveniles between 10 and 20 mm. in standard length have been observed in habitats other than the tide pools described above; however, the largest aggregations observed here have been in tide pools. In general juvenile maomao seem to favor relatively quiet water, inshore of the breaker zone, and they seem to be attracted to conspicuous objects such as piles of rocks, posts, floats, etc. The habitats on which they are seldom seen are those where heavy surf action is common, or where muddy or sandy bottoms exist. Apparently the juveniles migrate inshore from spawning sites in deeper water, as they are seldom seen in these latter areas. In shallow water they seem to seek out conspicuous objects around which they hover until they attain a length of 25 to 30 mm. at which time they take refuge in the substrate and are less conspicuous.

Numerous observations have been made of juvenile maomao congregating around floating objects such as boxes, palm fronds, rafts, debris, and even clusters of floating <u>Sargassum</u>. On April 17, 1957, thirty-nine juvenile maomao between 9 and 14 mm. in length were captured as they swam in and around a large cluster of <u>Sargassum</u> that had floated into the East Boat Channel at Coconut Island. Similar groups have been observed near a floating box, a piece of plywood, and a palm frond in the vicinity of Coconut Island. Large groups of juvenile maomao were also observed beneath rafts anchored in shallow water at Waianae and Fort De Russy on Oahu. From the previously discussed behavior of the larvae after hatching, it appears that they migrate to the surface and toward shallow water, congregating around the first large object offering shelter that is encountered. If no such objects are encountered, individuals appear to move on into tide pools and other sheltered areas along the shore. Periodic observations made along the walls surrounding Coconut Island during the late spring and summer consistently revealed aggregations of juveniles in areas indicated by the cross hatching in Figure 1. These areas are mostly in semi-sheltered locations, thus, substantiating previous observations that juvenile maomao avoid, or are eliminated by conditions of moderately heavy turbulence.

Associations

The associations of maomao juveniles in shallow water habitats, especially in tide pools, are pertinent to a study of this phase of the life history since a variety of species of fishes are in close contact with each other in this habitat, often in competition for food and space, and occasionally preying on one another. Within the tide pools, the maomao juveniles, as well as most of the other fishes, may be considered as transient occupants only. Smaller maomao (9 to 20 mm.) are usually found in aggregations well off of the bottom and in the deeper part of the pool. The juveniles of two other species of fishes have been observed in the same aggregations with maomao; the convict fish Microcanthus strigatus, and the butterfly fish Chaetodon lunula.

A fairly complete picture of the species complex of fishes was obtained during collections made at regular intervals over a four year period at Diamond Head Park. During this time certain pools were regularly poisoned with rotenone, yielding all of the fish occupants, and furnishing valuable information on the seasonal abundance and associations of various species. Greatest effort was expended during these collections toward obtaining juvenile maomao; however, a relatively constant, although lesser effort was expended toward the collection of the other species. Some of the species collected and an indication of their seasonal abundance are presented in Table 15. These fish represent the "casual species" category of Breder (1948), or those species which show no obvious tide pool specialization but are well adapted to tide pool existence, at least during some part of their life history. Also included among the casual species collected, but not as common as those listed in Table 15, are; *Abudefduf imparipennis*, *Pomacentrus jenkinsi*, *Apogon erythrinus*, *Thalassoma umbrostigma*, *Scorpaenopsis gibbosa*, *Scorpaena ballieui*, *Holocentrus lacteoguttatus*, *Lactoria fornasini*, and *Conger cinereus*. Under the category of "typical species" of those species which show specializations associated with tide pool life and are consistently found in tide pools, the small goby, *Bathygobius fuscus*, is the most abundant. Other species collected that probably belong in this category are; *Bathygobius cotticeps*, *Zonogobius farcimen*, *Istiblennius zebra*, and *I. gibbifrons*. A third category includes those species which are not well suited for tide pool life, but only enter the pools accidentally, or the "accidental species" of Breder (ibid.). Under this category *Kuhlia sandvicensis*, *Neomyxus chaptalii*, and *Pranesus insularum* might be included.

Of the twenty-four species listed as co-inhabitants of tide pools with maomao, over half may be in direct competition for food with the maomao to some extent according to a food survey of tide pool fish presented by Strasburg (MS., Tables 5 and 6). In regard to possible predators, Strasburg lists "fish fragments and scales" as found in the

TABLE 15

THE AVERAGE NUMBER OF CASUAL SPECIES* OF FISH COLLECTED FROM DIAMOND HEAD TIDE POOLS IN EACH MONTH OVER A FOUR-YEAR PERIOD

	1954 - 1957											
Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Abudefduf abdominalis	29	25	93	170	116	60	37	14	24	3	4	9
Abudefduf sordidus	1	1	2	3	3	6	13	9	4	3	5	4
Acanthurus sandvicensis	0	0	25	69	76	103	80	42	8	4	1	0
Stethojulis axillaris	0	0	3	7	6	4	8	8	9	10	1	7
Chaetodon lunula	0	0	0	6	7	13	21	4	2	1	1	0
Chaetodon miliaris	0	0	23	6	1	1	0	0	0	0	0	0
Parupeneus porphyreus	0	0	3	12	3	1	1	0	0	0	0	0
Microcanthus strigatus	4	4	11	10	2	0	0	0	0	0	0	0

*CASUAL SPECIES - Those species which show no obvious tide pool specializations but are well adapted to tide pool existence, at least during some part of their life history.

stomachs of four of the species of fishes commonly found in association with juvenile maomao. Of these, only one species, Bathygobius fuscus has shown aggressive action toward the maomao, although in examining the contents of eighteen stomachs of this species from individuals captured in areas where maomao were abundant, only crustaceans were found, and no fish or fish remains were evident.

B. fuscus was first suspected of preying on juvenile maomao when one was observed attempting to devour a maomao that had been partially overcome by poison. (The goby is much less sensitive to rotenone poisoning than the maomao.) In order to test this relationship further a group of ten juvenile maomao between 10 and 15 mm. were netted from a tide pool at Diamond Head and placed in a small glass bottle full of sea water which was then capped. This bottle was then placed back on the bottom of the same pool from which the fish had been taken. The struggling actions of the enclosed fish immediately attracted four B. fuscus, one from a distance of approximately 3 feet, to the point at which the jar had been placed. These gobies repeatedly butted up against the glass jar in an apparent effort to feed on the trapped fish.

Further evidence on the feeding habits of this goby resulted from a simple experiment in which a 47 mm. B. fuscus was placed in a fifteen gallon aquarium through which filtered sea water was circulated. After leaving the goby without food for one week a 12 mm. maomao was introduced into the tank, and the goby immediately darted to the surface and consumed the maomao. It is concluded, therefore, that this goby is a potential predator on maomao juveniles, but probably does not become a serious threat to young maomao unless it is deprived of other sources of food.

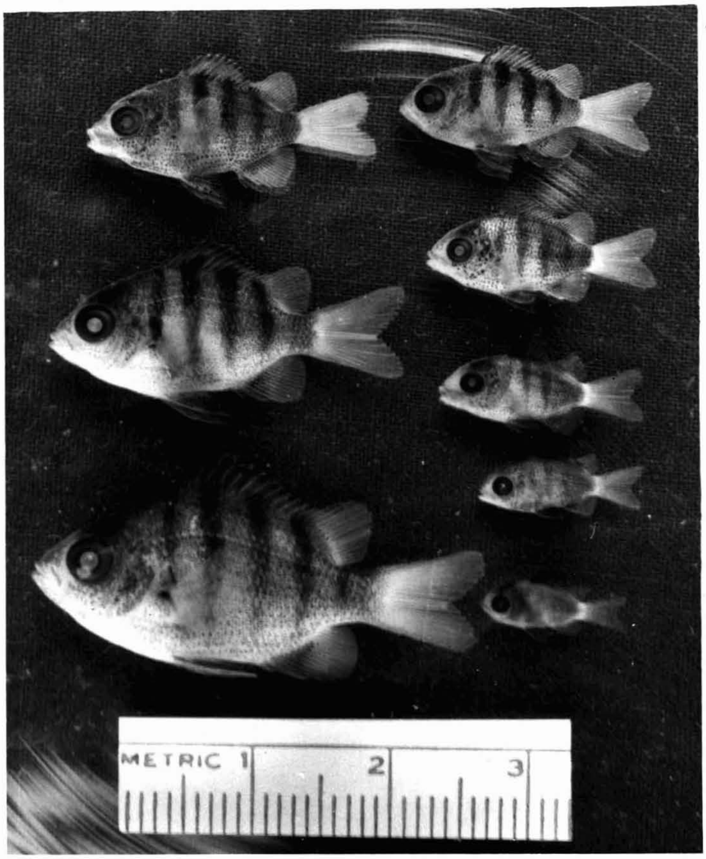


Figure 19. Juvenile Abudefduf abdominalis of the sizes most commonly inhabiting tide pools.

Of the other fishes listed by Strasburg (op. cit.) as having fish fragments and scales in their stomachs, only Abudefduf sordidus and Holocentrus lacteoguttatus are commonly found with the maomao. The former species is morphologically very similar to the maomao, and it is doubtful that the small specimens found in tide pools are capable of capturing and consuming a juvenile maomao of approximately the same size. An examination of the stomach contents of five specimens (45 to 50 mm. in length) of Holocentrus lacteoguttatus which were taken from pools containing a large number of maomao revealed only crustaceans.

Fluctuations in Abundance

The sampling program at Diamond Head Park supplied considerable information concerning fluctuations in the abundance of maomao juveniles migrating into tide pools, which verified the general picture of the spawning cycle obtained from other sources, (see section on reproduction). The numbers of juveniles under 20 mm. collected at intervals between April, 1954, and late December, 1957, are shown in Figure 20. During 1954 and 1955 collections were made monthly as close to the time of full moon as possible. The 1954 collections were made from one pool only (pool #1), whereas during 1955 the program of sampling was expanded to include all the tide pools between pool #1 and a large pool below the Diamond Head Lighthouse (designated as pool #18) about 300 yards east of pool #1. During 1956 and 1957 the sampling was increased to weekly intervals, and the area was further expanded to include all of the pools in Diamond Head Park, which includes a rocky shore of about 500 yards in length bounded by sandy areas on either end. An attempt was made to keep the effort expended constant during the 1956-57 period. An

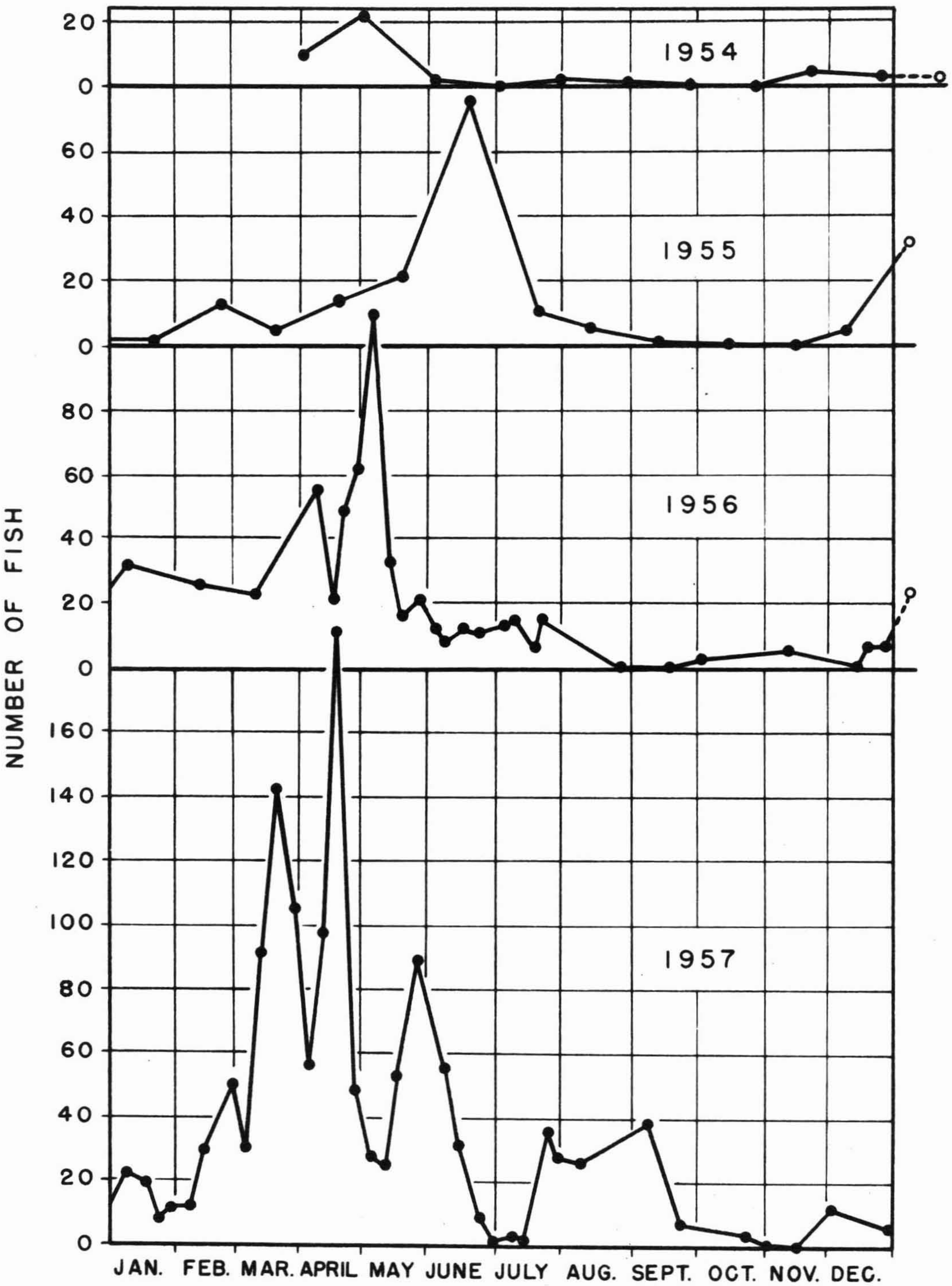


Figure 20. The number of juvenile maomao (20 mm. and under) collected from tide pools at Diamond Head, Oahu, during 1954, 1955, 1956, and 1957. During 1954 all collections were made from one pool only (designated pool No. 1), and during 1955 the sampling was expanded to include all pools between No. 1 and the large pool below Diamond Head Lighthouse (designated pool No. 18). During 1956 and 1957 the sampling area was further expanded to include all pools at Diamond Head Park.

increased proficiency at capturing these fish probably increased the yield by about 10 percent during this period.

These data show peaks of juvenile immigrants between the first of April and mid-June, and minimum numbers during October and November, probably reflecting earlier spawning fluctuations.

Food

The food of juvenile maomao was determined primarily by means of the examination of stomach contents of thirty-four specimens collected at Diamond Head, Waikiki, Makapuu Point, Hanauma Bay, Kaneohe Bay and Kahuku on the island of Oahu. All specimens examined were preserved in formalin within a few minutes after capture, and the stomach contents examined as soon afterwards as possible. The stomachs examined were opened under a binocular microscope, and thecontents were identified as far as possible with the literature available. Aid was obtained from specialists in order to gain more specific identifications of some of the dominant organisms such as the crustaceans.

The morphological modifications for feeding and digestion are discussed in some detail in the section on adult food and feeding, and these structures do not differ greatly in the juveniles except in size. The teeth vary from those of the adult in that the medial cusp described for the lateral adult teeth is more accentuated and sharply pointed in the juveniles, which results in a loosely held, uniserial, villiform type of dentition in individuals up to about 60-70 mm., at which time the more truncate structure of the adult begins to form. This dentition is displayed by the juvenile maomao appears to be fairly well adapted for feeding on small crustaceans, which appear to be their primary food.

The major items found in the juvenile maomao stomach contents are listed in Table 1. The dominant organism in the stomachs of juveniles from 10 to 30 mm. in length appeared to be a small red harpacticoid copepod identified as Dactylopus tisboides (Claus), although other similar harpacticoids were also found in abundance. The juvenile preference for a crustacean diet is indicated in the fact that when a stomach was found to be crammed with organisms, the contents usually consisted largely of copepods and amphipods of two or three species, and little else. When algal fragments were found in the stomachs, the latter were usually not full. Other food items were represented by a large variety of species from various groups. Although the number of samples does not justify any conclusive remarks, there is an indication that a definite preference exists for certain copepods and amphipods, and when these are not available, the choice of food organisms becomes quite broad. The data indicate (Table 1) that copepods, fine algae, and amphipods are dominant food organisms, considering both the number of juveniles containing the item and the bulk contained in the stomachs. Six juveniles had consumed a number of insects (springtails of the order Collembola, and one Hemisocus roseus (Hagen) of the order Corrodentia).

Larger juvenile maomao (from about 30 to 60 mm.) were found to be feeding primarily on copepods and amphipods also. However, the freqency of larger crustaceans, such as small crabs, found in these stomach contents increases. This is what might be expected in association with their increasing adaptation to recesses in rocks and coral for refuge, and with continued development of their dentition.

Feeding Behavior

The feeding behavior of juvenile maomao differs from that of the adults in that the juveniles are seldom observed in feeding aggregations of the type previously described for adults. In tide pools, feeding activity of the juveniles is normally at a low level during period of low tide when the pools are isolated or nearly isolated. During these periods juveniles are often observed in a relatively quiescent state, a few inches beneath the surface of the water, in groups of five to ten individuals. Only occasionally will they swim about slowly in what appears to be a subdued feeding activity. When the first water breaks into the pools on the rising tide, a marked increase in activity is noted in these young maomao, and by the time waves are breaking into the pool in rapid succession, the maomao are darting about rapidly near the surface in what is obviously feeding activity, although their prey is invisible to the observer. This exchange of water apparently carries a fresh supply of organisms into the pools from deeper water and from the barriers which isolate the pools from the open sea.

In the shallow water habitat of juveniles around coral reefs and other areas, the feeding is often by small aggregations of maomao, frequently situated in some area where currents carry organisms over a reef platform or other shallow water area. In these cases the juveniles face the current and individuals dart out from the aggregation a short distance apparently to feed on a small organism. As the juveniles reach approximately 30 mm. they begin to take refuge in cracks and shelters in the substrate, and in general move into the vicinity of the deeper water habitat frequented by the adults. At this time they tend to be solitary feeders, at least they do not join the feeding aggregation of adults when they are located nearby.

A definite hierarchy of feeding or peck order seems to exist among juvenile maomao observed in small tide pool aggregations, and this was confirmed with groups confined to aquaria. In order to observe the evolution of this behavior more closely, four groups of juveniles were placed in four 13.5 gallon, glass walled aquaria at the main laboratory at Coconut Island. Each group was composed of fish of exactly the same size, although a size difference existed between groups. A ration of prepared fish food was dropped onto the surface of the water once a day, and after a short time a definite peck order was established. This peck order was evident as soon as the food was introduced into the aquaria. The dominant juvenile would immediately rise to the surface and begin to feed, with intermittent periods of chasing other fish attempting to do likewise. Usually the dominant fish remained near the surface in the area that contained the most food, while those of lesser dominance were distributed out toward the periphery of that area and at lower levels in the water. Those individuals with the lowest rank in the peck order remained close to the bottom of the aquarium, and did not feed until the food drifted down to them. Although other factors may cause a differential growth rate, the difference in size of an individual is probably a good indication of the quantity of food he has consumed under these experimental conditions. It was therefore hypothesized that the size of a fish in these experiments indicated its position in the feeding hierarchy, and this was confirmed by observations of behavior and periodic measurements, at least as far as extremes in dominancy was concerned. (see Table 16). In each trial a dominant fish was clearly

TABLE 16

THE NUMBER OF SPECIMENS OF A GIVEN LENGTH INDICATING DIFFERENTIAL GROWTH OF FOUR GROUPS OF JUVENILE MAOMAO REARED IN AQUARIA ON EQUAL RATIONS OF FOOD

Standard Length of Juvenile (mm.)	Date examined															
	Group A				Group B				Group C				Group D			
	4/20	4/29	5/29	6/11	4/20	4/29	5/29	6/11	4/20	4/29	5/29	6/11	4/20	4/29	5/29	6/11
10	11	2														
11		4			24	7										
12		3	1			8			5							
13						5				1			8	3		
14			3							2				3		
15			1	3			1			2				1		
16			1	1			2									
17																
18			1	1							1				1	
19							3	1							1	1
20							1				1					
21								2								1
22							1				1	1				
23								2								
24			1	1							1					
25							1	1								
26																
27				1				1								
28												1			1	
29																1
30																

indicated by its size after thirty-nine days, and before this time by its aggressive feeding behavior.

This phenomenon appears to vary considerably in nature depending on the amount of confinement and the food available; however, even in situations where juveniles are not restricted to tide pools, and food is seemingly abundant, larger juveniles are often seen chasing their smaller competitors. This is probably a reason for the occurrence of aggregations of juvenile maomao consisting of individuals that are all of about the same size.

Growth

In an attempt to obtain an estimate of growth of juvenile maomao that was a close approximation of the average natural growth rate, the following three methods were employed: (1) marking and tagging individuals in nature, (2) following the progression of modes in length frequency determinations of the juveniles entering tide pools, (3) making periodic measurements of juveniles kept in tanks and nets in which natural food was available.

All attempts to determine the growth characteristics of juvenile maomao by the use of tags and markings failed. Four methods of tagging and marking were attempted in both juveniles and adults, and although some success was obtained with one method of tagging adults, all methods failed with the juveniles. Failure to tag or mark juveniles successfully was attributed partially to the lack of suitable methods and techniques; however, because of the delicate nature of the young maomao, high mortality resulted from excessive handling alone. In addition, recapture of marked fish released into their natural environment was extremely difficult, time consuming, and often resulted in injury to the fish.

Therefore, other approaches to the problem were adopted.

The rearing of juveniles in a nearly natural environment seemed to be a suitable method for obtaining an approximation of their growth, and was therefore attempted. Maomao used for this operation were obtained directly from the vicinity of Southwest Point, Coconut Island, and from advanced stages of larvae reared in previously described trials (see section on larvae). Three groups of juveniles were reared in various environments which approximated the natural environment during these trials. No food was given any of the broods directly; however, every effort was made to insure that a normal supply of natural food was available to them. A great deal of care was exercised in measuring these fish in order not to injure them in any way.

These fish were placed in the large outer net of the rearing apparatus, and a smaller holding net (21" x 28" x 23") which was anchored beside the rearing apparatus. Later these fish were transferred to a large concrete tank, and two specimens transferred from this tank to a live car anchored in the lagoon on the east side of Coconut Island (see Figure 1). The concrete tank utilized was the one described by Tester (1952) in which he kept tuna and other pelagic fishes. Its dimensions are 34.7' x 10.8', with a depth of 4.0' at the south end and 3.8' at the north end. Its volume is about 10,600 gallons, and during this study water was pumped into the north end from the nearby lagoon at the rate of 60 gallons per minute. The live car, to which some of the fish were later transferred, contains cages of ¼" mesh galvanized steel screening, with dimensions of 33" x 35" x 26", that are held by a floating platform anchored in about 5 feet of water.

The three broods used in these trials were designated as broods A, 3, and 4, and initially included a total of twenty-one individuals. Broods 3 and 4 were reared from hatching, and brood A consisted of captured juveniles which were all 12 mm. in standard length at the beginning of these trials on April 20, 1957. The age, length, disposition, and other data collected on these juveniles during almost nine months of observations is presented in Table 19 (Appendix B). The transfers of these juveniles was necessitated by the priority of other experiments, the availability of nets and tanks, and consideration of the space requirements of various sizes. It was unfortunate that the natural environment of some of the tidal ponds at Coconut Island could not have been utilized for this study; however, a method of juvenile recapture from these areas was not devised. Recapture of juveniles from the various rearing containers used was accomplished by the use of hand nets and seines. During the period from April 20, 1957, until January 3, 1958, when the study was concluded, periodic length measurements were made of these juveniles, and these data were averaged for each brood and plotted in Figure 21.

No published accounts on the growth of pomacentrids in nature were found; however, Verwey (1930a) reared Amphiprion percula in an aquarium on natural food obtained from the circulating water. He gives the following data on their growth: 4 mm. at hatching, 7 mm. at 12 days, an average of 8.7 mm. at 19 days, 12.5 mm. at 26 days, 16 mm. at 36 days, 25 mm. at 66 days.

According to Conrad Limbaugh, Scripps Institution of Oceanography, La Jolla, California, (personal communication) Chromis punctipennis

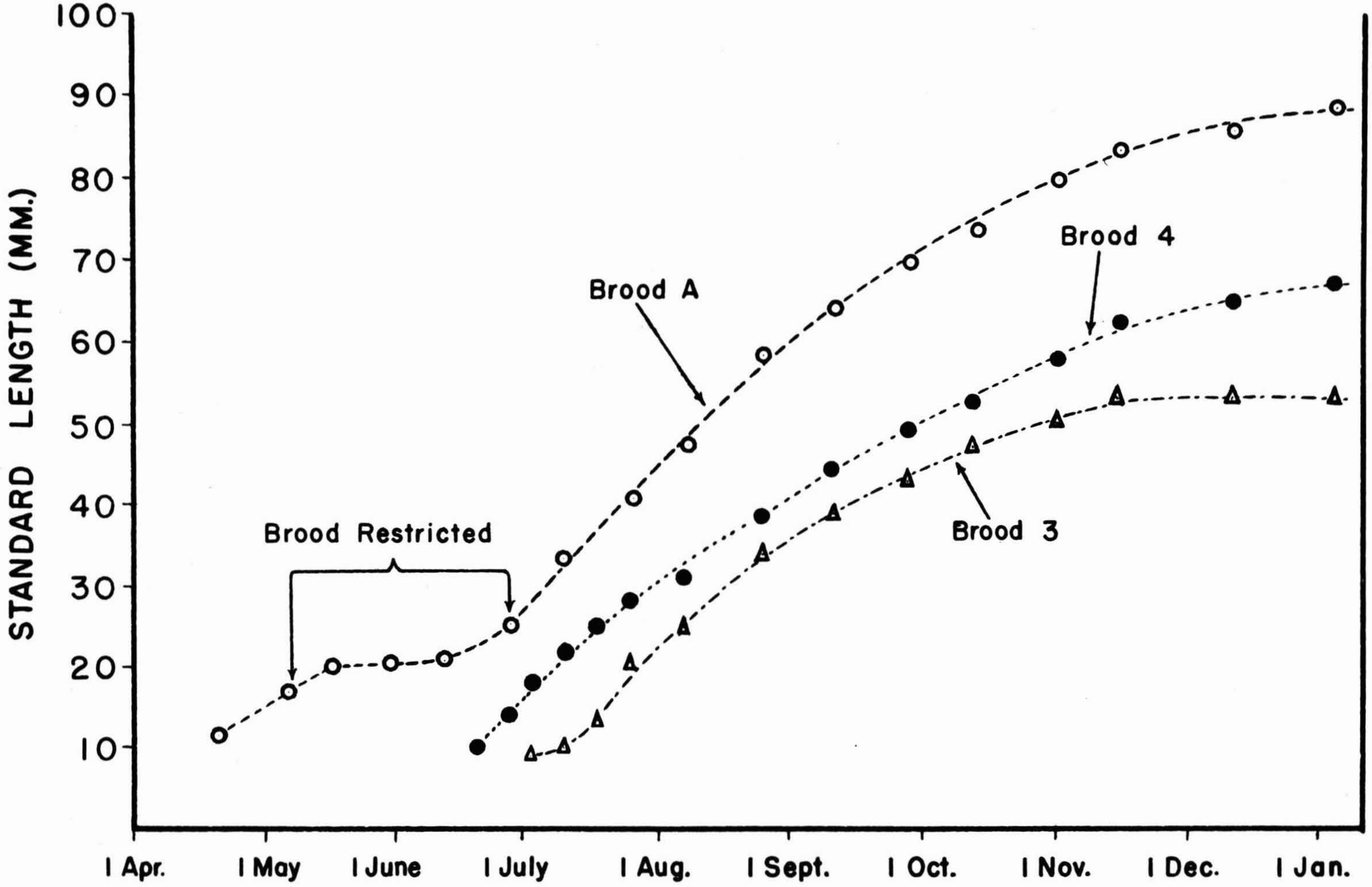


Figure21. Average growth rate of three broods of maomao kept in the rearing apparatus, the concrete rearing tank, and the live car at Coconut Island from April, 1957 until January, 1958. Brood A was restricted to a small holding net for the period indicated. For details of the disposition of each brood and a discussion of these curves see Table and the text.

(Cooper) in the vicinity of La Jolla requires 3 years to attain sexual maturity, and at that time is 5.5 inches long. He also states that the pomacentrid, Hypsypops rubicunda (Girard) is sexually mature at 8 inches for the female, and 8½ inches for the male, and that the "young mature at approximately three years, although aquarium-held specimens grow much slower." A further indication of the growth rate of this species is revealed in the observation that half inch young appear close to shore between July and November, and as the spawning period is between April and July, these half inch fish might be assumed to be approximately 4 months old.

During these rearing trials, brood A was restricted to the previously described small holding net on May 16, 1957, due to the lack of other available space, and these juveniles were retained in this container until moved to the large concrete rearing tank on June 26, 1957. During this period of restriction, these individuals experienced a marked decline in growth rate (see Figure 21), probably because of the lack of food available to them in this relatively small area. Following their introduction into the large concrete rearing tank, a marked increase in the growth rate was evident, followed by a steadily declining rate of increase to the last measurement on January 3, 1958. The average slopes of the growth curves seems to be somewhat less for broods 3 and 4 which were reared later in the season, thus indicating that the decline in growth rate may be associated with conditions encountered at this particular time of the year (winter months). Based on observations made during the fall and winter months of 1952-1953, Randall (MS.) noted that juvenile manini (Acanthurus sandvicensis) ceased to grow during November, December, and

January. Tester and Takata (1953) observed a similar retardation of growth between January and April in the aholehole (Kuhlia sandvicensis) reared in a tank at Coconut Island, despite the fact that these fish were fed regularly. They attribute this retardation primarily to lower water temperature and the deceleration of growth rate that usually accompanies increase in age of fishes.

In an attempt to analyze the growth data presented, certain considerations pertinent to the problems of growth of fishes in general should be discussed. Brown (1957) states that most fishes have annual cycles of growth, but in addition, if the annual growth is averaged, the annual specific growth rate decreases with age. Thus, the growth curves presented in Figure 21 may have the effect of an annual cycle of growth (such as a winter decline shown by Randall (op. cit.) and Tester and Takata (op. cit.)) as well as a general decline in the specific growth rate. If this were the case, and if we hypothesize that the annual growth cycle caused a decrease in growth during the late fall and winter, then we might expect that fish reared over the same size range in the period from early spring to summer might show a more rapid absolute growth rate. There is no reason to believe that these curves represent a growth rate that is greatly divergent from those exhibited by maomao in nature at this time of year, therefore, it is certainly within the realm of possibility that maomao could reach sexual maturity (about 125 mm. for females) within one year, if hatched early in the spring.

According to Brown (1957: 380), food supply is probably the most important factor affecting the growth of fishes, and maximum growth rate depends on sufficient and adequate food in any given environment.

It was not possible to measure the amount of food available to these reared fish nor were any fish sacrificed to examine the stomach contents. Since the food supply appeared to be primarily in the form of planktonic organisms (concluded from feeding behavior), the seasonal abundance of some of these organisms preferred by maomao may have affected their growth rate. In a survey of the abundance of copepod nauplii and adults, Hiatt (1951: 350) notes that they are either in great abundance or common occurrence during all months of the year in Kaneohe Bay. He also shows that shrimp and crab larvae are fairly abundant throughout the year with the exception of July.

The previously discussed hierarchy in feeding among juveniles may also have affected the growth rate of the juvenile maomao in these trials, especially those in broods 3 and 4 after August 23, 1957, when all broods were placed together in the large concrete rearing tank. As has been noted, a marked peck order, and a resulting difference in individual growth rates exists among smaller juvenile maomao (10 to 30 mm.). Although the size differences in these rearing trials were not sufficient to cause the individuals to form separate aggregations, more aggressive feeding tactics were observed among the larger fish. However, it is believed that the concrete tank was of sufficient size so that serious competition for food did not take place.

Regarding the early plateau in the growth curve of Brood A, caused by its restriction to a small holding net, it has already been suggested that this might be due to a paucity of food in this confined area. Another cause for a decrease in growth rate is suggested by Brown (op.cit., p. 385), and that is, evidence that crowded fish eat less and show less fluctuation in appetite.

Another method utilized to estimate the growth rate of juveniles was that of following the progression of length-frequency modes of juveniles between 10 and 20 mm. standard length in samples from the tide pools at Diamond Head. The collections analyzed were made at intervals of approximately one week, with a relatively constant effort expended, and the results obtained between November 12, 1956, and December 24, 1957, are shown graphically in Figure 22. It was noted that certain length groups have a greater relative abundance, and these dominant groups often tend to persist in time, and can be followed by the progression of their modes. In five cases the progression of modes appeared to be sufficiently clear to justify their use as an indication of growth, and these modes are marked "a" through "e" in Figure 22. From these modes the total growth over a certain period was determined, and the mean growth per day calculated. These data are summarized in Table 17.

The average growth rate shows a general increase between February and August. This increase may be due to some phenomena associated with a rise in water temperature that occurs during this period. The average growth rate ranged from 0.13 mm./day in February and March to 0.23 mm./day in June, July, and August, with an overall average of 0.19 mm./day, or 5.7 mm./month. The only other data on the growth of Hawaiian reef fishes using this method is that of Tester and Takata (1953) for the aholehole, which showed a growth rate of 7.4 mm./month, and Randall (1955) for the manini, which showed a growth rate of about 12 mm./month.

In comparison to the above growth rates, comparable rates of juveniles of a slightly larger average size were obtained from previously described

Figure 22. Length frequency distribution of juvenile maomao from Diamond Head tide pools.

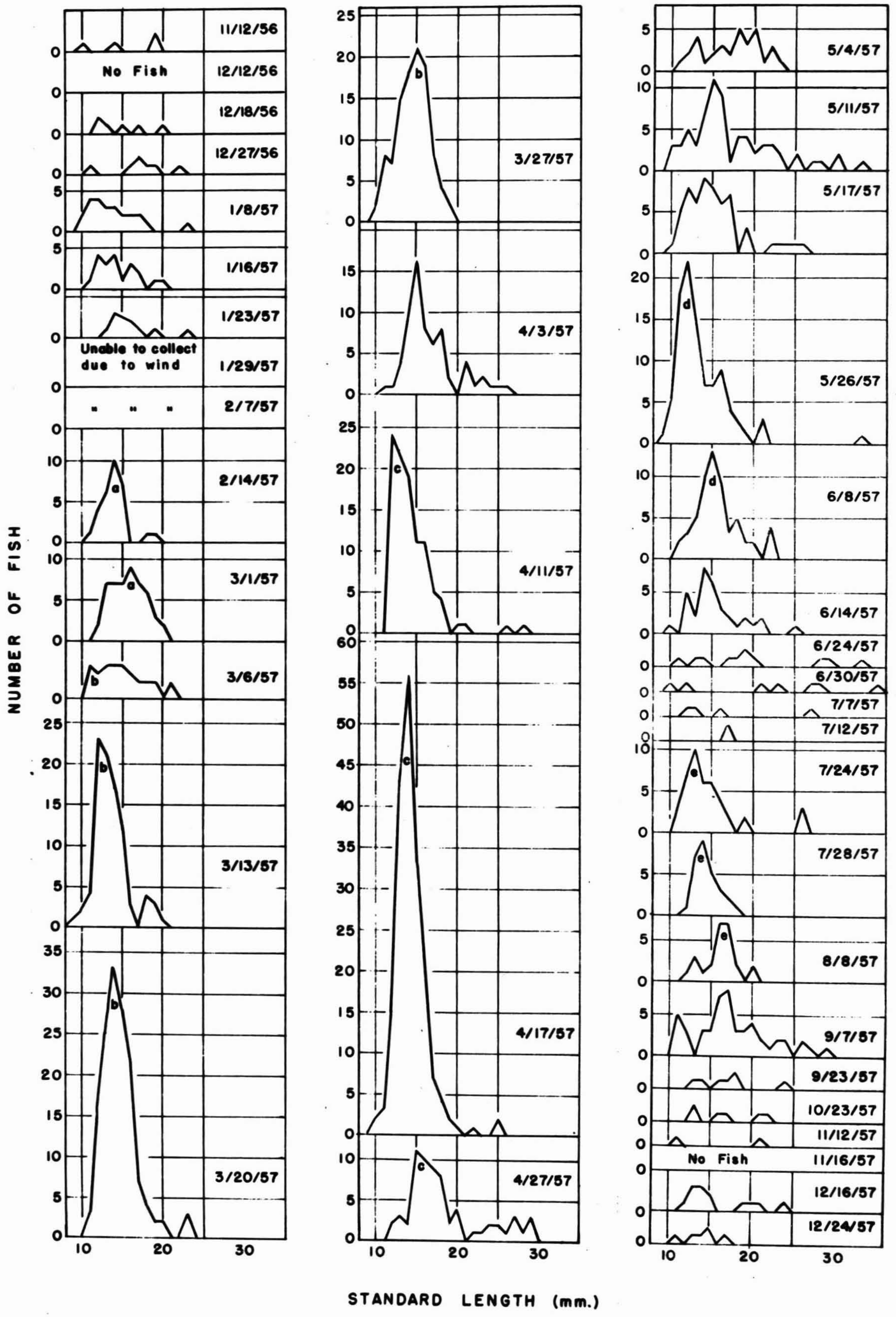

NUMBER OF FISH
STANDARD LENGTH (mm.)
10
20
30
11/12/56
No Fish
12/12/56
12/18/56
12/27/56
1/8/57
1/16/57
1/23/57
Unable to collect due to wind
1/29/57
" " "
2/7/57
2/14/57
3/1/57
3/6/57
3/13/57
3/20/57
3/27/57
4/3/57
4/11/57
4/17/57
4/27/57
5/4/57
5/11/57
5/17/57
5/26/57
6/8/57
6/14/57
6/24/57
6/30/57
7/7/57
7/12/57
7/24/57
7/28/57
8/8/57
9/7/57
9/23/57
10/23/57
11/12/57
No Fish
11/16/57
12/16/57
12/24/57
a
b
c
d
e

TABLE 17

GROWTH RATE FROM PROGRESSION OF MODES OF JUVENILE LENGTH FREQUENCIES FROM DIAMOND HEAD COLLECTIONS

Date (1957)	Mode Symbol*	Length at Mode	Total Growth mm.	Days	Mean Growth mm./Day
14 Feb.	a	14)	2	15	0.13
1 March	a	16)			
6 March	b	11)	4	21	0.19
13 March	b	12)			
20 March	b	14)			
27 March	b	15)			
11 April	c	12)	3	16	0.19
17 April	c	14)			
27 April	c	15)			
26 May	d	12)	3	13	0.23
8 June	d	15)			
24 July	e	13)	3.5	15	0.23
28 July	e	14)			
8 Aug.	e	16.5)			

Average Growth Rate From
Progression of Five Modes = 0.19 mm/day or 5.7 mm./month

*See Fig. 22

TABLE 18

GROWTH RATE FROM REARING TRIALS OF JUVENILE MAOMAO TO 25 mm. AT COCONUT ISLAND

Date (1957)	Brood	Average Standard Length	Total Growth mm.	Days	Mean Growth mm./Day
20 April	A	12.0)	8.2	26	0.31
6 May	A	17.9)			
16 May	A	20.2)			
19 June	4	10.3)	14.5	27	0.54
26 June	4	14.3)			
3 July	4	18.3)			
9 July	4	21.8)			
16 July	4	24.8)			
3 July	3	9.3)	15.7	33	0.48
9 July	3	9.5)			
16 July	3	13.5)			
24 July	3	20.5)			
5 August	3	25.0)			

Average Growth Rate
From Three Rearing Trials = 0.44 mm./day or 13.2 mm./month

rearing trials. The data utilized are presented in Table 18. The average growth rate of three broods containing juveniles between 9 and 25 mm. was 0.44 mm./day, or 13.2 mm./month. This is more than twice as great as the comparable figure obtained from the progression of modes of the length frequency of tide pool juveniles, and can probably be attributed to an abundance of food and a lack of serious competition for it. In comparison, Randall (op. cit.) has shown that the manini kept in captivity and consuming only natural food also showed a significantly larger average growth rate (20 mm./month between March 17, and May 13).

In conclusion, it has been noted that the growth rate as determined from three broods of juvenile maomao reared in a nearly natural environment displayed a gradual decline which was attributed to a seasonal decline as well as a deceleration normally associated with maturing fish. Food appears to be of primary importance to the growth of the maomao; however, crowding and other factors may also exert an influence. From two estimates of juvenile growth, it appears that those reared in captivity show more rapid growth than those in nature.

Orientation to Light

An interesting phenomenon has been observed regarding the orientation of juvenile maomao to light under certain specialized conditions. Apparently these fish are motivated by a phototropism such that they attempt to keep their dorsal side orientated toward the primary source of light, even though this requires swimming with their ventral side toward the water's surface. Although this topic was not included within the scope of the original problem, it is probable that this orientation of the juveniles has some bearing on their migrations, and perhaps their feeding, and therefore will be discussed briefly.

Examples of fish with their ventral side orientated toward the water's surface in the Blue Grotto cave in Italy are reported by Abel (1954); however, only an abstract of this paper was obtained. This behavior has been also observed by divers who have entered underwater caves in which most of the light is reflected from a light floor. Mr. Paul Adachi of Honolulu has informed me that he has seen a large number of fishes in an "up-side-down position" in such caves around Oahu, and Mr. Conrad Limbaugh of Scripps Institution of Oceanography, La Jolla, California, has reported similar experiences from the California area. Von Holst (1950) experimented with orienting reflexes in fishes and concluded that there was an interaction between geotaxis and phototaxis in fishes. He found that the degree of control of the two taxes depended on the strength of each taxis, but was also influenced by the activation of other instincts such as feeding and sleep. Thus he found that phototaxis was of greater influence when feeding, while geotaxis dominated at night when the fish was at rest.

This phenomenon was first observed in the maomao while diving beneath a raft anchored off of the Army Recreation Center at Waianae, Oahu, where a large number of juvenile maomao, ranging from approximately 15 to 50 mm. in length, were seen swimming under the raft with their ventral sides toward the water's surface. This raft was approximately 15 x 20 feet, constructed of wood, and held in place by means of a chain tied to a metal anchor on the white sand substrate approximately 15 feet below. This light substrate reflected a great deal of light, as was most evident when an observer swam beneath the raft and was sheltered from the overhead sunlight. These maomao were probably attracted to this raft as a refuge during their inshore migration as larvae, for no other shelter was evident on the substrate for a distance of about 300 yards in any direction.

In addition to the maomao, a number of other species of fish were seen under this and other rafts, all maintaining this unusual orientation despite the fact that it seemed to require considerable effort to do so. Many of these fishes were actively feeding among the moderate growth of attached algae and invertebrates that encrusted the underside of the raft. Other species of fish included: *Abudefduf sordidus* (100 to 120 mm.), *Chaetodon lunula* (20 to 50 mm.), *Dascyllus albisella* (80 mm.), *Acanthurus sandvicensis* (30 to 50 mm.), *Aulostomus chinensis* (200 mm.), and three unidentified species of acanthurids (probably including *Ctenochaetus strigosus* and *Acanthurus xanthopterus*).

Many additional observations were made under rafts at Waianae, and also at the Fort De Russy Recreation Area in Honolulu. Similar orientation of the juveniles was always observed; however, occasionally, when the reflected light was not as intense, larger fish would be seen swimming beneath the raft with their ventral side down, among smaller fish of the same species with their ventral side toward the surface. Thus, this orientation may be associated with the incomplete development of certain sense organs.

It seems as though the explanation for this phototropism involves an inherent drive to maintain the primary source of light on the dorsal side by the fish concerned; however, the orientation may also be influenced by the position of nearby solid objects in relation to the source of light.

SECTION III

REPRODUCTIVE BEHAVIOR

Observations on the reproductive behavior of maomao were made at infrequent intervals during 1955 and 1956, primarily in the Tuna Pond spawning area at Coconut Island. In the spring of 1957 almost daily observations were made of fish in both the Southwest Point and Tuna Pond spawning areas. During most observations periods, only one or possibly two seemingly unrelated phases of the reproductive behavior were observed. Many individual observations, however, began to reveal a sequence of actions which had the same relationship to each other, until gradually a fairly complete picture of the succession of major events that accompany reproduction evolved. This is by no means a complete picture, for, as is frequently the case in such animal behavior studies, the significance of some of the actions, and probably the existence of some of the more subtle maneuvers were not revealed.

In this behavior analysis, a description of the major phases of maomao reproductive behavior will first be presented, accompanied by notes on comparable observations on other pomacentrids. This is followed by a more detailed description of the individual actions of fish involved in each of these phases, and an analysis of the significance of these actions to the overall reproductive behavior of the maomao in the light of other research in animal behavior.

The major phases of maomao reproductive behavior observed are:

1. Choice of a spawning site and establishment of a territory by the male.
2. Preparation of the spawning site and pair formation.

3. Actions accompanying spawning and fertilization.
4. Parental care of the brood.

Throughout this discussion, individual maomao will often be referred to as "male" or "female", however in most cases these are merely assumptions. As stated previously, no readily observable sexual dimorphism ordinarily exists in the maomao although a distinctive coloration is associated with one phase of reproduction, and all captured maomao displaying this coloration were males. Reference to the sex of a maomao is, therefore, based on some positive identifications of captured fish, but primarily on color inferences. These determinations of sex are further supported by the actions and coloration of other pomacentrids with behavior patterns very similar to that of the maomao, in which sexual dimorphism is distinct.

Methods and materials

Practically all observations on maomao reproductive behavior were made in the vicinity of Coconut Island, Oahu, at the Southwest Point, and Tuna Pond spawning areas (see Figures 1, 23, and 24). Since a greater number of fish occupied the Southwest Point spawning area, a concealed observation platform was constructed at this location in the spring of 1957. This permitted detailed observation of the reproductive behavior of maomao at nearby spawning sites without detection by these easily frightened fish. This observation platform consisted of a narrow plank extending about 4 feet out from shore and it was surrounded by palm fronds which served to conceal the observer from the fish below. In addition, various other naturally concealed locations along the retaining wall from which spawning sites could be observed readily were utilized.

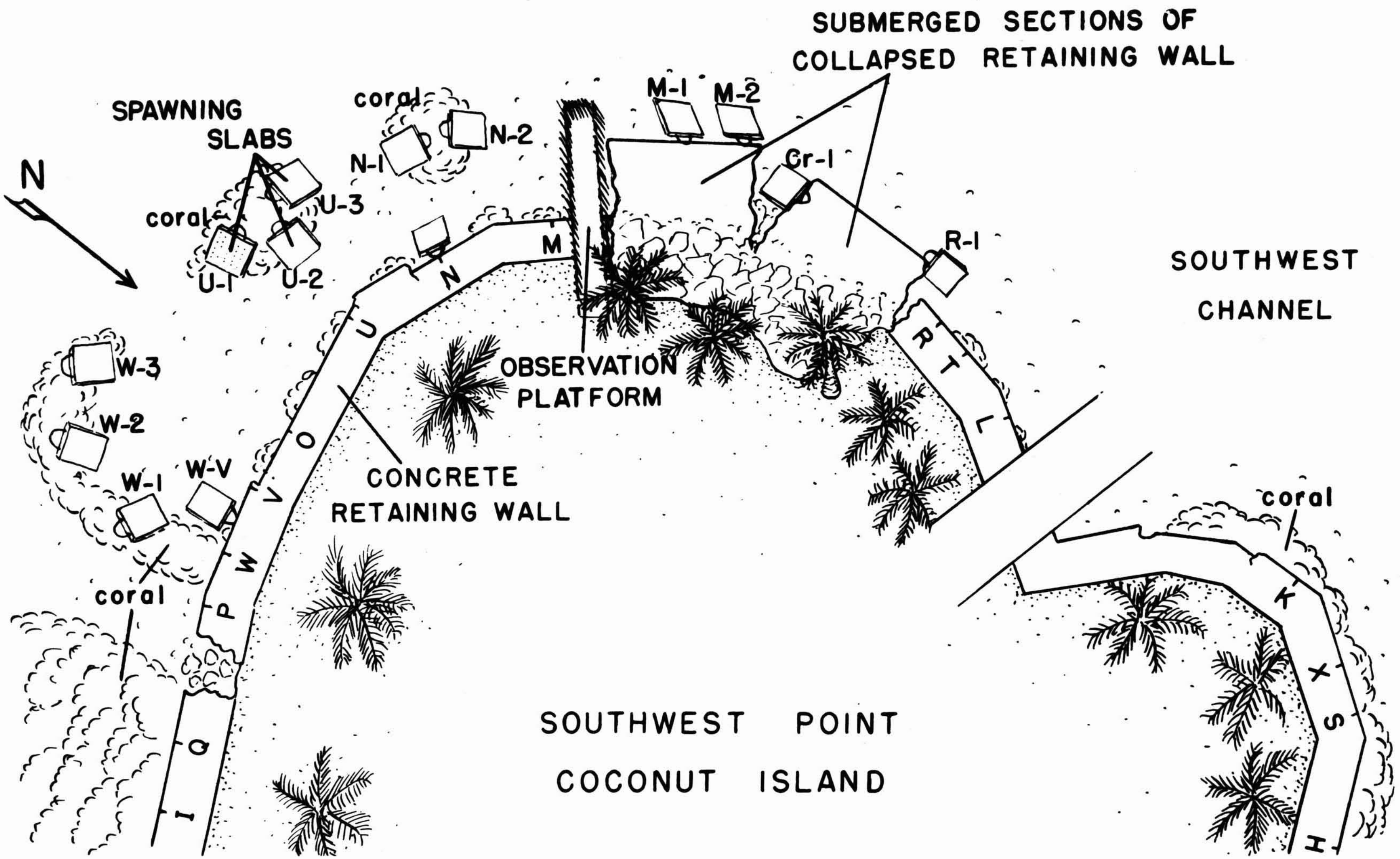


Figure 23. A sketch of the maomao spawning area at Southwest Point, Coconut Island, Kaneohe Bay, Oahu, where observations were made on the reproductive behavior of this species. Letters and numbers indicate the location of established spawning sites referred to in the text.

Figure 24. Views of the Southwest Point and Tuna Pond spawning areas on Coconut Island, where observations were made on the reproductive behavior of the maomao. Top - Southwest Point from the water with partially constructed observation visible in the center. Bottom - Tuna Pond spawning area showing gates to pond and observation house.

One of the disadvantages of observation from above the surface was that good visibility of the fish greatly depended on the clarity of the water and the lack of surface disturbances such as that caused by wind and passing boats. Although both spawning areas utilized for observations were located on the lee side of Coconut Island, the prevalent trade winds caused enough surface disturbance to make observations difficult much of the time, and for this reason many of the observations were made in the morning when the wind velocity was usually minimum. Small quantities of mineral oil were also used during observations to reduce the effect of surface disturbances.

Since a majority of the nesting sites in the two areas observed are on, or very close to the concrete retaining wall surrounding Coconut Island, observations on the behavior of this generally timid fish from points on the shore proved to be more fruitful than from beneath the surface. Repeated attempts to observe their behavior from beneath the water's surface resulted in little success, and the maomao involved would invariably flee to a hiding place as soon as a diver came close enough to their nesting area so that it was clearly visible. The shyness of this species varies considerably with the individual, the surroundings, and the concealment and actions of the observer; however, in no case was success obtained with underwater observations to equal that obtained from above the surface when observing conditions were optimum. Also in favor of observation from shore was the consideration that any disturbances of the natural environment might alter the normal reproductive behavior, and thus limit the value of results obtained.

In order to encourage maomao spawning in the Southwest Point spawning area, and to collect material for other phases of this study, concrete spawning slabs (previously described) were placed in readily observable locations in shallow water as shown in Figure 2. These slabs proved to be attractive to the spawning fish, as did the surface of the retaining wall, and they were frequently occupied during the late spring and early summer of 1957. In the months of April through July over 50 new clutches of eggs were observed on these sites at Southwest Point, and numerous valuable notes on the reproductive behavior were made. Broods of maomao eggs observed in two locations at Southwest Point are illustrated in Figures 25 and 26.

Pattern of reproductive behavior in the Pomacentridae

Reports in the literature on the reproductive behavior of pomacentrid fishes are limited to a few short descriptive notes; however, two workers have contributed more detailed accounts of reproductive activities in the genera Dascyllus, Premnas, and Amphiprion (Verwey, 1930a; Garnaud, 1951, 1957). Although often lacking detail, accounts of pomacentrid reproduction generally reveal a common pattern which is not unlike that found in many other teleosts which attach their eggs to a substrate and exhibit parental care. The pattern of pomacentrid reproduction includes the following: the male usually establishes a territory, and chooses and prepares a site where the spawning is to take place; the male is usually aggressive and courts the female by means of various maneuvers, frequently displaying special sexual coloration; the female, when accepted as a mate at the spawning site, attaches her eggs to the prepared substrate, and the male fertilizes them; one or both parents may care for the clutch of

Figure 25. A brood of maomao eggs (the large dark area surrounding the arrow), viewed from above, and attached to the retaining wall at site "O" Southwest Point, Coconut Island. The guardian fish is not visible.

Figure 26. A guardian maomao (circled) protecting a brood of eggs attached to a concrete spawning slab located at site "Cr-1" at Southwest Point, Coconut Island. This view is from the observation platform.

eggs until hatching, but the male is the most active guardian.

In order to illustrate some of the variations noted in the general pattern of pomacentrid reproductive behavior, a brief resume of the salient points of other behavior studies in this group is presented.

The ethology of the pomacentrid *Dascyllus trimaculatus* (Rüppell) is the subject of a recent publication by Garnaud (1957) in which the following activities associated with reproduction are described. The pre-spawning behavior is quite abbreviated: the male only cursorily cleans the substrate, he performs a "nuptial dance" along side of the female to attract her, and he undergoes a startling color change; when the female responds to the male's courting by following him, he indicates the spot where she is to deposit her eggs; the eggs are deposited early in the morning of the day following the "nuptial dance"; the female then leaves the clutch of eggs to the care of the male whose fanning is essential for their development; the male alone defends a territory around the spawning site from all possible intruders; a single pair undergoes repeated spawnings in a single season.

Longley and Hildebrand (1941) report the establishment and defense of a territory, and guarding of a "nest" of attached eggs for a number of pomacentrids from the Tortugas region of southern Florida. Among those observed, Chromis insolatus (Cuvier & Valenciennes) displayed spawning coloration and was extremely aggressive in its defense of clutches of eggs. However, the sex of the guardian fish was not determined. These authors also repeatedly observed spawning activities of *Abudefduf saxatilis* (Linnaeus), believed to be closely related to the maomao, and on three occasions captured a parent fish while it was in the process of guarding its "nest". In all three cases the guardian fish proved to be a male. While this species was being observed, a smaller fish (assumed to be a female) was tolerated in a nest guarded by a larger male, but no spawning was observed.

Brinley (1939) observed a strong territoriality associated with reproduction in the small pomacentrid, Pomacentrus leucostictus Müller & Troschel. This species frequently spawns in old gastropod shells, and the clutch of eggs is guarded exclusively by the male. Longley and Hildebrand, op. cit., describe the mating behavior of P. leucostictus, consisting of sexual dimorphism in the form of a rapid color change, and a series of postures and dashes apparently designed to attract a mate.

Breder (1932), and Breder and Coates (1933), describe some phases of reproduction in Pomacentrus leucoris Gilbert based on observations made on a few individuals brought to the New York Aquarium from the Galapagos Islands. With this species both the male and female took part in the preparation of the spawning site. They prepared a rocky surface by scouring it with sand brought up from the bottom in their mouths and blown against the surface. They then fanned the surface vigorously and picked off the remaining sand grains. After preparing and abandoning a number of areas, the female finally spawned in one, and the male fertilized the eggs. Although both the male and female took part in both the preparation of the site and guarding and care of the eggs, one individual (presumed by the authors to be the male) was much more active in both phases of reproductive behavior.

Additional notes on other species of the genus Pomacentrus indicate that the reproductive behavior generally conforms to the family pattern previously described. Longley and Hildebrand (op. cit.) have observed the establishment of a defended area around attached clutches of eggs in Pomacentrus partitus Poey, and Pomacentrus planifrons Cuvier & Valenciennes; the guardian of the latter species was identified as a male.

Some interesting variations in the general theme of pomacentrid spawning have been observed in Hypsypops rubicunda (Girard) by Mr. Conrad Limbaugh of Scripps Institution of Oceanography in California, however, these observations are as yet unpublished. The major events associated with reproduction in this species are as follows: the male establishes a territory, and within it an area on the substrate is cleaned except for a small portion in the center on which a certain red alga is allowed to grow; this alga is kept clean and cropped, and later the eggs are attached to it; when a ripe female approaches the site, the male challenges her by rushing at her emitting a loud thumping noise; unlike other invaders, the female, if ready to spawn, does not usually retreat even though she may be bitten by the male; the female is eventually accepted as a mate when she arrives within about 1 foot of the prepared spawning site; the female then spawns and leaves the area; the male remains and cares for the brood throughout their period of incubation, thus following the general pattern of other pomacentrids.

In still another genus of pomacentrids, the species Stegastes chrysurus (Cuvier and Valenciennes) observed by Longley and Hildebrand (op. cit.) strong parental manifestations were displayed by a single fish guarding clutches of eggs attached to coral branches. The sex of the guarding fish was not determined, nor were other details of spawning observed.

Some interesting modifications of the general reproductive pattern of pomacentrids exists in at least two genera with specialized habitats. These include species of the genera Amphiprion and Premnas which live among the tentacles of giant sea anemones in an apparent symbiotic association.[1] In a rather extensive investigation of this group, Verwey (1930a) describes various phases of the reproductive behavior of four species. From observations on Amphiprion percula (Lacepede) in the Batavia area he outlines the following reproductive behavior pattern for this species: these fish nip each other when sexually excited, but the female is larger and takes the initiative in this activity, nipping at the flanks of the male; the male cleans off an area on the substrate near the base of the anemone which it occupies, and the female attaches her eggs in the prepared site; the male then induces the nearby anemone to cover and conceal the clutch of eggs with its tentacles by rubbing and biting it; both parents guard, clean, and aerate the eggs, but all parental manifestations are shown to a greater extent by the male. Verwey (op. cit.) found that this species displayed a strong territoriality around its anemone habitat throughout the year, regardless of reproductive activities it might be undertaking. More recently Garnaud (1951) made additional observations on A. percula in aquaria at Monaco, and his findings were in substantial agreement with those of Verwey with the

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[1] This association of fish and coelenterate has attracted the attention of many naturalists, and notes of various aspects of the ecology of these anemone fishes are dispersed throughout the literature. For details not covered in the above review see: Crespigny, C. C. (1869); Sluiter, C. (1888); Kent, S. (1893); Horst, R. (1903); Plate, I. (1908); Weber, M. (1913); Ahl, E. (1925); Delsman, H. C. (1930); Verwey, J. (1930b); Moser, J. (1931); Gohar, H. A. F. (1934); Herre, A. W. C. T. (1936); Sachs, W. B. (1937); Mitsch, H. (1941); Gudger, E. W. (1946).

exception of details on the time of day that spawning took place, and the number of eggs deposited at one time.

Other anemone fishes observed by Verwey (op. cit.) included *Premnas biaculeatus* (Bloch), *Amphiprion polymnus* (Linne.), *A. ephippium* (Bloch), and *A. akallopisus* Blecker. The greatest detail was observed in the behavior of *A. percula*, but the behavior of these other species did not seem to differ from that species greatly. In all this group a strong territoriality and a degree of permanence in the existence of pairs is an outstanding feature. A more recent work on the anemone fish *Amphiprion bicinctus* Rüppell by Gohar (1948) sheds little light on the actual reproductive behavior of this group, except that in this case only one of the parents (of undetermined sex) acted as a guardian of the clutch of eggs.

At least two other workers have observed some aspects of pomacentrid reproductive behavior. However, their accounts were not available at this time. The work of Lo Bianco (1919) was not available, but according to De Gaetani (1932) Lo Bianco summarizes the preparatory behavior of *Heliastes chromis* Gunther (= *Chromis chromis*) prior to spawning. Other observations made include a description of the spawning of *Abudefduf saxatilis* (Linnaeus) by Mr. F. G. Wood of the Marineland Research Laboratory of St. Augustine, Florida, but this information was not made available as it is being prepared for publication.

The first published account of any aspects of maomao reproduction is that by Tester (1953) in which he briefly describes observations on parental care, and the eggs and larvae. This preliminary study stimulated interest that resulted in the present study in which the following details of reproductive behavior were revealed.

1. Choice of a spawning site and establishment of a territory by the male.

During the early spring male maomao begin to dissociate from aggregations to choose suitable spawning sites on the substrate. They then actively defend an area surrounding the chosen site, aggressively attacking intruders (within certain size limits) that enter the roughly defined territory. The territory usually extends out from the site in all directions to include an area with a radius of from 3 to 8 feet or more. The extent of this area defended by the male maomao varies greatly depending on the topography of the surrounding area, the plane of the spawning site in relation to the surroundings, the aggressiveness of the defender, and the amount of pressure exerted on the defending fish by intruders.

The substrate chosen for a spawning site is usually a hard, relatively smooth basalt or limestone surface free of large sessile organisms. Uncluttered areas on concrete structures such as pipes, walls, and pilings are also among preferred sites. Only rarely have maomao been observed defending territories around coral formations.

Maomao spawning sites have been observed from the surface to depths of about 90 feet, which is the approximate range of the observed adult habitat. The same site may be defended and utilized again and again; however, it has not been determined if the same individual occupies a site on successive occasions. Longley and Hildebrand (1941) observed a male Abudefduf saxatilis, identified by means of a malformed profile, defending the same territory on a coral head three times in one season, and for two successive seasons.

2. Preparation of the spawning site and pair formation.

After the male maomao has chosen a site and begun defense of a territory surrounding it, he prepares the surface selected for the future attachment of eggs. This preparation consists primarily of clearing the surface of small sessile algae and invertebrates by rasping them off with his teeth. Periods of rasping are interrupted by short periods of fanning of the surface by the male. Fanning is accomplished primarily by actions of the pectoral and caudal fins, similar to that executed later during aeration of the egg mass. Defense of the territory continues throughout this preparation phase.

Some time after the start of cleaning activities, the male begins to assume a nuptial coloration, and commences courting activities. During this color change the normal black stripes become a pale gray and are often indistinguishable, while the normal brassy green to yellow base color is transformed into a pale blue. This bluish hue is more intense on the dorsal portion of the body, and the pale ventral portion is usually unchanged. The intensity of this sexual coloration changes very rapidly and varies with the activity and level of excitement of the male maomao during courting.

Female maomao, when ready to spawn, hover near the periphery of the male's territory or mingle with circling maomao aggregations which appear to be feeding nearby. These females display no apparent distinctive marking or coloration to indicate their sex or readiness to spawn.

Male courting behavior consists of displays and maneuvers in various sequences performed in the vicinity of a waiting female. The maneuvers include "looping" and zigzag swimming" as illustrated in Figure 27A and B, and they are executed by the male as he swims toward and away from the female. The male maomao may also assume a vertical stance in the vicinity of the female as illustrated in Figure 27C. The possible significance of these and other modes of courtship behavior will be discussed in a later section.

Since the male maomao still maintains an aggressive defense of his territory, his courting activities also take on aggressive overtones. If during one of the male's courting maneuvers a female approaches him, the male immediately rushes at her, and she usually retreats. Then as the male turns from his attack to swim back to his spawning site, the female also turns and attempts to follow. This behavior is often repeated a number of times until finally the female is permitted to follow the male and is temporarily accepted as a mate at the spawning site. The pair then engage in chasing each other in a tight circle, or "tail-on-tail chasing" (Figure 27D) on the spawning site. This "tail-on-tail chasing" which may continue intermittently for some time, results in an ultimate acceptance or rejection of the female as a mate.

3. Actions accompanying spawning and fertilization.

During spawning, the female maomao swims slowly back and forth over the substrate along semicircular paths maintaining contact between the ventral surface of her body and the substrate. Expulsion of the ova and the disposition of the genital papilla were never observed during spawning. The female maomao exhibits considerable diligence in spawning, often maintaining contact with the substrate for 20 to 30 minutes at one time.

Behavior of the male maomao during the time the female was depositing her eggs included four major activities: release of sperm over the recently deposited eggs, inspection and fanning of the egg mass, stimulation of the female, and driving intruders from his established territory. The

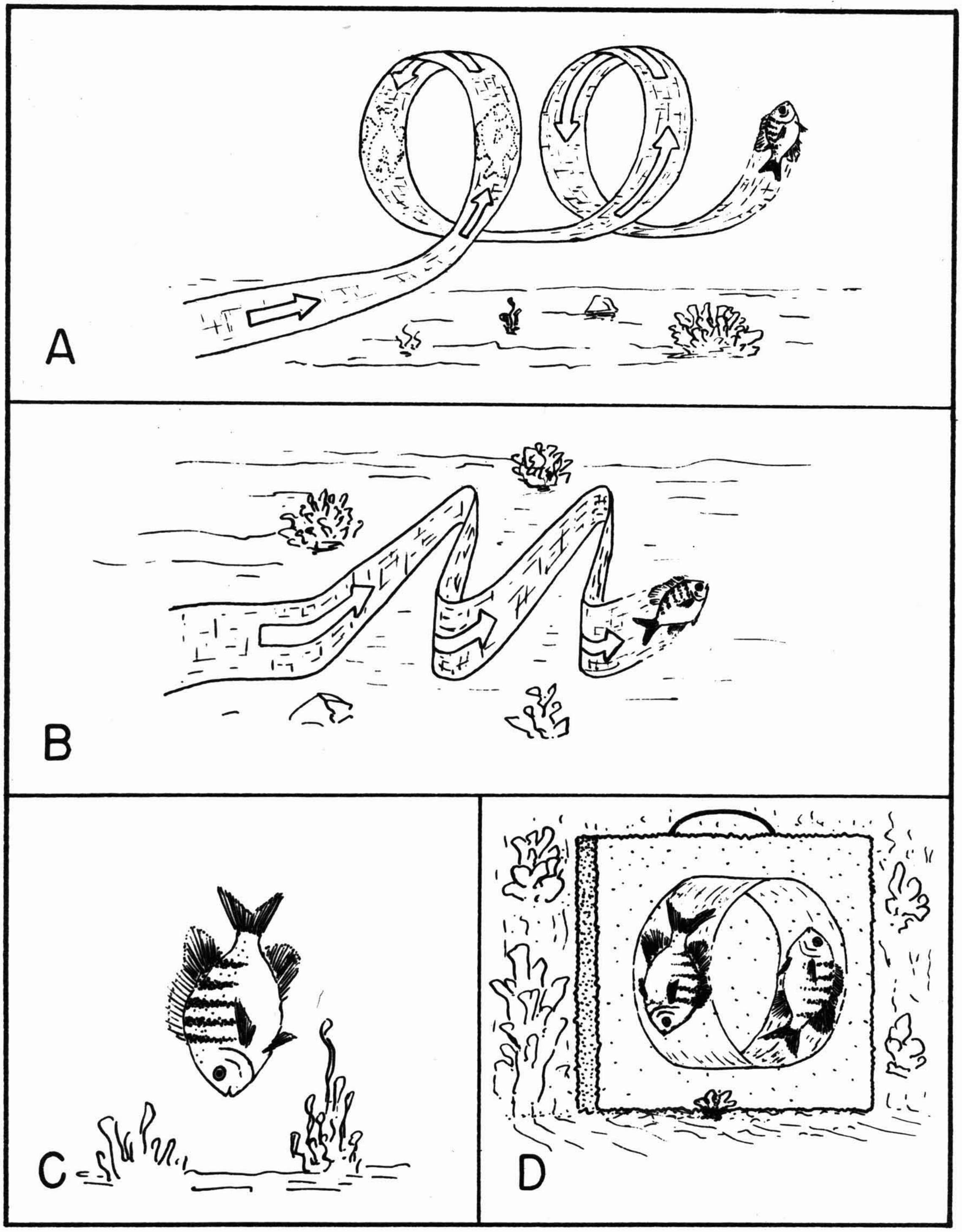

Figure 27. Diagrams of some maneuvers recorded during observations on the reproductive behavior of maomao. A. Looping. B. Zigzag swimming. C. Vertical stance. D. Tail-on-tail chasing.

accomplishment of these tasks results in a frenzy of activity by the male which is in direct contrast to the slow steady movements of the female during spawning.

The release of sperm by the male maomao appears to be a relatively rapid action. The male swims up to the nest every few minutes, and for three or four seconds swims across the surface of the "nest" with his ventral body surface pressed against the egg mass, presumably releasing sperm; however, no direct evidence of the release of seminal fluid, such as cloudiness in the water at the suspected point of release was observed.

As the spawning female swims slowly over the substrate in an almost uninterrupted action, the male occasionally enters the "nest" to nudge or nip her in the region of the ventral caudal peduncle or genital area. This action occasionally results in "tail-on-tail chasing"; however, when the male leaves the site the female continues to spawn. On occasion, when the male is away from the immediate vicinity of the spawning site chasing territorial intruders, the female ceases her spawning activity and hovers in a normal upright position at a point about 12 inches from the "nest". On his return, the male immediately rushes at her, and a brief session of "tail-on-tail chasing" ensues; the female then resumes her spawning activity.

Occasionally the male inspects the "nest" by swimming up to the spawning site until his snout almost touches the egg mass. Here he remains motionless for a short period of time as though he were visually examining the eggs. The male maomao then usually fans the egg mass, which is an action frequently observed during the period following spawning when the male is exclusive guardian of the brood.

While the female is busy spawning, most of the time the male remains about 2 feet away from the nest, nervously swimming back and forth as though held by two antagonistic drives: one attracting him to the nest to fertilize and inspect the eggs and stimulate the female, the other drawing him away from the "nest" to drive away the ever-present intruders who are attempting to devour the newly laid eggs. In driving off intruders, the male maomao swims rapidly toward them, and without exception, they turn and flee.

4. Parental care of the brood.

After spawning the female leaves the site. It appears that the guardian of the developing eggs is primarily the male maomao, as is the case in all of the other pomacentrids thus far observed. During the care of the brood, the male maomao is primarily engaged in the following activities: chasing territorial intruders; fanning the egg mass; inspection and picking of defective eggs from the "nest"; and periodic preparation of an adjacent area for spawning, and the attraction of a mate.

Chasing of intruders during this phase of reproduction appears to be less aggressive than during the spawning period, although considerable variability exists among different guardian males. Chasing of intruders continues throughout this period of caring for the brood; however, male maomao have been observed merely to threaten intruders by moving a short distance toward them with raised dorsal fin. This often serves to intimidate the intruder making pursuit unnecessary.

When not chasing intruders, the guardian maomao may spend much of his time fanning the clutch of eggs, apparently to insure adequate aeration and to keep the egg mass free of silt. As pointed out in the section on development, the time spent fanning seems to vary with the stage of development of the eggs, and perhaps with other factors such as the pressure exerted by intruders.

Periodically the guardian male maomao visually inspects the egg mass to remove defective or unfertilized eggs. During this activity he faces the surface of the nest, examines it visually at close range, and occasionally makes a short lunge forward, picking off the undesirable egg with his mouth.

Preparation of an area adjacent to an existing egg mass, and attraction of a female to spawn on it is a fairly common occurrence among guardian maomao. When such activity is observed, the previously described behavior for site preparation and pair formation is superimposed on that for parental care. This often results in a frenzy of activity by the male maomao, especially when he is plagued with a large number of predators attempting to invade his territory. As many as five separate broods have been observed under the care of a single male maomao at one time; however, spawning seldom extends over a period of more than 4 days after the first spawning.

When all of the eggs have hatched or have been removed as defective, the male maomao abandons the site and no longer exhibits territorial behavior.

Analysis of Maomao Reproductive Behavior

An analysis of some aspects of maomao reproductive behavior is undertaken at this time in order to understand better the behavior of this species in the light of present concepts of animal ethology and to compare certain aspects of maomao behavior with similar actions observed in other fishes. Such an analysis may lead to a better understanding of the significance of specific actions in the maomao and serve to define more clearly avenues of approach to further research on the behavior of this species.

In order to present an analysis of this type it will be necessary to introduce some concepts and terms utilized by behaviorists and deemed necessary to the following discussion. These concepts were adopted because they lend themselves readily to aid in the interpretation of observations such as have been made in this study of maomao behavior. These concepts have been introduced and developed in various works by Tinbergen, Lorenz, Noble, Baerends, and others, and have been summarized by Tinbergen (1951, 1953), Thorpe (1951), and Baerends (in Brown, 1957).

According to these behaviorists, both external and internal stimuli are necessary to activate instincts. However, since external stimuli are more readily observable, they are of primary concern in this study. It has been found that of the many external stimuli received by an animal in a given situation, only a certain few serve to release and direct a specific response. These few stimuli are termed "sign stimuli" and act as "releasers" for they release a specific innate action in the animal receiving them. Individual stimuli have different values as releasers of a definite response, depending on their various qualitative and quantitative properties. Tinbergen (1953) shows that during the breeding season of the three-spined stickleback, Gasterosteus aculeatus, the male assumes brilliant nuptial coloration. This includes red underparts and shining blue eyes, in contrast to previous drab coloration, while the female assumes a silvery gloss and displays an abdomen swollen with eggs.

The male then establishes a territory and constructs a nest. When a suitable female approaches the male he performs a dance around her. By the use of models it has been determined that the sign stimuli in this case are rather simple and conspicuous, as apparently is the case with most sign stimuli when both the actor and reactor are animals of the same species. It was found that a simple model, almost regardless of shape, with a red lower and greenish-blue upper side, would evoke attack by the male or courting by the female stickleback, and in further observations the red underside proved to be the most important character. In the female, the swollen abdomen is the most important character causing the male to react. Thus the sign stimulus of the male consists primarily of a red underside, and this acts as a releaser, releasing the female's innate drive to follow the male to the nest. The swollen abdomen, in turn, is the primary character making up the sign stimulus of the female which releases the next action in the reproductive behavior of the male. A continuous chain of reactions of sign stimuli displayed by the male releasing actions in the female, which in turn result in the sign stimuli that release actions in the male, etc., is illustrated by Tinbergen for the entire reproductive process in the three-spined stickleback.

Another concept to be utilized is one which occurs when two antagonistic drives of approximately the same strength are activated simultaneously in the same animal. Under such circumstances so-called displacement activities result in order to release the tension created by the two antagonistic drives. This displacement activity is in the form of a third action, different from either that might result from the original drives. An example of this is seen in border fighting of the three-spined stickleback. A male stickleback, meeting a stranger away for his territory exhibits an escape drive, but when meeting a stranger as an intruder to his territory he exhibits attack. A meeting at the border of his territory elicits the drives both to attack and to flee simultaneously. This results in a displacement activity of "sand digging" which happens to be the first step in nest building and quite unrelated to both attacking and fleeing.

Although these concepts are corroborated by convincing experimentation, interpretation of the results is subject to some controversy; however, they are extremely useful and readily adaptable to some aspects of observations made on maomao behavior, and therefore will be utilized in the following discussion.

1. Territoriality.

Examples of territoriality are numerous among the vertebrates and are commonly associated with reproductive activities. In fishes, a territory, which is generally defined as any defended area, is commonly established and maintained by substrate spawners that guard their broods during early development. Territorial behavior has been described in a number of fishes by Noble (1938), and in his examples he points out that the male usually establishes and defends the territory. In addition, strong territorial behavior is generally associated with fewer eggs in the spawn and marked sexual dimorphism in which the male is most conspicuously adorned (Noble, op. cit.; Aronson in Brown, 1957).

The establishment and defense of territories by adult maomao has been observed many times in the spawning areas at Coconut Island (stippled areas in Fig. 1). The general pattern of activity is one in which a mature male maomao begins actively to defend the area around a suitable spawning site. The defending fish aggressively attacks all other fish including his own species, which enter the roughly defined limits of his territory. This instinct for maintaining territories seems to be strongly developed throughout the family Pomacentridae (Verwey, 1930a), as is evident in the previous review of the literature.

The size of the territory defended by the maomao seems to depend largely on the location of the chosen site, and the aggressiveness of the defending fish. It may also be influenced by the density of other territories in the vicinity, the depth of the water, and the type of substrate. When the site chosen is on a sloping bottom, or vertical concrete or rock substrate, the territory is usually a region in a sphere around the nest with a diameter of about 5 feet, although this distance ranged from 3 to more than 8 feet in some cases. Limits of the territory are often defined by prominent objects in the vicinity such as protruding rocks, coral heads, and other structures.

The position of nesting sites chosen by male maomao appears to be controlled primarily by at least two factors; a suitable substrate for the deposition and development of eggs, and proximity to some recess that affords protection from approaching danger. The proximity to the normal maomao habitat also seems to be of importance. The general distribution of nests in a spawning area appears to be regulated by the availability of desirable sites and the pressure of males competing for them. Breder (1936) describes a similar situation in a discussion of the reproductive habits of the Centrarchidae (sunfishes) in which the distribution of nests is controlled by two antagonistic forces:

(1) the centrifugal effect between competing males, and (2) the centripetal effect induced by limitations of suitable bottom, and probably some form of population hierarchy. In addition he found that the position and form of the nests constructed by the male sunfish are influenced by a large number of purely physical factors in the environment including temperature, sunshine, depth of water, rate of flow of water, nature of the bottom, and proximity of protecting objects.

Evidence of the factors controlling the distribution of maomao nests was observed a number of times during the breeding season at the Southwest Point spawning area on Coconut Island. When only a few nests were observed in the area, they were well distributed among the most desirable locations; however, when the area was crowded with spawning fish, and the better sites all taken, a number of clearly less desirable spawning sites were occupied.

The limitation of suitable space to meet the minimum requirements for spawning sites and accompanying territories may limit the number of maomao spawning, and, indirectly, the size of the population, although only a few observations support this hypothesis. One example that may apply is that of the West Reef spawning area (Fig. 1), which apparently contains a very limited number of suitable spawning areas. These sites are restricted to three discarded sacks of concrete that had been thrown into a large, dense growth of living coral. The sacks disintegrated leaving their hardened contents as very suitable spawning surfaces for the large population of maomao that inhabit this area. The fact that all of these sites contained egg masses almost whenever they were observed, including one period when maomao spawning elsewhere was rare, suggested that the competition for space on which to spawn was high in this area, and perhaps even limited the number of fish able to spawn. Since no other suitable spawning sites are to be found for some distance around this site, it is possible that migration is limited and such competition for spawning space does exist. Further observations of this situation and others like it are necessary before this hypothesis can be accepted or rejected.

In a discussion of the space requirements for territories by cichlids, Baerends and Baerends-van Roon (1950) point out that the number of fish that become dominant and establish territories depends on the size of the available area, and also the size of the fish establishing territories, since the larger fish seem to occupy larger territories. Breder (1936) observed that in centrarchid spawning, if only a few fish are spawning, they distribute themselves equally over the most desirable areas. As more individuals begin to spawn, the territories become more crowded together, and less desirable locations on the periphery of the most suitable area are occupied. Finally, a point of saturation is reached, and when too many fish are crowded together to spawn it was found that the genital products were resorbed into the gonads, and spawning did not take place. In this way, the population is limited and yet the reproductive potential is retained in reserve to help stabilize the population in case of heavy mortality.

As previously stated, maomao seem to occupy the most desirable spawning sites first, and then as the number of individuals spawning in a given area increases the less desirable sites are occupied. The total number of established sites in the Southwest Point spawning area were never all occupied at one time, and therefore, a situation in which extreme competition for spawning space existed was never carefully scrutinized.

Some puzzling observations were made in regard to the priority with which spawning sites were chosen and occupied, which did not conform to the general pattern described above. On one occasion at the Southwest Point spawning area, a maomao "nest" was observed on a very undesirable site while choice sites remained unoccupied nearby. In this case the eggs were deposited on a small fragment of concrete that had broken off of the retaining wall and was protruding out of the muddy substrate. Besides being of inadequate size to hold the usual number of eggs spawned, the parent fish had difficulty in attempting to keep them free of silt. Another example of a poorly chosen site in the midst of an area containing better sites, was observed on a reef in the eastern portion of Kaneohe Bay in September, 1954. The spawning site was in the center of an oval sandy area about 12 x 15 feet, and surrounded by large heads of Porites lobata and P. compressa. The depth of water was about 10 feet over the sandy area, and 6 to 8 feet over the surrounding coral. The eggs were deposited on a small dead head of Porites compressa which was being vigorously defended by a guardian maomao. This location seemed to lack both characteristics of sites chosen by most maomao: a suitable substrate for the deposition and development of eggs, and proximity to some recess affording protection from approaching danger. The cause of such apparently aberrant behavior in the choice of a spawning site is obscure and requires a more thorough knowledge of the stimuli responsible for initiating reproductive behavior in the male maomao.

Some evidence exists among the pomacentrids of the establishment of territories that are not directly associated with reproduction. Among the anemone fishes, Amphiprion percula displays a certain degree of territorializing, even though a pair may inhabit a large individual anemone with five or six other fish of the same species. A strong territoriality is also displayed by Premnas biaculeatus which lives between dense patches of Acropora hebes and does not hesitate to attack any intruder in its territory, including a human diver, (Verwey, 1930a). Strong territoriality has been observed in Pomacentrus jenkinsi Jordan & Evermann; however, it is uncertain if this behavior is associated with reproductive activity. This Hawaiian species usually follows a solitary existence, and on a number of occasions individuals have been observed vigorously defending a territory in their shallow water habitat. On one such occasion in October, 1955, a mature P. jenkinsi was observed on Coconut Island reef ardently chasing a large number of fish milling around its territory. Because of the apparent interest in the area shown by all of the fish in the vicinity, the defending pomacentrid was suspected of guarding a clutch of eggs; however, a thorough search of the site failed to reveal any such nest. This fish was then captured, and subsequent dissection revealed that it was a moderately ripe female. Since no other individual of this species was observed in the vicinity, it is assumed that this female had established a territory for other than reproductive purposes, or that the pattern of reproductive behavior in this species does not follow that reported for other pomacentrids in which the male predominates in the establishment and maintenance of a territory.

It is assumed that some selective advantages are conferred on a species by its establishment and defense of a territory in which to mate and spawn, and therefore, these advantages are briefly reviewed with comments on their application to the maomao. The establishment of territories may limit the breeding population according to the available space and suitable substrates, and in this way may exercise a control of the population so that it does not increase beyond the carrying capacity of the habitat. Although some areas seem to present almost unlimited surfaces suitable for egg deposition, other factors such as the proximity of shelter for the guardian fish, and the occurrence of predators may make such areas hazardous from the standpoint of survival. Conversely, the establishment and occupancy of a territory for a period of time gives the occupant a familiarity with the area that puts him at an advantage in defending it and hiding from dangerous predators. Also, an established territory, which nearby potential predators learn to respect, affords an additional advantage to a guardian fish in protecting his brood. In the maomao, establishment of territories may limit the spawning population and thus create a reserve of males and females to insure population stability in the case of unusual mortality among the spawners; however, observations thus far indicate that this probably does not apply in most cases with the maomao as previously pointed out. The established territory may also afford the defending fish a feeding advantage, creating an area for his exclusive feeding; however, this may prove to be of little advantage to the maomao as often the pressure of intruders is so great that he has little time to feed and is busy in almost constant pursuit. Also, as pointed out in the section on feeding habits, this species often rises toward the surface in pursuit of certain elements in the plankton, and in such cases being restricted to a territory near the bottom might prove to be a disadvantage. Finally, an increased defensive vigor in fish associated with the establishment of a territory and the onset of sexual activity allows it to defend better its chosen area and thus insure maximum survival of brood. Increased aggressiveness during spawning coupled with a familiarity of the territory both seem operative in conferring survival advantage on the guardian maomao and his brood.

2. Aggressive behavior in defense of a territory.

The first behavioral manifestations of the activated reproductive instinct appear to be aggressive actions utilized by the maomao in the establishment and defense of a territory. Threatening and chasing are the main forms of aggressive behavior observed in the maomao, and these appear to be greatly intensified during certain periods in the breeding season. When a certain level is reached, this aggressive behavior serves a definite purpose in the male maomao: it results in the exclusion of all other fish from an area on the substrate necessary for successful mating and propagation of offspring. As previously mentioned, only the male takes the initiative in maomao reproductive behavior, with forceful, pugnacious actions, while the female remains largely passive.

Increased aggressiveness associated with his reproductive state confers at least two advantages on the male maomao which aid him in the establishment and maintenance of his territory. It permits him to rise above his usual shyness and possible subordinate position in his normal social hierarchy; fishes in the area soon learn to respect him and his defended domain. Also, it allows him to become increasingly familiar with the one area which he is defending, and thereby, he places himself at a definite advantage over the casual intruder. Every advantage possible is required when attempting to protect a large number of eggs that are highly prized as food by a great number of reef fishes.

Aggressiveness associated with reproduction in fishes is usually in the form of a bluff or threat, and combat involving physical contact and resulting in injuries is uncommon (Tinbergen, 1953). This was confirmed in numerous aggressive acts observed in maomao in which actual physical contact was seldom observed. Only in the so-called "kissing behavior" (described later) did such contact appear deliberate. Maomao aggressive behavior may take two forms as previously mentioned; that of threat, and an extension of threat, the chase. A great deal of variability exists in both of these forms of aggressive behavior. However, repeated observations revealed that belligerant acts of male maomao are expressed at three levels: (1) rapid and forceful chasing, with close contact maintained between the pursuer and the intruder; (2) reserved pursuit, in which the defending fish does not swim as fast or as far, and close contact with the pursued fish is not made; (3) threatening, with little of no pursuit. Aggressive behavior varied between individuals at the same site on different occasions, and among guardian males on adjacent sites at the same time. An example of the latter case was observed at the Southwest Point spawning area, where two male maomao simultaneously guarding their respective broods at sites "U-1" and "U-2" were observed to react quite differently to what appeared to be approximately the same stimuli. This took place when an invader entered the territory of one fish, and after being chased away, entered the territory of the second fish in about the same manner. The first maomao pursued the intruder in a very reserved manner; however, when the intruder entered the territory of the second maomao, he was threatened, and almost before he had a chance to react, he was attacked and forcefully chased from the territory.

The circumstances surrounding these occurrences may shed some light on the cause for such differential behavior. The first maomao was a normal colored male guarding a small clutch of eggs whose color indicated that they were in an early stage of development. The second maomao guarded a larger clutch of eggs in a later stage of development, and the coloration displayed by this fish was the pale blue of a mating male. Further observations confirmed that the stage in the mating sequence, or what might be called the "reproductive status", affects the belligerancy of a guarding fish, with the peak of aggressiveness coinciding with the peak of sexual excitement just prior to and during mating. The blue coloration of the second maomao described above, indicated this latter state. Despite repeated observations, no consistent relationship was revealed between the number or stage of development of the eggs per se and the plane of aggressiveness of the guardian fish.

Another factor that seems to influence the level of aggressiveness in the guardian male maomao is the amount of pressure exerted by intruders. This is illustrated by observations made at site "C" in the Tuna Pond spawning area of a guarding maomao, on three consecutive days, during periods in both the morning and afternoon. An aggregation of about fifty maomao, accompanied by a number of other fishes, was seen actively feeding in this area during the three morning observation periods, but had dispersed in the afternoon. These fish were feeding adjacent to the guarded area at site "C" and the guardian maomao was kept busy forcefully chasing individuals invading his territory. During the afternoons, when very few fish could be seen in the vicinity, the guardian fish displayed a greatly reduced state of aggressiveness. This correlation between guardian aggressiveness and predator pressure was corroborated by similar observations on two other occasions.

The stimuli required for the release of aggressive behavior associated with reproduction appears to be primarily visual in nature; however, the relative influence of various components of the visual stimuli as releasers has not been determined. During the course of observations, aggressive behavior was demonstrated by the maomao toward all of the common species of reef fishes entering its territory, with the exception of some of the acanthurids, notably the common "manini", Acanthurus sandvicensis Streets. Fishes pursued included other pomacentrids, butterfly fishes (Chaetodontidae), wrasses (Labridae), parrot fishes (Scaridae), goat fishes (Mullidae), mullet (Mugilidae), and other less common fishes including the spiny puffers (Diodontidae). On two occasions, maomao were observed attacking spiny puffers (Diodon sp.) which appeared more than twice as large as the defending maomao, and a very uninviting target. In both cases the defending maomao rushed at the puffer, stopping about six inches short of the intruder. The maomao then turned and circled around to repeat his bluff, and after he had made three rushes at the puffer, the puffer turned and slowly swam away.

The size, shape, color pattern, and actions may all contribute to the recognition of potential predators by the guardian maomao, and thus allow him to reserve his energy for attacking only those predators potentially dangerous to his brood. Guardian maomao never seem to be bothered by the small, plankton-feeding atherinid, Pranesus insularum (Jordan & Evermann) that frequently passes through its territory in large numbers. Also, the juvenile stages of species normally attacked, such as Dascyllus albisella Gill, are usually ignored by a guardian maomao until they reach a length of about three inches or more.

As previously mentioned, some of the acanthurids appear to be recognized as harmless to the maomao brood and casually pass through the territory of a male maomao unmolested. As the manini is the most common acanthurid around the maomao spawning sites, its relationship to the guardian maomao has been observed most frequently. On one occasion, two manini were observed feeding within 6 inches of a recently spawned maomao egg mass without causing any aggressive action by the male guardian. In another instance of this apparent lack of aggression toward the manini, a male maomao preparing a nest at site "B" in the Tuna Pond spawning area was seen grazing algae off of the substrate while a manini fed alongside him in the same manner at a distance of only a few inches. Randall (1955, p. 280) points out that the manini is an obligate herbivore, and would not feed on the eggs of the maomao when afforded the opportunity. Apparently, the manini fails to release the aggressive drive normally released in the maomao by most other species; however, the nature of the sign stimulus in the manini was not determined. Apparently, this sign stimulus can be neutralized by increased aggressiveness in the maomao, for when a defending maomao is being hard pressed from all sides by intruders, he has been observed to chase manini from his territory.

Recognition between guarding maomao and some potential predators is apparently mutual, and in such cases a threatening display or perhaps a very limited chase is sufficient to cause intruders to avoid a defended area. Such limited aggressiveness was seen displayed in the presence of five goatfish swimming along the bottom toward a "nest" at site "U-2" in the Southwest Point spawning area, and illustrated in Figure 28G. The guardian maomao moved toward the intruders a short distance with elevated dorsal spines, and the intruders immediately recognized the threat and changed the direction of their movement. The guardian maomao gradually turned so that he continued to face the intruders until they passed.

The actions of a guardian maomao were never observed in the presence of some of the larger, more voracious predators such as moray eels and sharks; however, a human diver in the area often incited curiosity from the guardian maomao which caused him to proceed cautiously out from his spawning site and hover in the water. As soon as the diver moved closer, an alarm response was exhibited, and the guardian maomao, as well as other maomao in the vicinity, fled to the protection of recesses in the substrate.

One of the puzzling aspects of reproductive behavior in the maomao is that involving the establishment of two spawning sites by separate males in close proximity to each other while many other established spawning sites in the area are unoccupied. Such a situation was observed in May, 1957, at the Southwest Point spawning area on Coconut Island, where two nests were observed on a portion of the fallen retaining wall at sites "M-1" and "M-2" within about one foot of each other. This situation is apparently uncommon in other groups of substrate spawners such as the centrarchids and the cichlids in which a uniform spacing is maintained between nests and territorial limits are defined and sustained by means of border fighting (Breder, 1936; Baerends and Baerends-van Roon, 1950).

In the case cited above, it is difficult to visualize how the second maomao in the area was able to establish his territory, if indeed a territory was established. Unfortunately, this situation was not observed until after both fish had persuaded females to spawn at their chosen sites. It was interesting to note that these two male maomao did not exhibit any particular antagonism toward each other while caring for their respective egg masses during the short period they were observed; however, when one male attempted to attract a female onto his spawning site for the purpose of additional spawning, the other male displayed aggressive action, and it appeared as though he began to chase the female. It was not possible to be certain of this activity, as the rapid chasing action always involved at least three fish, and in the resulting confusion, it was impossible to determine who was chasing whom. Since further observation was not possible on this or simialr situations, difficulties involving the maintenance of adjacent territories in close proximity to each other were not resolved. Since a number of egg masses have been observed fairly close to each other in deeper water areas at Waianae and Lanikai, Oahu, it may be that under certain conditions some sort of social cooperation is established whereby mutual defense of two or more "nests" is accomplished by some sort of division of effort. Such a system would require a more complex system of recognition, probably involving a distinct sign stimulus for cooperating males.

3. Mating Behavior

The primary purpose of courting among maomao is simply to have a male and a female brought together in the proper place at the proper time for purposes of reproduction. In an analysis of the courting behavior of the maomao, a general sequence of events is revealed leading to the ultimate goal of a simultaneous release of gametes by the male and female at a prepared spawning site. This sequence of events includes the following: (1) recognition of a gravid male by a gravid female, and vice versa; (2) aggressive persuasion of the female by the male; (3) submission by the female to the male's persuasion (the female submits to the male's aggressiveness and attempts appeasement); (4) direction of the female to the spawning site by the male; (5) final acceptance of the female by the male at the spawning site. In order to accomplish each of these steps, various sign stimuli in the form of nuptial coloration, postures, and maneuvers must be displayed and executed in the proper sequence by the mating maomao. Maomao mating behavior is, therefore, analyzed from the standpoint of these sign stimuli in so far as they have been revealed during observations on this species.

a. Nuptial coloration.

The most striking morphological expression of sexual readiness in the male maomao is a rapid and marked color change. Such color changes are secondary sexual characters associated with the onset of sexual maturity and the approach of a peak of reproductive activity. The exact timing of this color change is not well understood. The male maomao seems to assume the nuptial coloration gradually after the establishment of his territory and a period of site preparation at about the time he begins to execute mating maneuvers.

Although this nuptial coloration displayed by the mating maomao is quite variable, most of the variability is quantitative, and repeated observations revealed the following apparent consistencies: the pale bluish-gray hue is most evident dorsally, while the ventral half to one third of the body usually remained pale yellow to white; the black blotches on the soft dorsal and anal fins remained distinct, although other black markings faded to a pale bluish-gray, often to the point of imperceptibility; the margins of the soft dorsal, caudal, and anal fade to whitish; the bluish coloration appears to be more intense in the region of the pectoral insertion and dorsal portion of the head; during periods when the blue is very intense, the spinous dorsal fin appears whitish.

The association of nuptial coloration with the elaboration of gonadal hormones has been quite well established by experimental work with the teleosts, (Dodd, 1955; Hoar, 1955; Odiorne in Brown, 1957). The mechanism by which this color change takes place in the maomao has not been investigated in detail. However, a comparable color change has been observed in the cichlids by Baerends and Baerends-van Roon (1950). They were able to distinguish six separate types or systems of chromatophores in the cichlids studied, and attributed various color changes to changes in specific systems of chromatophores. One species they describe, Cichlasoma severum (Haeckel) displays a color change roughly comparable to that of the maomao, and they attribute a change from green to blue in this cichlid to the expansion of melanophores and melanoiridosomes of a type which are large, deeply situated, and regularly associated with rapid changes in coloration.

Since mutual recognition of a gravid male and female is the first step toward mating and reproduction, the role of nuptial coloration as a mark of recognition warrants first consideration in this discussion. Noble and Curtis (1935) conducted experiments in which the nuptial coloration of the jewel fish, Hemichromis bimaculatus, could be controlled. They were even able to induce nuptial coloration in males that exhibited no courtship movements. From this study they found that females responded primarily to color, that they chose the most highly colored of several possible mates, and that no response was incited by the male's courtship movements in the absence of any color. In a further analysis of nuptial coloration in this species, Noble (1938) believed that colors may serve to emphasize gestures which are essential to the formation of nuptial bonds. According to Tinbergen (1951, 1953), nuptial coloration serves as a mark of recognition by which a female recognizes a sexually ripe male who has prepared a nest. In addition, however, nuptial coloration also serves as a sign stimulus by which the female is "released" to move into the vicinity of the male so that he might begin the next action in the series that leads the female to the nest and results in spawning. In the case of the three-spined stickleback (Gasterosteus aculeatus), a simple visual stimulus of the color red appears to be sufficient to actuate a response from a ripe female, as was shown by presenting a ripe female with a crude red model in the experiment previously described.

Nuptial coloration in the courting maomao was observed a number of times, expressed in various degrees of intensity, and coupled with various maneuvers; however, its relative importance in recognition and persuasion of a female in relation to other sexual gestures was not determined. Failure to determine the exact role of nuptial coloration was apparently due to the extreme shyness of the maomao, and inexperience of the observer with techniques employed in animal behavior studies. Attempts to place any objects in the water, regardless of their shape or size, resulted in an immediate alarm response by maomao in the vicinity, and a cessation of normal activity.

Observations suggest that since nuptial coloration often intensifies rapidly during certain maneuvers, it is probably not a stimulus per se for recognition or persuasion, but rather is coupled with maneuvers to give emphasis to the key gestures that serve as sign stimuli. Such a hypothesis helps to explain some of the variability in intensity with which nuptial coloration is displayed. If color alone was utilized to stimulate a female to recognize and enter into a spawning situation, then it might be expected that the intensity of coloration would affect the rate at which mating was accomplished. But this does not seem to be the case, although observations on this point are not adequate. In a few cases the bluish hue appeared to be hardly noticeable, and yet mating seemed to be successfully carried out with about equal ease and dispatch as when nuptial coloration was intense. In such a case a substitute must have been made for the color stimulus. An example of such a substitution of one set of stimuli for another set without affecting the response is given by Baerends (in Brown, 1957). He calls this phenomenon "heterogeneous summation", and cites an example in the cichlids in which the tail beating of a male showing no sexual coloration has the same effect as a quietly posturing male with intense nuptial coloration. Applied to the maomao, some additional action may be effectively substituted for the blue coloration in the male to obtain the proper actions to result in pair formation and reproduction. Further observations and carefully designed experiments are necessary; however, to confirm the existence of such phenomena in maomao courting behavior.

b. Looping, zigzag swimming, and vertical stance maneuvers.

Various combinations of the basic looping, zigzag, and vertical stance maneuvers (Fig. 27A, B, and C) have been seen executed by the mating male maomao, and they all appear to be manifestations of the reproductive drive. In most fishes with a similar reproductive pattern, the male initiates action leading to pair formation and must persuade a female to join him in a cooperative act. As previously pointed out, the male's persuasive actions may be rather aggressive in nature, and therefore, the female must appease the male in order to be courted. These maneuvers of the male maomao, which are quite aggressive, are apparently intended to persuade the female to mate and direct her to the spawning site. Various combinations of the basic maneuvers, some involving both the male and female maomao, were repeatedly observed during the courtship of maomao, and some of the more common patterns of behavior are illustrated in Figure 26A-F. The looping and zigzag maneuvers appear to be the primary mating actions or signals, judging from the frequency with which they were observed executed by the mating male maomao, and the vertical stance was least observed.

The vertical stance gesture (Figures 27C, 28C) was always executed near the border of the male's territory, and it was never combined with other maneuvers, nor was it ever observed to induce a female to follow the male back to the spawning site. A possible explanation of the vertical stance behavior is proposed, based on its timing and location. As previously pointed out, when mutually inhibiting instincts are activated simultaneously by intense motivations, an activity associated with a third instinct may result (Tinbergen, 1953). In this case, it is suggested that the two motivations in the male maomao are the aggressive instinct to drive off nearby intruders, and the mating instinct to attract a gravid female into the nest. The simultaneous activation of these two instincts, may be what causes the activation of another form of behavior displacement activity in the form of the vertical stance. The significance of this third action is unknown, and its explanation would require further observations. The vertical stance might also be a simple threat or recognition signal, but this explanation is discounted because this gesture was so infrequently observed.

Often the various patterns of behavior involving these maneuvers by the male maomao would fail to incite any visible response from the female. It should be pointed out, however, that the male was the primary object of observation due to his conspicuous color and behavior, and the female was not always distinguished as such until she reacted to the male's persuasive actions and approached him. Examples of maneuvers which stimulated no response from female maomao are illustrated in Fig. 28A-C. The simple zigzag swimming maneuver was never observed to cause a female to follow the male back to the spawning site, and it is, therefore, suggested that this may be a preliminary or preparatory display by the male for recognition and/or to arouse a female.

Looping is apparently a more advanced persuasive maneuver as it appears to be the most successful action by the male in attracting a female. Figures 28D-F illustrate the maneuvers of a male maomao resulting in the successful attraction of a female, although in some cases permanent mating did not result. A characteristic of all of these maneuvers, with the exception of the vertical stance, is the rapidity with which they are performed. Often these maneuvers by the male maomao are accentuated by an increased intensity of the nuptial coloration.

In some cases during these maneuvers, the female joins the male in his looping, (Fig. 28D). However, due to the rapid action of the pair, it was never possible to observe which fish was leading during the looping.

The most common patterns of behavior observed were those illustrated in Figure 28E, F, in which the male loops while swimming away from the spawning site and meets the female near the periphery of his territory. The female retreats before the male a short distance, attempting appeasement, but as soon as he turns to swim back to the spawning site, she turns and follows him closely. He may return directly to the nesting site, or may loop on his return. The most common occurrence during the male's return to the spawning site with a female following is to have the male repeatedly turn and chase her away, but eventually allow her to arrive at the spawning site (Fig. 28F).

c. Tail-on-tail chasing.

A typical action of a pair of maomao in which the female has just been accepted onto the spawning site is chasing of each other in tight circles over the surface of the spawning site, or tail-on-tail chasing (Fig. 27D). This is interpreted as a continuing act of appeasement by the female, and it may serve as mutual stimulation to induce spawning. This chasing behavior only lasts for a few seconds and may result in the rejection of the female from the site. When rejected, the female either swims away from the area altogether or she travels to a point a few feet away, usually returning after a short time. This circular chasing is usually repeated until the male is finally appeased or the female becomes discouraged and does not return after being chased away. On the second of April, 1957, a female at site "M-1" in the Southwest Point spawning area was observed to be chased from the site six times after tail-on-tail chasing before she was finally discouraged and did not return.

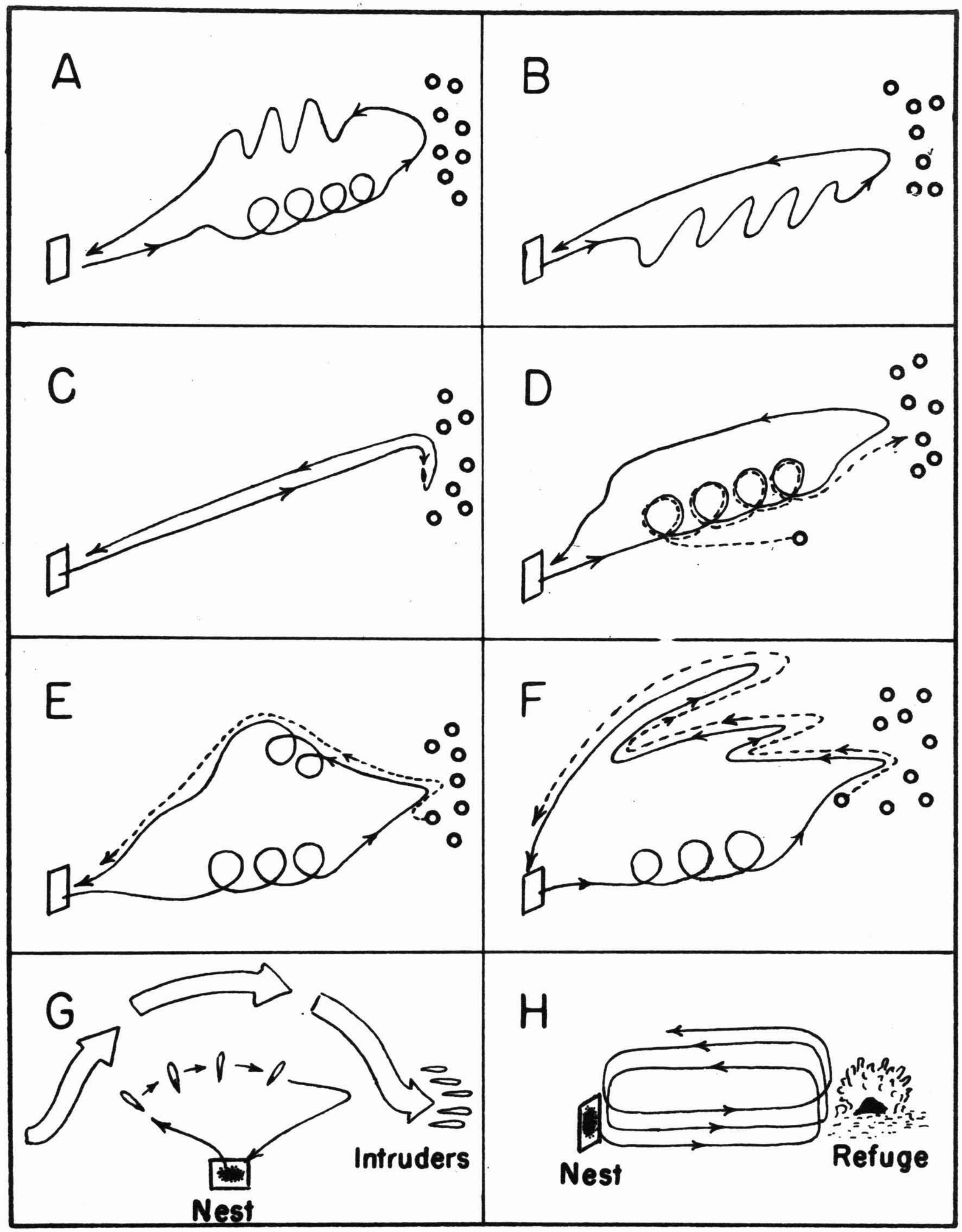

Figure 28. Diagrams representing some patterns of behavior exhibited by male maomao in an established territory. Rectangles represent spawning sites, solid lines represent routes of males, broken lines represent routes of females, and small circles represent aggregations of maomao. For explanation of diagrams, see text.

More than one female may follow the male back to the spawning site after the execution of courting maneuvers, and it was not unusual to see a second, and even third maomao (all assumed to be female) occupy a nesting site simultaneously with the established male. Such situations involving supernumerary females occupying a site simultaneously were observed to be short lived and always resulted in the expulsion of all of the occupants by the male guardian.

4. Parental care.

Parental care in most animals is the manifestation of both internal and external stimuli; the former, probably hormonal in nature, creates a "reproductive mood", while the latter produces more specific responses. An example of this is seen in the maomao by comparing the reactions of individuals of both sexes when confronted with an unprotected maomao egg mass before and after they are conditioned for parental care. To the unconditioned, non-breeding maomao such an egg mass is a highly desirable source of food and its visual and perhaps chemical stimuli incite an immediate feeding response. To the maomao who is properly conditioned by internal stimuli, the very same external stimuli release a number of responses which are all manifestations of the parental instinct, including fanning of the eggs, picking out defective eggs, protecting the brood from predators, etc. In this discussion, an attempt will be made to define the nature of the external stimuli instigating various phases of parental care.

In questioning what stimuli induce a male to guard a clutch of eggs in a given territory, investigations involving fish with such habits have shown that both innate and learning factors are involved. It is instinctive for the three-spined stickleback to seek out a place in shallow water with liberal vegetation; however, the relative position of objects in the surrounding area are learned by the defending male and it is only when stimuli from these objects are coupled with those of an intruding rival that they cause the male to initiate an aggressive defense of the area (Tinbergen, 1953). This was demonstrated by placing two fish, each guarding separate territories, in separate glass containers and bringing them together, first in one fish's territory, and then in the other's. When brought together in Territory A, the guardian of A tried to attack the intruder, B, and B attempted to flee. When brought together in territory B, the situation was just reversed, and A attempted to flee while B attacked. In this case the same innate behavior is modified by external stimuli to produce very different results when the same situation is modified by different surroundings.

Care of the brood appears to be primarily an instinctive drive actuated periodically by internal stimuli during the breeding season; however, evidence exists that learning is involved in the discrimination of the eggs and the young. The jewel fish, <u>Hemichromis bimaculatus</u> Gill, cannot distinguish the eggs of other species of cichlids from their own until the eggs reach a certain stage of development, and then they only recognize them by means of the size and color learned from previous spawning experience. If eggs of a pair spawning for the first time are removed and the eggs of another species are substituted, they will rear the substituted eggs, but in subsequent spawnings they will fail to recognize their own due to previous learning, and will eat them (Noble and Curtis, 1939; Tinbergen, 1953). There is further evidence that recognition of the eggs depends on the visual acuity of the parent. In some of the cichlids the eggs are examined and removed by the guardian when they become defective and turn white.

In an attempt to identify the stimuli which cause a guardian maomao to undertake various kinds of parental care, some simple experiments were attempted.

Some factors in both the territory in general and in a specific brood appear to stimulate parental care in fishes that attach and protect their eggs during incubation. In order to determine if the maomao received a greater stimulus from the egg mass per se, or from it in relation to its relative position to surrounding objects, egg masses that had been deposited on experimental concrete spawning slabs were moved from one location to another and the reaction of the guardian fish observed. One slab chosen was located at site "W-2" in the Southwest Point spawning area (see Fig. 23) and it contained a moderate sized clutch of eggs that had been spawned about two days previously. This brood was exchanged with an unoccupied spawning slab at site "W-1", which was located about four feet further along on the same coral ridge. This transfer was made with a minimum of disturbance by hooking the wire handle constructed on the spawning slab for this purpose with a long handled boat hook. Thus the slabs were exchanged in a few seconds without removing them from the water. During this transfer the guarding male maomao retreated to a refuge in deeper water. Although the intervening activities of the guarding male were not clearly observed, he returned to his displaced brood in about ten minutes and resumed his normal parental care. On the following day, this same slab containing the brood, now located at site "W-1", was exchanged with a vacant slab at site "W-3", also on the same ridge, but about nine feet away from site "W-1". Unfortunately, a large number of fish, including a number of other maomao, were milling around in the area, and they immediately proceeded to consume the transferred brood. The guardian parent could not be observed, and it was not determined whether he abandoned his brood because they were moved too great a distance and he could not locate them, because they had been destroyed before he had a chance to find them in their new location, or for other reasons. This experiment did indicate that the parent fish continued to recognize his brood, as such, when moved a distance of four feet. It is not implied that he recognized the individual eggs, as the stimuli may be more generalized than that; in fact, such a disowned guardian may have been attracted to any unattended brood in the area.

In order to specify further the nature of the stimuli inducing parental care, and possibly to shed some light on the acuity of maomao vision, an artificial egg mass was attached to one of the concrete spawning slabs. This was constructed by gluing small white glass beads onto the slab with waterproof glue, and spraying them with black paint to produce the general color of a mass of maomao eggs in an advanced stage of development. Unfortunately, the only glass beads that could be obtained were roughly rounded, 2.0 mm. in diameter, and perforated with a single large hole, about 0.8 mm. in diameter. These beads were somewhat larger than maomao eggs, which average about 1.2 mm. in length and are elliptical in shape. This artificial egg mass was placed in a tank through which sea water was circulated for a period of two weeks in order to remove any possible soluble residues from the glue or paint. This preparation was then exchanged for a live egg mass of approximately the same size and color at site "U-2" in the Southwest Point spawning area. The live egg mass was removed from the area altogether. The guardian fish remained in hiding during the exchange, and since he did not display a distinctive coloration, he could not be identified afterward; however, none of the maomao returning to the area showed more than a brief curious interest in the artificial brood. A short time after the exchange, a disturbance was created in the water and observations were terminated until the following day. The next day the artificial slab remained abandoned, and during many subsequent observations no fish were observed to take any special interest in it. Although the results of this attempted experiment are very inconclusive, they do indicate that gross color and shape of an egg mass alone probably do not act as releasers for acts of parental care as is the case for some of the actions in reproductive behavior of fishes previously reported.

It is unfortunate that this experiment, and others like it, could not have been repeated; however, by the time the general reproductive pattern of the maomao had been worked out, and the various phases and elements identified, the spawning season was about over. Despite the shy disposition of this species, it is believed that a continuation of this behavior study of the maomao, utilizing well planned experiments and more adequate aids to observation, could result in valuable contributions to the study of animal behavior.

An observation was made on a guardian male maomao beset with a conflict involving two antagonistic drives which shed some light on the operation of conflicting stimuli associated with parental care. The resulting behavior was that which might be classed as displacement activity of the type previously discussed. In this case, a maomao was guarding a clutch of eggs at site "I" on the face of the retaining wall at the Southwest Point spawning area. During previous observations, this guardian fish proved to be quite shy, and on the approach of an observer along the wall above he would retreat to what was apparently his established place of refuge beneath a coral head about four feet from the wall in a slightly deeper area. When observed on the sixth of May, 1957, from a point on the wall directly above the nest, this fish was beset by the release of two antagonistic drives; to flee to the protection of his place of refuge in deeper water, or to remain close to the egg mass, now requiring greater attention due to the advanced stage of development of the eggs. Apparently, fear about equalled the paternal protective instinct, for the fish swam nervously along a roughly elliptical path between the nest and the refuge for about two minutes as illustrated in Fig. 28H.

5. Miscellaneous behavior.

a. "Kissing"

Kissing behavior was only observed twice with maomao, but on both occasions the water was clear and quiet, the observer seemed to be unnoticed by the fish involved, and the entire action was clearly viewed. This activity was termed "kissing" in lieu of "mouth fighting" as described for some fishes because of the docile nature of the individuals involved, and the slow, unexcited manner in which it was carried out. This type of behavior has only been reported in a few fishes and its association with the reproductive behavior of the maomao is largely speculative.

A well known tropical aquarium fish, the "Kissing Gourami" (*Helostoma temminicki* Cuvier & Valenciennes) derived its common name from a similar kissing habit; however, the significance of this strange behavior is not revealed, (Axelrod and Schultz, 1955). Ray and Campi (1956) describe several species of grunts of the genus Haemulon which have the peculiar habit of rushing at each other with open mouths and "kissing". These authors have photographed two blue-striped grunts, Haemulon sciurus (Shaw), engaged in this activity, and state that such sights are common during the breeding season. Baerends and Baerends-van Roon (1950) describe activity of cichlids in defense of a territory in which the mouths of two fish are locked together during combat. In this case, however, the entire action has been repeatedly observed and analyzed, and the behavior is believed to be aggression motivated by the entrance of an intruder into an established territory.

Kissing behavior was observed in a pair of maomao near site "M-1" in the Southwest Point spawning area on Coconut Island on the 12th of April, 1957. When the pair of fish involved were first observed, they were already engaged in this activity, and it continued for approximately two minutes. This action took place just beneath the surface of the water, in an area where the depth of water was about three feet. One of the fish involved displayed the blue hue previously described for mating maomao, while the other individual displayed normal coloring. The observed kissing behavior consisted of the following sequence of events. The two individuals approached each other head-on, swimming in an extremely slow and casual manner. No rapid flicking of fins or other rapid body movements indicating the least excitement were noticed. The approach continued at the same slow rate until actual contact was made. It was not determined if the mouths were open or closed; however, it appeared as though the lips met with the mouths closed. As soon as firm contact was made both fish began to thrash violently, giving the observer an impression that they were attempting to push each other. During this phase, which lasted about four seconds, they broke the surface of the water repeatedly. The thrashing terminated when the broke contact, one fish swimming to the right, and the other to the left. They swam away slowly in a circular clock-wise path until they again faced each other, and the entire action was repeated as before. The entire action was repeated seven times in approximately two minutes. As they approached each other for the eighth contact, they seemed to simultaneously turn away from each other when about 6 inches apart, and the fish with the mating coloration returned to guard an egg mass at site "M-1". The other fish was not observed thereafter; however, an inspection of the area revealed a brood at site "M-2", only a short distance away from "M-1", (see Fig. 23). A second display of kissing behavior was observed in the same area about two months later, and it appeared to follow the same general pattern; the distribution of broods in the area was not determined on this occasion.

The significance of such behavior must be limited to speculation until further observations can be made. It is possible that this is a display designed to establish some sort of position in the social hierarchy among the maomao in this area. It seems more probable in the light of the close proximity of the two broods at sites "M-1" and "M-2", and the similarity to the border fighting described by Baerends and Baerends-van Roon, op.cit., that this is an aggressive display of some sort in which a boundary is contested. This is not at first evident, as all other aggressive displays thus far observed in the maomao have been accompanied with rapid movements and other manifestations of excitement; however, in the approach phases of this behavior, the docile action may have been mistaken for one of extreme caution.

SECTION IV

SUMMARY AND CONCLUSIONS

During this investigation of the life history and reproductive behavior of the Hawaiian pomacentrid, Abudefduf abdominalis, ("maomao"), the following salient points were revealed resulting in the formulation of the accompanying conclusions.

1. The habitat of the maomao is varied, extending over a considerable range of depths and substrate types, with the exclusion of extensive sandy and muddy areas. This species usually remains close to the substrate, and a primary habitat requirement appears to be suitable refuge, although the availability of food, the availability of suitable spawning sites, and a possible association with other species of fish, all appear to influence its distribution.

2. The maomao is a broadly omnivorous species, and its adaptation to a variety of dietary items probably endows it with considerable resilience to survive large fluctuations in the environment. Two specialized feeding aggregations of maomao are occasionally observed: (a) a "curtain" of fish in deeper water may utilize such a formation to efficiently pick plankton from the passing current, and (b) a "ball" of maomao may form near the surface in shallow water to prey on small crustaceans. Copepods are usually the dominant organisms consumed, but other crustaceans, filamentous algae, and fish eggs are often found in abundance in the stomach contents. Choice of diet apparently depends largely on availability, and may include a wide variety of organisms.

3. Maomao coloration is included under two categories, normal adaptive coloration, and nuptial coloration. Two phases of adaptive coloration,

light and dark, are gradually adopted by maomao in order to present a minimum of contrast with their background. Sudden excitement of a maomao in the dark phase of coloration will often cause a rapid fading of color or "excitement pallor".

4. The structure of the maomao reproductive system is similar to other teleosts which exhibit external fertilization. In both the male and female maomao the left gonad was larger than the right in most of the specimens examined. Stages of maturity were assigned to the gonads from 760 females and 1,625 males, indicating a majority of the "ripe" gonads occurred between January and September, with a maximum in May and June, and a minimum in October and November. Multiple spawnings in one season by a single maomao are indicated; apparently a common occurrence among other pomacentrids investigated.

5. The sex ratio of 2,313 commercially caught maomao was 68.6 percent males and 31.4 percent females, but there is some evidence that this was due to selective sampling. The sex ratio determined from these samples was not consistent with time, but variations were not correlated with spawning seasons or other phenomena. No apparent sexual dimorphism was seen in the maomao, although males were consistently larger than females in fish obtained from traps. Sexes can be distinguished by close examination of external genitalia in which a slight difference between the sexes exists.

6. Examination of maomao ovaries showed uniform contents in transverse sections taken at any point along the longitudinal axis of either gonad. Ova develop in clusters of germinal epithelium on the periphery of the ovary, and when nearly mature, they are deposited in the lumen. The distribution of egg diameters usually indicated three distinct groups

of eggs: a stock pile of primordial eggs, and two separate groups in more advanced stages of development.

7. The fecundity of female maomao were not determined, although a single female was estimated to spawn an average of 21,400 eggs at one time. The number of eggs deposited by a female at one time was correlated with its body weight ($r = 0.625$, $p \quad 0.05$). Maomao probably conform to the spawning pattern of other pomacentrids investigated, which deposit small numbers of eggs at frequent intervals throughout the spawning season.

8. The nature of the maomao spawning cycle was investigated from a number of aspects, and all confirmed the previously mentioned pattern of continuous spawning throughout the year with increased spawning from mid-December to September, and a peak in May or June. The period of maximum spawning roughly corresponds to a period during which surface water temperatures are lowest in the Hawaiian Islands. A similar spawning pattern has been shown for five other species of Hawaiian reef fish. Observations on maomao spawning sites in Kaneohe Bay revealed that an increase in spawning activity takes place during periods around the time of full and new moons. This phenomenon is not well understood but it is believed to be caused by a stimulus complex associated with bilunar periodicity which augments or accentuates the normal spawning stimuli.

9. Maomao eggs are attached in a single layer by means of an adhesive membrane to a suitable surface on the substrate (usually rock, dead coral, or concrete). Normally a nest contains more than one clutch of eggs, and as many as five clutches have been observed in a single nest, cared for by a single guardian maomao. The average density of eggs in nests

examined was 1.2 eggs/mm.^{2}. The number of eggs per nest ranged from 10,100 to 116,900, with a mean of 56,800.

10. The mature maomao ova is roughly elliptical with an average length of 1.29 mm., and a width which varies between 0.62 and 0.67 mm. The yolk is red or yellow, the latter color more infrequently observed and thought to be associated with some item in the adult diet. Developing maomao ova normally hatch early on the sixth day after fertilization with an average water temperature of 24.5° C. A description of the stages of development is presented.

11. The major sources of mortality of developing maomao eggs are attributed to (a) predation by other fishes, (b) oxygen deficiency, and (c) invasion by microorganisms. Predation appears to be primarily by butterfly fishes, wrasses, and goat fishes. Oxygen requirements of developing embryos is shown to increase steadily for 5 days after fertilization, and this is accompanied by increased aeration of the brood by its guardian. Both bacterial and protozoan invasions of developing maomao eggs were observed and described. A guardian maomao usually removes infected eggs from the nest, and his presence is considered essential to the successful development of the brood in nature. Mortality of broods in nature prior to hatching is estimated to average somewhat less than 10 percent, and was never observed to exceed 30 percent.

12. Maomao larvae at various stages of development are described and figured. Larvae average 2.7 mm. in length at hatching, gradually develop adult characteristics, and by approximately 20 days (at about 12 mm. fork length) the adult markings are clearly visible. The average growth rate of 24 individuals between 1 and 17 days after hatching was 0.43 mm./day.

Larval stages of maomao up to three days old are positively phototaxic, under the influence of strong light. The larvae are planktonic and incapable of extensive migrations until seven to eleven days after hatching, at which time they migrate into shallow water along the shore.

13. Use of a specially designed apparatus permitted the rearing and observation of broods of larval maomao for more than a week after hatching. Five broods successfully reared all displayed high mortality during a "critical stage" on the second and third day after hatching. Factors affecting larval mortality are discussed. In addition to an exhaustion of the yolk supply during the "critical stage", the adequacy of a number of larval organ systems is probably tested during this time. Larval survival in nature was estimated at 0.01 percent of the original brood ten days after hatching, whereas in rearing trials survival averaged 1.9 percent of the initial brood. Increased survival in the apparatus was attributed to the exclusion of predators and a decrease in the turbulence usually encountered by larvae in nature.

14. Juvenile maomao inhabit tide pools in the lower and midde intertidal zone, and in other relatively quiet, shallow areas close to shore. The physical and biological characteristics of twenty tide pools at Diamond Head Park were analyzed, and it was concluded that juveniles are most abundant in, and apparently prefer, pools possessing certain qualities. The relative position of the access from a pool to deep water appears to be of importance, as does available concealment within the pool. When juveniles attain the length of 25 to 30 mm. they begin to move out of the tide pools into deeper water, and take refuge in recesses in the substrate. The associations of maomao with other species of fish in tide

pools is discussed. The seasonal abundance of juvenile maomao observed in tide pools follows the general pattern of spawning determined by other means, and the peaks of abundance between 1954 and 1957 varied between mid-April and mid-June.

15. The food of juvenile maomao is similar to that of the adults, with copepods and amphipods being preferred. A hierarchy of feeding or peck order exists among juvenile maomao resulting in differential growth of confined fish. Estimates of juvenile growth rates were made from (a) rearing trials, and (b) the progression of length frequency modes of tide pool samples. Rearing maomao juveniles on natural food resulted in a growth rate of 0.44 mm./day, or 13.2 mm./month, while progression of length frequency modes showed a growth rate of 0.19 mm./day or 5.7 mm./month. A gradual leveling of the growth curve of reared juveniles was attributed to (a) a seasonal decline during the winter months, and (b) a deceleration of growth normally attributed to maturing fish.

The orientation to light by juvenile maomao is discussed. These fish are subject to a phototropism which motivates them to orient so that their dorsal side is always toward the primary source of light, even though they must swim with their ventral side toward the water's surface to accomplish this in some situations.

16. From a sequence of actions accompanying maomao spawning observed at Coconut Island, the general pattern of reproductive behavior was worked out. Most of the observations of maomao spawning in shallow water were made from concealed points along the shore, thus a fairly reliable picture of natural, undisturbed activities was obtained. The literature on pomacentrid spawning is reviewed, revealing a similar pattern of

reproductive behavior throughout this family. The maomao conforms to this pattern displaying the following sequence of activities: (a) the male maomao chooses a suitable site on the substrate and establishes a territory, which he defends while preparing a surface for egg deposition. (b) While preparing this site, the male gradually assumes a pale blue nuptial coloration and begins to attempt to attract a female. Various sequences of displays and maneuvers are then performed by the male in the vicinity of the female in an attempt to gain her recognition and attract her to the prepared site. The male's courting maneuvers often take on aggressive overtones, while the female's actions appear to be aimed at appeasement. (c) After the female has been attracted to the site and spawns, she leaves the nest, and the male commences to fan the clutch, pick out defective eggs, and defend the area against potential predators. Additional females may be attracted to spawn on the same site beside the existing clutches of eggs.

17. An analysis of the maomao reproductive behavior is attempted, in the light of recent literature in this field. The primary requirements for a spawning site appear to be a suitable substrate for egg deposition, and convenient refuge for the guardian parent. Male maomao usually occupy the most desirable spawning sites first, but some puzzling exceptions were observed. Some selective advantage is believed conferred on a species by its establishment of a territory in which to mate and spawn. Establishment of territories may serve to limit the population according to the available substrate and thus help to restrict the population to the carrying capacity of the habitat. If the spawning population is limited by available space, this may create a reserve of spawners, and thus insure population stability. An increased defensive vigor associated

with reproduction, as well as familiarity with the area, allow the male maomao to better defend his territory and thus insure maximum survival of the brood.

Aggressive behavior associated with reproduction in the male maomao usually takes the form of a bluff or threat; however, three levels of expression have been observed: (a) rapid and forceful chasing, (b) reserved pursuit, and (c) threat without pursuit. It has been observed that the peak of aggressiveness in the male maomao coincides with a peak of excitement just prior to and during spawning, and is also influenced by the pressure exerted by territorial intruders. Visual stimuli are believed important in initiating aggressive behavior, as certain herbivorous fishes (such as the manini) are usually allowed to swim unmolested in a territory except when the defender is highly excited and confronted with a number of intruders at the same time.

Mating behavior in the maomao involved the following sequence of events: (a) mutual recognition of a reproductively suited pair, (b) aggressive persuasion of a suitable female to accept the male's overtures, (c) the female's submission to the male, (d) orientation of the female to the site, and (e) a final acceptance of the female by the male on the site. The male maomao's nuptial coloration is a striking morphological expression of sexual readiness, and appears to act as a mark of recognition and attraction when coupled with other maneuvers. The significance of three maneuvers (looping, zigzag swimming, and vertical stance), and their role in recognition and attraction of a mate is discussed. A fourth maneuver, tail-on-tail chasing, is executed on arrival at the nesting site, and is interpreted as a continuing act of appeasement.

Parental care is believed to be a manifestation of both external and internal stimuli. Internal stimuli create a "reproductive mood" that causes breeding fish to respond differently to the same stimuli than non-breeding fish. Exchange of egg masses attached to movable spawning slabs showed that a male guardian recognizes his brood when moved as far as 4 feet. Evidence indicates that a guardian recognizes more than the gross color and shape of his brood.

An unusual "kissing" behavior is described, although its significance in regard to reproductive behavior is speculative.

APPENDIX A

APPARATUS FOR REARING LARVAL FISH

The original purpose in constructing an apparatus in which to rear larval fish was to create an enclosure that would restrict the larvae, and at the same time maintain an environment as close to that of the surrounding waters as possible (except for the exclusion of large predators). This was accomplished with reasonable success in rearing maomao larvae and therefore the apparatus used is described and illustrated in order that details of its construction may be available to other workers with similar problems.

This apparatus consists of two main parts, a large-mesh outer net and a fine-mesh inner net. The outer net (Figure 29) is constructed of fiber glass screen with a mesh size of 14 fibers to the inch, with a maximum opening of 1.5 mm. This material was sewn with linen fishing line to form a rectangular container 66 inches long by 60 inches wide and 46 inches deep, open at the top and suspended from a wooden frame. Beneath each corner of this frame was attached a metal float of approximately one gallon capacity (aircraft oxygen bottles were used) to add buoyancy to the frame. Each corner was fitted with a metal eye to which a wire was attached leading to a single overhead line that held the apparatus in place beneath a small bridge. This overhead line was fitted with a length of heavy rubber tubing that served to maintain tension on the line during tidal fluctuations.

A similar smaller net (Figures 30, 31, and 32) was suspended in the center of the outer net by means of a wooden frame with extensions that rested on the frame of the larger net. The inner net was constructed of an industrial plastic filter material that resembled nylon, produced by the National Filter Media Company of New Haven, Connecticut. This product is available in a number of mesh sizes and weaves; however, the primary consideration for purposes of this investigation was to obtain a screen with the largest possible mesh size that would still retain the larvae in order to minimize clogging of the openings with organic matter suspended in the water. The screen chosen was made of a material called "Saran" (trade mark of the Dow Chemical Company), style No. MS - 900 (32 x 32) which had a simple cross lap weave sealed at each contact, with strands 0.5 mm. apart, and a maximum opening of 0.65 mm. This net was also sewn into a rectangular container, 30 inches by 30 inches by 34 inches deep, using nylon thread on a mechanical sewing machine. This inner net was tacked to a light wooden frame the components of which are 3/4" x 3/4" in cross section. The inner net is tied to a framework that rests on the outer net frame and consists of two parallel boards, 12 inches apart, joined by cross pieces at either end and in the center. From this center cross piece the concrete slab containing the mass of attached maomao eggs was suspended by means of a heavy wire hook. The entire inner net is easily moved to one side of the outer net for examination of its contents from a nearby boat. A cover made of fiber glass screen was fitted over the entire apparatus to keep small fish from jumping into the nets.

The primary purpose of the outer net was to restrict floating debris and keep the inner net from becoming seriously clogged. It was found that normally the outer net became heavily clogged with debris in four to five weeks and therefore had to be cleaned periodically. The outer net was removed without disturbing the inner net merely by suspending the inner net from above, submerging one side of the outer net, and pulling it off to one side. Both nets were easily cleaned using a high pressure stream of water.

After being in the water for four months, the fiber glass net became brittle and tore when folded sharply. The inner net exhibited no such signs of deterioration.

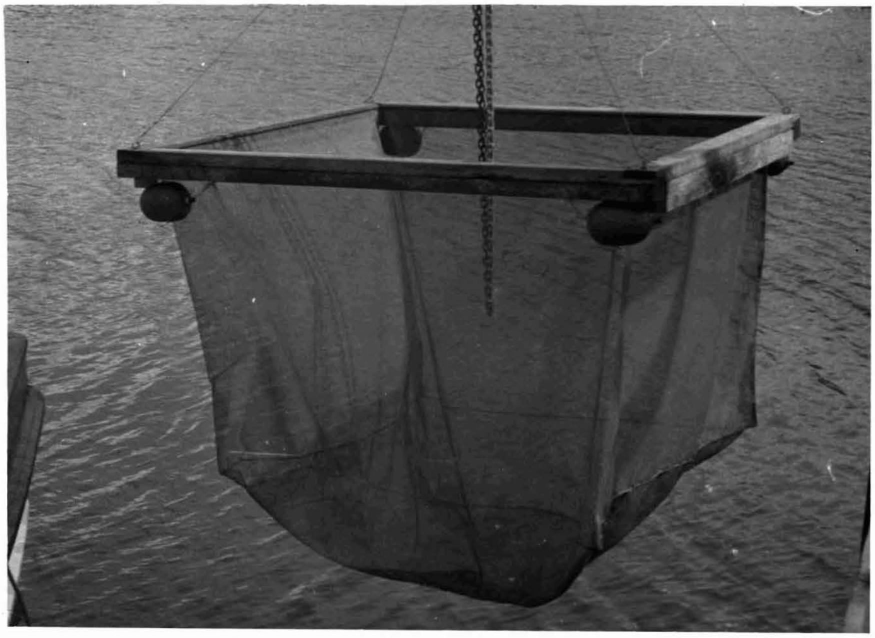

Figure 29. Outer net of the rearing apparatus removed from the water. The chain shown is not part of this apparatus.

Figure 30. Inner net of the rearing apparatus in the water and viewed from above. A concrete spawning slab is suspended from the frame in the center.

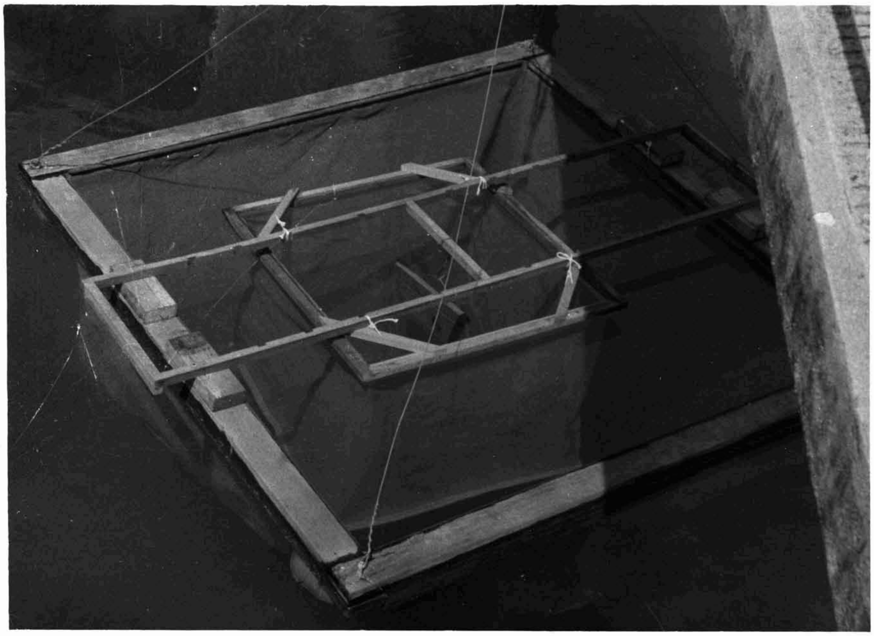

Figure 31. Rearing apparatus with the screen cover removed, in the Tuna Pond spawning area at Coconut Island.

Figure 32. Rearing apparatus with the screen cover removed, in the Tuna Pond spawning area at Coconut Island, showing the line attached to the bridge above holding it in position.

APPENDIX B
TABLE 19

THE AGE, LENGTH, AND DISPOSITION OF JUVENILES DURING REARING TRIALS AT COCONUT ISLAND

Date (1957)	Brood Symbol	Total No. of Indiv.	Location	No. at Various Std. Len. (mm.)	Mean Std. Len. (mm.)	Age (Days)	Remarks
20 IV	A	15	Outer net	15 - 12	12	24	
30 IV	A	15	Outer net	3 - 15 6 - 16 5 - 17 1 - 18	16.3	34	
6 V	A	15	Outer net	2 - 16 3 - 17 5 - 18 4 - 19 1 - 20	17.9	40	
16 V	A	15	Holding net	4 - 19 5 - 20 5 - 21 1 - 22	20.2	50	Into holding net on 6 May
29 V	A	15	Holding net	1 - 19 3 - 20 4 - 21 7 - 22	21.1	63	
11 VI	A	9	Holding net	1 - 20 1 - 21 5 - 22 2 - 23	21.9	76	Some escaped
19 VI	A	7	Holding net	1 - 21 3 - 23 1 - 24 1 - 25 1 - 26	23.6	84	
19 VI	4	4	Outer net	1 - 9 1 - 10 2 - 11	10.3	30	
26 VI	A	8	Holding net	1 - 22 2 - 23 1 - 24 1 - 26 2 - 28 1 - 29	25.4	91	One fish recaptured. Moved to concrete tank.

TABLE 19 (CONT'D)

Date (1957)	Brood Symbol	Total No. of Indiv.	Location	No. at Various Std. Len. (mm.)	Mean Std. Len. (mm.)	Age (Days)	Remarks
26 VI	4	4	Outer net	1 - 13 1 - 14 2 - 15	14.3	37	
3 VII	3	2	Outer net	1 - 8 1 - 10	9.0	22	
3 VII	4	4	Outer net	1 - 17 2 - 18 1 - 20	18.3	44	
9 VII	3	2	Outer net	1 - 8 1 - 12	10.0	28	
9 VII	4	4	Outer net	1 - 20 2 - 22 1 - 23	21.8	50	
9 VII	A	8	Concrete Tank	1 - 25 1 - 30 3 - 33 1 - 38 2 - 39	33.8	104	
16 VII	3	2	Outer net	1 - 11 1 - 16	13.5	35	
16 VII	4	4	Outer net	2 - 24 1 - 25 1 - 26	24.8	57	
24 VII	3	2	Outer net	1 - 20 1 - 21	20.5	43	
24 VII	4	4	Outer net	3 - 28 1 - 29	28.3	65	
25 VII	A	7	Concrete Tank	1 - 34 3 - 40 1 - 45 2 - 46	41.6	120	One indiv. not measured
5 VIII	3	1	Outer net	1 - 25	25	57	One indiv. escaped.
5 VIII	4	3	Outer net	1 - 29 2 - 32	31.0	75	One indiv. escaped.

TABLE 19 (CONT'D)

Date (1957)	Brood Symbol	Total No. of Indiv.	Location	No. at Various Std. Len. (mm.)	Mean Std. Len. (mm.)	Age (Days)	Remarks
6 VIII	A	8	Concrete Tank	1 - 39 1 - 45 1 - 47 1 - 48 1 - 49 1 - 50 1 - 52 1 - 53	47.8	132	
23 VIII	3	1	Outer net	1 - 34	34	75	Placed in concrete tank.
23 VIII	4	3	Outer net	1 - 38 2 - 39	38.6	93	
23 VIII	A	8	Concrete Tank	1 - 48 2 - 57 1 - 58 1 - 59 1 - 61 1 - 63 1 - 65	58.5	149	
10 IX	3	1	Concrete Tank	1 - 39	39	95	
10 IX	4	3	Concrete Tank	1 - 44 2 - 45	44.6	113	
10 IX	A	8	Concrete Tank	1 - 54 1 - 62 1 - 63 1 - 65 2 - 66 2 - 69	64.3	167	
27 IX	3	1	Concrete Tank	1 - 43	43	112	
27 IX	4	3	Concrete Tank	1 - 48 1 - 49 1 - 50	49.0	130	
27 IX	A	8	Concrete Tank	1 - 59 2 - 67 1 - 69 2 - 71 1 - 72 1 - 77	69.1	184	

TABLE 19 (CONT'D)

Date (1957)	Brood Symbol	Total No. of Indiv.	Location	No. at Various Std. Len. (mm.)	Mean Std. Len. (mm.)	Age (Days)	Remarks
12 X	3	1	Concrete Tank	1 - 47	47	127	Into Live Car
12 X	4	3	Concrete Tank	1 - 51 1 - 53 1 - 54	52.6	145	
12 X	A	8	Concrete Tank	1 - 64 2 - 72 1 - 73 1 - 75 1 - 76 1 - 77 1 - 78	73.3	199	73 mm. specimen into live car.
1 XI	A & 3	2	Live Car	1 - 50 1 - 73		3- 145 A- 218	
1 XI	4	3	Concrete Tank	1 - 57 1 - 58 1 - 61	58.6	164	
1 XI	A	7	Concrete Tank	1 - 73 1 - 78 1 - 79 1 - 80 1 - 81 1 - 82 1 - 86	79.8	218	
14 XI	A & 3	2	Live Car	1 - 53 1 - 75		3- 158 A- 231	
14 XI	4	3	Concrete Tank	1 - 60 1 - 62 1 - 64	62.0	178	
14 XI	A	7	Concrete Tank	1 - 81 1 - 82 3 - 83 2 - 86	83.4	231	
8 XII	A & 3	2	Live Car	1 - 53 1 - 75		3- 182 A- 255	
8 XII	4	3	Concrete Tank	1 - 62 1 - 65 1 - 67	64.6	201	

TABLE 19 (CONT'D)

Date (1957)	Brood Symbol	Total No. of Indiv.	Location	No. at Various Std. Len. (mm.)	Mean Std. Len. (mm.)	Age (Days)	Remarks
8 XII	A	6	Concrete Tank	1 - 82 1 - 83 2 - 86 1 - 88 1 - 89	85.6	255	One indiv. not caught
(1958)							
3 I	A & 3	2	Live Car	1 - 53 1 - 80		3- 208 A- 281	
3 I	4	3	Concrete Tank	1 - 66 2 - 68	67.3	227	
3 I	A	7	Concrete Tank	1 - 83 1 - 86 1 - 87 1 - 88 2 - 90 1 - 92	88.0	281	

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