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San Diego

The Ecology of Patch Reef Fishes

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Marine Biology

by

Ron Scott Nolan

Abstract
P 51-59
P 88-91-93

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1975

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ACKNOWLEDGMENTS

I thank these good people.

Committee: Rosenblatt (Chairman), Benson, Connell, Dayton, Isaacs.

Past Director Enewetak Marine Biological Laboratory, Helfrich.

Friends that assisted: McConnaughey, Stearns, Kiwala, Dana, Taylor, Johnson, Sertic, Cuell, McNair, Scanland, Allen, McCosker, Warner, Stover, Susie, Barbara, Sharon, Janice, Copp, Dockins, Diener, B.J., Ray, Marsh, Noskin, Reese, Barlow, Morrison, Losey, Miller's, Van Patten, Coates, Sarras, Roth, Cross, Hobson, Randall, Stewart, Struhsaker, Hoese, Fritzche, Luke, Erickson, Johannes, Wiebe, Loomis, Hubbs, Wisner, Wetzel.

Financial support: The Institute of Marine Resources of Scripps Institution and the Hawaii Institute of Marine Biology.

My Father and Mother.

Special thanks to Betty Stover.

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"Artificial Reefs as Experimental Tools." Proceedings of the Artificial Reef Conference. Houston, Texas, 1975.

FIELDS OF STUDY

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Studies in Oceanography
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ABSTRACT OF THE DISSERTATION

The Ecology of Patch Reef Fishes

by

Ron Scott Nolan

Doctor of Philosophy in Marine Biology

University of California, San Diego, 1975

Professor Richard H. Rosenblatt, Chariman

This study was intended to (1) describe the assemblage of fishes living on Enewetak lagoon patch reefs, their species composition, relative abundance and stability over time; and (2) to describe the colonization patterns of fishes to defaunated natural reefs and to artificial reefs in order to determine the means by which recruitment, immigration, and extinction shape the structure of the assemblage. Sixteen small (roughly 16 m^3) natural reefs were designated study reefs, of which nine were defaunated and five remained as controls. Nine artificial reefs comparable in size to the natural reefs were installed in bare sand regions. The fish populations on study reefs were monitored using SCUBA over a period of three years.

The fishes of the patch reef assemblage are very diverse and most are restricted to the immediate proximity of the reef. Fishes belonging to other nearby lagoon assemblages also seek shelter in patch reefs when quiescent at night. The species composition of the patch reef assemblage varied considerably about an equilibrial value over an observation period of two and a half years. Likewise, the variability found in defaunation collections of comparable reefs was found to be high. The sources of variability are believed to result from stochastic events that influence the availability of propagules and, also, the availability of appropriate types of shelter as interspecific and intraspecific competition, predation, and natural mortality free niche sites for potential colonists.

The colonization of defaunated natural reefs was characterized by the early invasion and persistence of 17 species--of which Pomacentrus pavo, P. vaiuli, Paramia quinquelineata, and Apogon novaeguineae were the most frequent. No defaunated reef ever achieved the exact pre-defaunation composition; and in many cases, the species composition at 600 days differed markedly from that of the baseline condition. The reefs did, however, attain a species number comparable to the original state. The characteristic oscillation about a value of about 22 species (accountable by census) following defaunation, supports the equilibrium theory of island colonization. The basic theoretical equation describing the equilibrium species value nicely models the colonization of the patch reef assemblage. Short-term rates of immigration that were measured within ten days of defaunation adequately predicted the equilibrium number of species found after 100 to 200 days.

Equilibrium theory predicts that small islands or islands depauperate in habitat diversity will achieve a lower species equilibrium than that of large or habitat diverse islands. In this study, a larger reef was found to have a higher species equilibrium while artificial reefs that lacked habitat diversity had fewer species. The first invaders of artificial reefs were the same species that successfully colonized natural reefs, but the assemblage structure of artificial reefs can be shaped by providing dense Pocillopora heads. These were rapidly colonized by Chromis caerulea, Dascyllus aruanus, and D. reticulatus. It is clear that an increase in artificial reef habitat diversity was accompanied by an increase in equilibrium species number. The recovery following perturbation of the patch reef assemblage proceded very rapidly, and this must have been due to the nearby proximity and abundance of colonizing propagules. It is apparent, however, that the sequence of invasions had repercussions throughout the history of patch reef colonization.

PART I

Patch Reef Assemblage Structure and Species Composition

INTRODUCTION

This study investigates questions relating to the ecology of fishes inhabiting small patch reefs in a coral atoll lagoon. The first major study to emphasize reef fish ecology was that of Hiatt and Strasburg (1960) who examined the feeding habits of Marshallese fishes and made extensive skin diving observations of habitat preference. Several studies of fish feeding habits have been performed in other coral habitats such as the Society Islands (Randall and Brock, 1960), West Indies (Randall, 1967); Gulf of California (Hobson, 1968), and Hawaii (Hobson, 1974).

General discussions of reef foraging mechanisms can be found in Bakus (1969) and Davis and Birdsong (1973). The browsing and grazing activities of reef fishes may have significant effects upon the presence and abundance of benthic organisms. Hayne and Ball (1956) found that the productivity of "fish food" in a freshwater lake was higher (but the standing crop lower) when fishes were allowed access to a particular area. Studies of the influence of herbivorous fishes on the flora of the West Indies (Randall, 1961a, 1965; Randall and Hartman, 1968; Earle, 1972) and in the Marshall Islands (Bakus, 1967), suggest that the foraging habits of browsing and grazing fishes can dramatically determine the floristic topography of a region. By providing artificial shelter, Randall (1963) was able to attract herbivorous fishes to a source of food that previously was inaccessible. The effects of browsing fishes on shallow-water reef sponges has been described by Bakus (1964) and Randall and Hartman (1968).

It is readily apparent to any observer in tropical waters that many fishes utilize coral reefs for shelter. Some means by which this resource is shared among fish species have been suggested by Collette and Talbot (1972) and Fishelson et al. (1974). Reefs are significant refugia from predators and strong currents during the night as well as the day. Many schooling herbivores (which often constitute a considerable proportion of the fish biomass) forage over the reefs or in rubble areas during the day and at night seek shelter in reef caves or crevices. Conversely, some species found deep within shelter during the day become active at night where they forage in the water column or over bare sand areas (Longley, 1972; Longley and Hildebrand, 1941); Randall, 1961b, 1962; Hobson, 1968, 1972, 1973).

Tagging studies have shown that many species have limited home ranges (Bardach, 1958; Randall, 1961b, 1962; Springer and McErlean, 1962; Nolan et al., 1975). Behaviorists have examined the mechanisms of territoriality in damselfishes and butterfly fishes and found a diversity of territory holding strategies (Zumpe, 1965; Stevenson and Myrberg, 1966; Myrberg et al., 1967; Myrberg, 1971; Emery, 1968; Cummings, 1966, Swerdloff, MS; Sale, 1968; Low, 1971; Allen 1972; Reese, 1973).

There are numerous in-depth studies of the autecology of various reef fishes, i.e., Abudefduf (Helfrich, 1958), surgeon fish (Randall, 1955), Dascyllus (Stevenson, 1963), Gymnothorax (Brock, 1972), damselfish (Allen, 1972). Species of Lutjanus have been investigated by Starck and Schroeder (1971) and Talbot (1960) and species of Chromis by Swerdloff (1970).

The analysis of reef fish assemblages and communities, however, has yet to achieve the level of understanding found in the study of most terrestrial ecosystems. The problems and limitations inherent in conducting research in the sea are being circumvented by use of underwater habitats and underwater television. Considerable insight into the daily activity routines (i.e., interactions with conspecifics, other species, and their environment) was achieved during the Tektite Program (Collete and Earle, 1972) and the underwater television experiments of Smith and Tyler (1973). In both cases ecologists restricted their attention to a small reef region and observed fishes over a period of time. The intimacy achieved in this fashion is essential to the study of reef fish ecology and behavior.

The two major goals of this study were:

1. To describe the assemblage of fishes living on Enewetak patch reefs and in adjacent regions; their species composition, relative abundance, and stability over time.
2. To describe the colonization patterns of fishes to defaunated patch reefs and to artificial reefs in order to determine the means by which recruitment, immigration, and extinction shape the structure of the assemblage.

The warm clear waters of a coral atoll provide comfortable conditions in which to observe a diverse and highly colorful fish fauna that is little disturbed by man. In his final book, Geographical Ecology (1972, Harper and Row), MacArthur introduced the ecology of tropical organisms with this comment:

> A few decades ago it was fashionable for ecologists to study communities in the arctic on the grounds that these would be very simple communities and hence easy to understand. Many excellent ecologists still follow this belief, but there are others who feel that it may be easier to understand the extremely complex communities of the tropics. This sounds paradoxical: How can a more complex community be easier to understand? A possible answer might be that the complex community has strong interactions among species so that the lives of the separate species are less independent than in a simple community. Where there is greater interdependence, patterns may be more conspicuous.

At Enewetak, the strong interactions between predator and prey, between food and shelter, are clearly shown by the experimental manipulations described here.

METHODS

The study took place at Enewetak Atoll in the Marshall Islands of the Pacific Trust Territory (11°20'-11°40' N, 162°00'-162°30' E) during the period of September, 1971, to September, 1974. The study reefs are located along the windward edge of the atoll in water depths less than 10 m, and between the islands of Enewetak (site of the Mid Pacific Marine Laboratory) and Parry (Figure 1). The coral development forming the patch reefs in this region is especially luxurious primarily because of currents supplying nutrients and food to the reefs from the windward outer reef. Reefs in the lee of Parry and Enewetak Islands consist predominantly of dead corals, whereas lagoon reefs on the leeward side of Enewetak are not discrete isolated units but mostly form a consolidated shelf. Descriptions of the geology of Enewetak and nearby Bikini can be found in Tracey, Ladd and Hoffmeister (1948); Ladd, Tracey, Wells and Emery (1950); and Emery, Tracey and Ladd (1954).

The reefs in the study area range from small Pocillopora heads (less than .5 m in maximum dimension) to massive pinnacles (over 100 m across). Small reefs separated from other reefs by sand expanses and roughly 3 x 3 x 3 m in size were abundant and proved to be excellent study sites. They offer a rich variety of fishes, corals, and types of shelter. To investigate the effects of variable amounts of shelter on the reef fauna, small, standardized artificial reefs were employed. A typical natural patch reef is shown in Plate 1A.

Current flow is predominantly lagoonward from the windward reef with the swiftest flow (5 kts) behind the inter-island reefs north and

south of the small, rubble island (here designated Isaac's Island) (Figure 2). The sand substrate in these regions has been swept clear, thereby exposing rubble and cobble bottoms. Directly behind Isaac's Island the flow is much reduced, but with a complicated fine structure due to eddies formed behind the reefs and in the channels. The prevailing trade winds augment flooding tides and may cancel the returning ebb flow. The mean tidal amplitude of Enewetak is about 2.7' and the mean spring tide range is approximately 2.9' (Hiatt and Strasburg, 1960). This range is sufficient to expose and alternately cover great expanses of reef flat but has little effect on the study reefs.

Water clarity is normally quite good with horizontal visibility to 50 m. At times a large surf pounding the windward reef may dislodge algal filaments and coral mucous reducing visibility to 10 m. Occasionally, large numbers of salps and fish larvae reduce visibility. Water temperatures are a uniform 23° to 24°C.

Enewetak is generally considered to be at too low a latitude to frequently experience typhoons (Wiens, 1962). In the late summer and winter of 1972, however, three typhoons struck Enewetak, resulting in six to eight foot surf breaking on the lagoon shore of Isaac's Island. Although most of the study reefs were too deep to receive breaking waves, the heavy surge did dislodge many fragile "table-shaped" Acropora and removed much of the sand substrate in the area of the shallowest reefs. This sand was deposited on Isaac's Island, creating a 3 m high sand bar extending continuously from Parry to Enewetak. With the resumption of the trade winds, the sand was blown back into the lagoon and currents dispersed the sand uniformly between the reefs by December, 1972.

Sixteen small (roughly 2.5 x 2.5 x 2.5 m) natural patch reefs were designated study reefs, of which nine were defaunated and five remained as controls (the history of study reef manipulations is shown in Table 1).

All study reefs lie in water depths from four to six meters and are isolated by sand expanses for a distance of at least 15 m in all directions. Reef size was defined by measuring reef height, reef circumference at the base and circumference at midreef. An index of reef volume was derived based on the assumption that the reefs approximate the shape of cylinders (the circumference values were averaged to obtain a mean reef radius). Calculated reef volumes are listed in Appendix Table 1, along with reef depth.

Galvanized steel spikes were driven into the reefs to provide photographic reference points to document changes in coral cover. No other specific invertebrate or plant sampling program was conducted, except to note unusual invertebrates or algal blooms.

The reefs were defaunated by the ichthyocide, powdered derris root (5% rotenone) which is believed to be less toxic to invertebrates than synergized, emulsified agents (Richard Rosenblatt, Scripps Institution of Oceanography, pers. comm.). Six pounds of powdered derris was mixed with water to paste-like consistency and applied to the reefs with plastic bags. Currents had to be relatively weak to prevent dilution and dispersal of the poison. Some fish species (such as Pomacentrus pavo) were ineffectively sampled by this method because they fled to nearby reefs immediately after application of ichthyocide. To contain these within the cloud of ichthyocide, a large 1/4" mesh

nylon bag was dropped over the reef before application. At times, considerable numbers of stunned and dead fish were lost to predators attracted to the area. Losses were especially high on reefs that harbored large schools of small species (e.g., apogonids, pomacentrids). Censuses conducted immediately preceding the defaunation permitted compensation for these losses.

In single poisonings, Smith (1973) obtained only 75% of the species collected by repetitive poisonings of Bahama patch reefs; on a 4 x 5 x 2.5 m reef sampled for five consecutive days, the second and third collections each added five new species to the initial sample of his collection. The incomplete kills on Bahama reefs were probably due to insufficient amounts of rotenone (22 g of emulsified rotenone) administered, or to weak batches of poison (the variability in potency of liquid rotenone is well known to ichthyologists). One would expect a more complete kill on such small reefs if sufficient amounts of fresh, powdered rotenone were used.

Poison stations on Enewetak reefs were very successful, killing nearly all the fishes. The use of the net was effective in containing species that would normally flee the reef. Forty-six poison stations were conducted on natural and artificial reefs in the study area. Each defaunation was preceded and followed by censuses. Only on one occasion, when currents unexpectedly swept away the rotenone, was the kill ineffective. Reef No. 13 was poisoned on 23 February 1973, yielding 17 species and 194 individuals. A census conducted the following day showed ten individuals of two species present. These were Pomacentrus pavo and Halichoeres trimaculatus, which had escaped before the net was

placed. Six days later, however, 75 individuals of ten species were present. Extremely rapid recruitment was also seen on reef No. 15, poisoned on 9 July 1973. Two days later, this reef was inhabited by two adult Pomacentrus pavo (that had probably escaped prior defaunation) and 25 newly settled juveniles. In addition, there were 24 Cheilodipterus macrodon about 1 cm in total length and a very dense cloud, about one cubic meter in size, of recently settled, nearly transparent juveniles. Three Chromis coelestis (one adult and two juveniles) also were noted for the first time. Colonization of patch reefs is discussed in detail elsewhere (Part II).

It is felt that the defaunation method used on the Enewetak study reefs was extremely effective--especially in eliminating fishes from the reef. The lack of comprehensive kills in the Bahama reefs was probably a result of an insufficient application of ichthyocide.

Specimens from ichthyocide stations were collected with handnets and placed on ice within thirty minutes of death. At the laboratory, they were identified, measured, weighed, and then preserved in 10% formalin. Spear collections of fish predators were made during the study, and results will be presented elsewhere (Nolan, 1975). Fish identifications are largely based upon Schultz et al. (1953).

Visual censuses ("point censuses" in the terminology of MacArthur, 1964, and Slobodkin and Fishelson, 1974) were used to follow patch reef fish populations; and in many cases, individual fish were recognized throughout the two-year period of censuses. This method is well suited to the clear waters of Enewetak. The number, size, and zone of occurrence of all fishes were recorded on pre-printed Underwater

Ascot data sheets. The censuses were conducted in a specific, sequential manner. About 15 m from the reef, I looked for fishes that might flee upon closer approach, time of day, tide state, water visibility, current direction and magnitude were also noted. Midwater feeding species were next censused. This was best accomplished by staying very close to the bottom and making only slow movements (including breathing). Otherwise these species would dart back to the shelter of the reef. Cavern-dwelling fishes were recorded by looking into holes and cracks. By tapping the entrance of a cave, a procession of squirrelfishes and cardinal fishes could often be induced to file conveniently past (these species sometimes could be more easily censused at night). Two replicate censuses were conducted on all study reefs during the following periods: December, 1972; February-March, 1973; July, 1973; October, 1973; February, 1974 (no sample on reef No. 30); and May, 1974 (Table 1). Each census consisted of six to eight navigations around the reef and required 30 to 45 minutes. Most ecological studies are forced to rely upon sampling techniques to estimate population and diversity values; here, however, the absolute values can be determined. As pointed out by Wass (1967) in his study of the re-colonization of a large patch reef in Kaneohe Bay, Hawaii, some species are more accurately censused than others (based on collections subsequent to the census). On Enewetak study reefs, for example, most gobies and blennies were not censused because of their small size, cryptic coloration, and reclusive habits.

The precision of the visual technique was assessed by comparing four replicate censuses on a control reef (reef No. 12 was selected by random means). These censuses were conducted at the same time of day,

tide, and current condition over a period of seven days. Species composition was found not to vary by more than two species on replicate censuses (Table 2); Myripristis murdjan and Flammeo sammara were absent on a single census. This may be an artifact of the method or they may have returned to different reefs than those they inhabited the preceding day or may have been taken by predators. Obvious species like Chaetodon ephippium, Coris aygula, and Zanclus canescens are undoubtedly transients on reef No. 12.

The visual census technique is then quite precise for species presence and sensitive enough in terms of numbers of individuals to allow the detection of small additions or deletions. The method becomes even more refined when size data are considered. This permits specific individuals (presumably) to be followed over considerable periods of time.

The accuracy of the visual method was established by comparing pre-poison censuses on a particular reef with the results of a later poison collection. In this case, only species number is considered. Reef No. 5 was censused on 10 May 1974 and poisoned the following day. The collection contained 39 species of which the census revealed 29. This is exclusive of gobies, microdesmids, scarids, synodontids, and tripterygiids. Fishes not detected during the census were either indistinguishable from conspecifics in the field (e.g., Myripristis murdjan and M. argyromus) or dwelled deep inside the reef (e.g., Adioryx spinifer).

Transects were designed to assess fish populations in adjacent sand and rubble plain areas using the method described by Brock (1954).

The numbers of free ranging fishes (e.g., surgeon fishes and parrot fishes) were counted along a 100 m transect line located on the sand plains near the middle of the study area. The line ranged between four and six meters in depth and was intentionally placed as far as possible from nearly patch reefs. Small, sub-surface floats attached at 10 m intervals on the line provided reference distances to judge 10 m^2 quadrants lateral to each side of the transect. This resulted in 20 10 m^2 quadrats for a total sample area of 2000 m^2. The number of fishes per quadrat was counted and their size (total length) estimated as the transect was traversed. On the 100 m inter-reef transect, only large, roving species were counted. Shorter, 50 m transects (1000 m^2) were placed in rubble and sand regions where the numbers of smaller fishes (e.g., gobies) were counted. The same census techniques were utilized on all transects. All data were recorded on pre-printed Underwater Ascot paper (Appleton Papers, Appleton, Wisconsin). The percent cover of living coral, rubble/cobble, or sand substrates was visually estimated for each quadrat of three transect types.

ENEWETAK LAGOON FISH ASSEMBLAGES

The fish faunal component of a reef community can be separated into categories based on habitat preference or foraging habits (Smith and Tyler, 1973; Hiatt and Strasburg, 1960). At Enewetak, the fishes inhabiting the shallow, windward lagoon community can be readily divided into four assemblages on the basis of the distinct regions that they inhabit. These assemblages may constitute a community in that they are linked energetically. Not only do they depend on common sources of primary production, but many species prey upon larvae or adults of differing assemblages or may spend considerable energy in excluding them from their territories.

This investigation deals primarily with the Patch Reef Assemblage, defined as those fishes that reside on small coral patch reefs, and restrict their activities to within a few meters of the reef. The Roving Fish Assemblage consists of free-ranging schools or solitary individuals of both herbivores and carnivores (e.g., jacks, parrot fishes, trigger fishes, snappers, surgeon fishes, and goat fishes). This category is analogous to the "midwater visitors" and "supra benthic nomads" of Smith and Tyler (1973), and the "fishes associated with the midwater and pelagic community" of Hiatt and Strasburg (1960). The remaining two assemblages consist of fishes intimately associated with the substrate over which they seek shelter, feed, or defend territories: the Sand Assemblage and Rubble Assemblage. These consist of smaller sized species: damsel fishes, gobies, blanquillos, and wrasses that escape predators by diving into sand burrows or between cracks in the rubble. Most of the area of the study region consists of sand or rubble

plains; reefs occupy only about 30% of the area. The Sand, Rubble, and Patch Reef Assemblages consist of species in which the adults are restricted to shelter refugia. The perpetuation of a species depends upon the recruitment of juveniles from the plankton, where they spend their larval stages. Roving Fish Assemblage species are not restricted to shelter (during the day) and avoid predators by schooling or by means of their large size, fast swimming ability, sharp spines, or cryptic coloration. Thus they are able to exploit infaunal organisms as well as prey upon unwary patch reef fishes. Many of these species do, however, seek the safety of reefs at night when their feeding schools disperse.

ROVING FISH ASSEMBLAGE

Observations were made at all hours of the day throughout the duration of the study on this assemblage; however, no obvious relationships between time of day or tide condition and the presence or abundance of fishes was detected. When the water was turbid, fewer individuals were seen, probably as a result of movements to nearby clear areas where prey detection and predator avoidance might be facilitated. The presence of Carnax melampygus and Carangoides ferdau along the transect was sporadic and their foraging activities may be related to time of day or tide level.

Table 3 depicts ten daytime censuses conducted along the inter-reef tansect (all tide conditions are lumped). Acanthurus nigricans, Monotaxis grandoculis, Lethrinus miniatus, Parupeneus barberinus, Odonus niger, Carangoides ferdau, Caranx melampygus, Epinephelus flavocoeruleus and E. macrospilos were the most often encountered species; and A. nigricans was the most numerous species ($\bar{x}$ = 19.8 ± 7.0). The Roving Fish Assemblage contains substantial numbers of piscivores (frequency $\bar{x}$ = 5.2) which exert a large predation pressure on the patch reef fishes.

A foraging goatfish, Parupeneus barberinus, is likely to be followed by juvenile P. barberinus, P. pleurostigma, and Halichoeres trimaculatus. These species are probably capturing crustaceans and polychates that flee when the goatfish disturbs the sediment. The associations are a common sight on the sand plains surrounding the reef; however, it is not known if this behavior is more than a chance feeding pattern.

Other species of this assemblage were seen on most dives; however, they did not occur in the transect area at the time of census. These include species of belonids and hemirhamphids. Epinephelus macrospilos and E. flavocoeruleus were the most abundant serranids, but seldom left the proximity of shelter unless briefly swimming between reefs. Schools of Lutjanus vaigiensis, L. gibbus, and L. monostigma were numerous around the large reefs at the south end of Isaac's Island. A pair of large (1.5 m total length) hump head wrasses, Cheilinus undulatus, also lived in this region. Very cryptically colored fishes, including Bothus mancus, Saurida gracilis, and Synodus variegatus, were sometimes seen resting on the sand between reefs. More commonly they were noted in sand at the base of patch reefs.

Large carnivores were also present in the area. Once a dogtooth tunny, Gymnosarda unicolor, was observed in deeper waters near reef No. 31. Blacktip reef sharks, Carcharhinus melanopterus, the white tip reef shark, Triaenodon obesus, and the eagle ray, Aetobatus narinari, were commonly seen at the study site. Two grey sharks, C. amblyrhynchos, were observed on most dives during the two years, suggesting a limited home range for this species. A 1.5 m grey shark was captured on a night line off reef No. 31 in October, 1973. Grey sharks and, to a lesser extent, blacktips sometimes became aggressive during ichthyocide stations or while spear fishing, biting at flippers or taking wounded fish from spears. On a night dive in November, 1972, a large unidentified shark attacked a grouper that had just been speared and placed in a net collecting bag. This shark was also believed to be a grey.

In conclusion, the areas between reefs at Enewetak are the feeding grounds for many large and small herbivores and carnivores. With the exception of jacks and sharks, most species of this assemblage are dependent upon patch reefs to avoid predation at night. During the day, jacks, snappers, and serranids feed upon the patch reef fishes and parrotfishes and surgeon fishes browse upon the algae growing on or within the reefs.

RUBBLE FISH ASSEMBLAGE

A 50 m transect was placed along the south side of reef No. 16 on a rubble plateau approximately 5.2 m in depth. The transect substrate averaged 41% rubble cobble and 59% bare sand. Reefs in this region receive heavy swell and breaking surf during typhoons. Consequently, the bottom consists of shards of broken coral and rubble that was exposed during the 1972 storms (Figure 3). During the siege of typhoons, the sand that previously separated reef Nos. 2, 3, 4, 10, 11, 16, and 17 was removed and deposited on Isaac's Island. The large rubble patch at the northern extreme of the study region is, however, a result of scouring from tidal flow over the inter-island reef.

The results of two censuses conducted on the rubble and sand transects are shown in Table 4. In this case the range of total transect abundance per species and mean number of individuals per m^2 quadrat have been tabulated. There were several small living or dead coral heads (the largest was 1 m across and .5 m in height) in the transect data which support populations of Patch Reef Assemblage Fishes. These species are denoted by asterisks in the table and their numbers were not included in the total densities. In some cases, e.g., Pomacentrus pavo, individuals were both in the coral heads and in the rubble. Total density values were adjusted accordingly for these species.

Two common, shallow-water dwelling pomacentrids, Abudefduf biocellatus and Pomacentrus coelestis, were found only in rubble areas. The wrasse, Stethojulis axillaris, is less restricted, moving between rubble areas and patch reefs as is Halichoeres trimaculatus which was

recorded in sand, rubble, and at the base of patch reefs. This wrasse is the most generalized of any species considered in this study, foraging in all habitats and often occurring in large numbers. Hiatt and Strasburg (1960) noted that H. trimaculatus is primarily a carnivore that opportunistically feeds on "virtually any prey occurring on sandy bottoms." Rhinecanthus aculeatus and Sufflamen chrysoptera are found only in rubble areas where they rigorously defend territories intra- and inter-specifically. Pomacentrus pavo is also restricted to shelter, living in either rubble areas or at the base of patch reefs.

The most abundant species were gobies of the genus Pogonoculis. Pogonoculis sp. excavates burrows in sand spaces between cobbles and, therefore, is not strictly a rubble dweller. Pogonoculis zebra, on the other hand, inhabited rubble crevices or excavated sand to gain access beneath fallen table Acropora. Species of this genus feed 2 to 3 m above the bottom, rapidly plunging into their burrows when approached. Malacanthus sp. is like P. zebra in habits and is mostly a rubble dweller.

Ctenochaetus striatus was found in the rubble mostly as juveniles and in fewer numbers than at the base of reefs. Juvenile Acanthurus olivaceous were consistent members of this assemblage, although they were not abundant on the rubble transect.

More replicates would be desirable for both rubble and sand transects; however, the census data reflects my general impressions of this assemblage. Most representatives are small species or juvenile stages, and either feed in the water column (Pogonoculis and Malacanthus)

or pick at the substrate (Abudefduf biocellatus, Pomacentrus pavo, and most juvenile wrasses). Serranids and jacks are the major daytime predators on this fauna.

SAND FISH ASSEMBLAGE

The sand transect was placed west of the rubble transect in comparable water depths. It lacked the small coral heads found in the rubble region and consisted mostly of sand (91.5%) with small amounts of rubble.

This assemblage is of much lower diversity and density than the rubble assemblage (Table 4). Here again, the most numerous species is Pogonoculis sp. with a mean of .22 per m^2. Halichoeres trimaculatus was next in abundance (all Pomacentrus pavo recorded were associated with a broken table Acropora). Of species recorded only in the sand transect, Odonus niger probably is the only species restricted to sand substrate (possibly due to its foraging technique of blowing away the sand to reveal invertebrates), with the exception of the sand burrowing gobies and blanquillos. The microdesmid, Gunnelichthys unimaculatus, and the goby, Ptereleotris tricolor, were seen hovering in midwater over many sand regions; however, they were not recorded along the transect. Other species not censused along the transect but believed to be abundant in some regions, were a small callionymid, Synchiropus sp., and the lizard fishes, Saurida gracilis and Synodus variegatus. A Carangoides ferdau seen foraging over a sand area and later speared contained 15 fresh Synchiropus sp. Bothus mancus, Carangoides ferdau, Caranx melampygus, Saurida gracilis, Synodus variegatus, Thysanophrys arenicola, Parapercis clathratas, and P. cephalopunctatus are the most important predators on the sand fauna.

STRUCTURE OF THE PATCH REEF ASSEMBLAGE

The fish inhabitants of patch reefs were determined by poison collections from 12 reefs that were defaunated in order to follow subsequent colonization. The data from all 12 reefs were combined to form a representative portrait of species composition, frequency of occurrence, and abundance (Table 5). Reefs A, B, C, and D were collected in May, 1972; reef Nos. 3, 5, 8, 9, 13, 15, and 17, in August, 1972; and Reef No. 10, in February, 1974. All were of comparable physical characteristics and seemed typical of the numerous small reefs occurring in shallow depths along the windward side of the lagoon. Pre-poison censuses were conducted and species abundances in the collection were corrected for loss due to predation during the rotenone stations. The abundance of pomacentrids and apogonids is most biased because of difficulty in picking up the large number of small specimens, and population values should be regarded as minimums (more reliable estimates of these species were obtained by replicate visual censuses reported in a later section). In Table 5, species composition, frequency (number of reefs out of 12 where present), and mean number of individuals per reef (where present) of the 12 reefs are combined (number of individuals per species is listed in Appendix). Abundance range and quartiles were used as suggested by Fager (1968) to depict the actual distribution of abundances. For example, in the pomacentrid Chromis caerulea, the range and quartile values were 0-3-12-19-54 indicating that the minimum number found on the 12 reefs was zero, and the maximum number was 54. Twenty-five percent of the samples contained fewer than three individuals, 50% contained fewer than 12, and 75% contained fewer than 19. Relative

abundance was scored by the categories (A) Abundant, (C) Common, (S) Single Occurrence. Fager's criteria (1968) again were used. In each of the 12 samples, species were listed in decreasing order by number of individuals until a sum equal to half of the total was reached--these then were classified as Abundant (A). This process was then continued until 75% of the total individuals were summed, yielding the category Common (C). Species that were found only as single individuals were listed as (S). Chromis caerulea (A = 2, C = 2, S = 0) was abundant on two reefs, common on two reefs, and never occurred as a single individual.

About 150 species have been either collected or observed in the proximity (within 1 m) of the study reefs. These represent a modest proportion of the Enewetak and Marshallese fish fauna. Hiatt and Strasburg (1960) estimated there to be 225 Marshallese genera and 600 species; Bakus (1969) estimated 880 species, which still may be an underestimate. Most of the resident species on the windward patch reefs are carnivores or omnivores. Herbivores are often present as juveniles (especially species of Ctenochaetus) during the day and are represented by adults wedged in crevices at night.

The most numerous fishes living on the reefs are apogonids and pomacentrids. Pomacentrus pavo, Chromis caerulea, Apogon novaeguineae, A. erythrinus, and A. gracilis ascend above the reefs (when not threatened by predators) to feed upon items transported over the reef by tidal flow. The cardinal fishes school during the day beneath ledges or in caverns, ascending at night to feed; pomacentrids seek shelter at night and feed continuously during the day.

Assemblage structure can be derived from Table 5. The following is a summary of the table, listing ranges and means for number of individuals and diversity on 12 defaunated study reefs:

	Least-Mean-Greatest Per Reef
Number of Individuals	138-452.3-1514
Number of Species	26-39.3-61
Number of Abundant Species (A)	1-3.0-11
Number of Common Species (C)	1-3.8-10
Number of Single Occurrence Species (S)	7-15.2-22

There was a considerable range in number of individuals and species. Species are distributed very unevenly; reefs B, C, and D all had large numbers ($\bar{X}$ = 535.0) of juvenile Apogon gracilis when collected in May, 1972, while reef A collected at that time lacked A. gracilis. Reef No. 9 had 420 specimens when collected three months later, while reef No. 13 had only 21 individuals at the same time. Although subsequent observations of reefs in the vicinity of the study area have shown that some occasionally support large schools of A. gracilis, they were not seen nearly as frequently as in May, 1972.

In the community of invertebrates inhabiting decaying oak wood, natural and artificial logs in Wythan Woods Estate, Berkshire, Fager (1968) found a significant positive correlation between number of individuals and number of species per log. In this reef assemblage, there is a trend towards an increase in number of species with number of individuals; however, it is not significant at .05 level. Even when A. gracilis populations are subtracted from total number of individuals, the correlation is still not significant (Pearson r = 5.88, n = 7) at the .05 level.

The number of individuals was not correlated with the number of either species category A or C. However, as predicted by the binomial distribution, number of species was significantly correlated (at .05 level) with number of single-occurrence species (Pearson r = .65, n = 12) merely indicating that as the number of species increased, the number of single-occurrence species increased. This suggests that the defaunation method was effective in collecting the most common species. The trend toward increasing (S) with number of individuals is partly a function of reef size and the type of shelter available.

A portrait of a typical reef based upon the collection data, would consist of about 40 species and 500 individuals. The more frequent species on these reefs in daylight are apogonids (Apogon gracilis, A. exostigma, A. erythrinus, A. novaeguineae, and Paramia quinquelineata) which are found in the lower half of the reef in either caverns or beneath overhanging table Acropora, and pomacentrids (Pomacentrus pavo, Chromis caerulea, Dascyllus aruanus, and D. reticulatus) which would be feeding on plankton in the water column above and to the side of the reef, seeking shelter when approached by predators. Many apogonid species similarly feed in the water column at night. Solitary Pomacentrus vaiuli and Abudefduf dicki would be ranging over the reef, occasionally picking at the substrate. At the apex of the reef, Pomacentrus nigricans would be defending territories among Acropora formosa and filamentous algae. Most reefs would support a single or paired Chromis dimidiatus and/or Abudefduf curacao feeding high in the water column with Pomacentrus pavo and Chromis caerulea. Labrids would be abundant, represented by three or four adults and 10 to

15 juvenile Halichoeres trimaculatus foraging at the base of the reef. Juvenile and adult Gomphosus varius and Thalassoma lutescens would also be present. In August, 1974, Thalassoma amblycephalus juveniles and adults were observed to be abundant, feeding in midwater over the reef. The most common and obvious day-active blenny, Ecsenius bicolor, would be present, paired or solitary, resting on corals. Several Paracirrhites arcatus would be propped on coral heads, mostly in the lower half of the reef. Many gobies (difficult to identify in the field) would inhabit a variety of coral species. At the base of the reef or resting in a crack between Acropora heads would be one or two adult or juvenile Epinephelus merra (Table 5 probably underestimates their numbers). Also present would be a single individual or pair of Cephalopholis urodelus or C. leopardus which remain largely within the reef during the daylight, being more secretive than Epinephelus merra. These species may be crepuscular feeders. Looking into a cave, we would find a single Adioryx spinifer, a pair of Flammeo sammara (or F. opercularis) and four to five Myripristis murdjan (or M. argyromus). These species feed at night.

Family contributions to biomass as percent total weight are listed in Table 6 (reefs, B, C, and D are tabulated independently to illustrate the influence of large numbers of A. gracilis). The greatest contribution to biomass ($\bar{X}$ = 247.2 gms per reef) was by the apogonids, followed by serranids, pomacentrids and anguilliforms (muraenids and echelids), holocentrids and miscellaneous families grouped in the category "other". Although they are small, apogonids and pomacentrids were very numerous; eels were less common but of greater body weight.

The weight value for serranids may be underestimated in that most reefs observed were characteristically inhabited by one to two individuals. In Virgin Island reefs, serranids constitute a high proportion of reef fish biomass (Randall, 1963). Frequency of ranks for these reefs are given in Table 7. Here the importance of the families Serranidae, Holocentridae, Apogonidae, Pomacentridae, and the Anguilliforms may be seen.

The residence time of particular individuals of some patch reef species is unknown. For example, Ctenochaetus striatus, C. binotatus, Halichoeres trimaculatus, Scarus jonesi, and S. unimaculatus freely range between reefs. Still, the feeding activities of these species may have a profound effect on the reef flora and fauna. The fidelity of "resident" apogonids is also uncertain because they emerge from the reefs at dusk and have been observed several meters from the reef at night. At dawn they may return to the nearest available shelter, which may not be the reef initially inhabited.

The 12 reefs poisoned showed considerable variability in their fish fauna. Reef No. 8 has a significantly greater volume than other reefs and also ranked high in diversity and biomass. The other reefs have approximately equal sizes (S.D. = 1.9, Table 1), yet diverged greatly in number of species, number of individuals, and biomass (Table 8). Many reef fishes show preferences for particular shelter types and/or coral species. At present, not enough is known about the specific substrate requirements of these fishes to assign this as a cause of variability. The reefs do seem roughly comparable in amount and type of shelter. The only exception are reefs that lacked healthy Pocillopora

heads; these lacked Chromis caerulea, Dascyllus aruanus, and D. reticulatus. To determine whether the observed variation was due to differences in amount or type of shelter available, small, standardized artificial reefs were installed in the study area. The variability on artificial reefs was also high (although there were fewer species involved) and probably is a result of stochastic factors affecting the recruitment of potential colonizing propagules (Part II).

Enewetak patch reefs support distinct day and night faunas, as do the reefs in the Gulf of California and Hawaii (Hobson, 1968; 1972). Table 9 presents the species composition, percent frequency of occurrence, and abundance values for nine censuses conducted on six study reefs between dawn and dusk. There are two obvious categories: those fishes active at night and those that are quiescent. The dawn/dusk transitions are particularly interesting in that members of both groups are exposed (but near shelter) at this time. However, the predation was no more intense at this time than during the day or night; it was so described by Hobson for the Gulf of California (1968), and assumed for other tropical reefs (1972). This difference may be due to the greater number of piscivores constantly patrolling the study reefs at Enewetak, resulting in a more even diurnal feeding period distribution.

Apogonids are generally assumed to be nocturnal feeders (Randall, 1967; Starck and Davis, 1966; Hobson, 1968, 1974). Apogon novaeguineae is often observed at night foraging up to 10 m horizontally from the nearest reef and within 2 m of the bottom. Apogon exostigma and A. erythrinus, however, remain within 1 m horizontally of the reefs and are seldom seen higher than 2 m above the sand bottom. Myripristis

murdjan, M. argyromus, Flammeo sammara, F. opercularis, and Adrioyx spinifer were observed swimming at the apex of cavernous reefs. The presence of diving lights caused these species to seek shelter in the caverns. Lutjanus vaigiensis and L. kasmira are active nocturnally, foraging over bare sand bottoms. Lutjanus vaigiensis schools during the day near the larger patch reefs near the south end of Isaac's Island - probably as a means of avoiding predation. These habits are similar to those of other snappers, e.g., Lutjanus griseus in the Atlantic (Starck and Davis, 1966) and L. argentiventris (Hobson, 1968). Adult Lutjanus kasmira were not present during the day near the study reefs, although juveniles were seen on reef No. 13 and several artificial reefs.

Many fishes were quiescent on the reefs at night. The surgeon, Acanthurus nigricans, was seen on 91% of night censuses. They, along with several species of scarids, Chaetodon trifasciatus, C. auriga, Cheilinus chlorourus, Epinephelus merra, and Pterocaesio tile wedged themselves in crevices or caverns. Individual Acanthurus nigricans were often observed during the day near reefs that later harbored specimens at night. When approached during the day, they would frequently enter the reef cavern before rejoining the feeding school. This behavior is similar to that of the trigger fish, Rhinecanthys aculeatus. When mildly threatened, it repeatedly enters its dwelling - as if to inspect its escape route and the security of the shelter. It would be of interest to tag Acanthurus nigricans and Pterocaesio tile at night (both are easily captured when quiescent) to determine whether individuals return nightly to the same reefs and if A. nigricans near a reef during

the day is the same individual sleeping in it at night. Schools of P. tile abound in deeper water (15-20 m) during the day. At dusk, the schools disperse and individuals seek shelter in the reefs. Schooling is believed to be a means of reducing predation, hence, this species and others may be very vulnerable at the dawn and dusk transition periods.

Carangoides ferdau is a common predator that forages actively over sand bottoms - sometimes in small groups, but usually as solitary individuals. Repeatedly during night censuses, a tight school of approximately 50 C. ferdau was observed cruising between reefs in the study area. Their nocturnal/diurnal pattern is the reciprocal of snappers that school during the day and feed solitarily at night. Nocturnal feeding is not known in carangids, but Hobson considers Caranx melampygus in Hawaii to be a crepuscular feeder (Hobson, 1974). At Enewetak, C. melampygus is occasionally observed feeding on patch reef pomacentrids and labrids during the day. Jacks may be excluded from nocturnal feeding by their dependence upon visual cues for prey detection. Adults must survive the night by avoiding large night feeding sharks and the juveniles must avoid moray eels. Schooling behavior may be an effective way of reducing the chance of being eaten with a minimal expenditure of energy (Brock and Riffenburgh, 1960; Shaw, 1970).

STABILITY OF THE PATCH REEF ASSEMBLAGE

The faunal composition of comparably sized reefs was highly variable within the 11 defaunated reefs. To test for temporal fluctuations in number of species and individuals, five reefs (designated control reefs) were censused (two replicates within a week) at approximately 100-day intervals. The results were used to establish the signal-to-noise ratio necessary to evaluate the effects of manipulations on experimental reefs.

The species composition of control reefs fluctuated considerably over the two and a half years of observation, and likewise, the number of species present. In Figure 3, the change in number of species over time for undisturbed control reefs can be seen. All reefs (except No. 10) initially had 18 to 21 species and all terminated with 20 to 24 species. Reefs No. 11 and No. 30 declined over the first 200 days while No. 10 and No. 12 increased. Reef No. 10 had the largest change in number of species, starting with 13 and ending with 23 species. Reef No. 7 showed the least variation (CV = 6% as compared to a mean CV of 21% for the other control reefs), beginning with 21 species and ending with 20. Reef No. 30 began with 18 species and ended with 20, but after 200 days had dropped to a low of 11 species. All reefs had returned to the original number of species, except No. 10 which had gained ten species by 445 days.

The temporal variation in number of individuals of all resident species on control reefs is shown in Figure 4. High population peaks reflect the addition of juveniles to already complete species lists (e.g., 350 Cheilodipterus macrodon and 500 Apogon novaeguineae to reef

No. 12 in May, 1974, 400 Apogon gracilis to reef No. 7 in March, 1973, 200 Chromis caerulea to reef No. 12 in October, 1973, and 300 Pomacentrus pavo to reef No. 10 in July, 1973). When increases due to juvenile recruitment were subtracted from the resident adult populations, the curves appeared much more uniform (as do those of reefs No. 11 and No. 30).

Changes in the species composition of control reefs can be seen in Tables 10 through 14. Reefs No. 10 and No. 12 will be discussed in detail to illustrate actual species additions and losses. Over one half of the new species of reef No. 10 were present as juveniles when first observed on the reef. This does not preclude that others may have invaded as larvae and attained adult size by a subsequent observation period. Species lost from the period of 232 to 440 days were predominantly juveniles when last censused in July, 1973--size data are not included here.

The 12 invasions and extinctions of reef No. 12 are shown in Table 13. Eight species were present at every census period. Individuals of Pomacentrus nigricans, P. pavo, P. vaiuli, Paracirrhites arcatus, Chromis agilis, Centropyge flavissimus, and Paramia quinquelineata were consistently present on the control reefs and characterize the Patch Reef Assemblage in this region. In the cases of the sudden disappearance of Chromis caerulea and Apogon novaeguineae, the adults may have been taken by predators or died of other natural causes.

The occurrence of some species was sporadic (e.g., Flammeo sammara, F. operculatis, Adioryx spinifer, Gomphosus varius, Cephalopholis leopardus, Ecsenius bicolor, and Ptereleotris tricolor). If

holocentrids do not always return to their original daytime caverns, this would result in occasional losses from the censuses. Adult Gomphosus varius were seldom observed on small reefs, but common on nearby large reefs. Juveniles may move to larger reefs as they grow to adult size. The fidelity of Cephalopholis leopardus to specific small reefs is not known, and it is likely that their home range may encompass several reefs. The increase of reef No. 12 from 19 to 24 species during the period 440 to 526 days (Figure 6) came as juveniles of all species but Labroides dimidiatus.

The numbers of individual Pomacentrus pavo and Chromis caerulea on reef No. 12 demonstrated considerable variation as adults were lost and replaced by juveniles that settled from the plankton (Table 15). By May, 1974, adults of both species had severely decreased in number, but P. pavo had begun to re-invade the reef. In the period 232 to 331 days, there is a paucity of midwater feeding pomacentrids on reef No. 12. This period corresponds to an interval of new species invasion, but it is not known if there is any causal relationship.

Two studies that monitored selected species over time periods of up to a year, have shown them to be fairly stable systems. Wass (1967) monitored the fishes inhabiting a large patch reef in Kaneohe Bay, Hawaii, and found fish diversity to be fairly uniform over a period of 180 days (if parrotfishes were not included). Numbers of individuals in six out of nine monitored species, however, did undergo large variations during the same period. Smith and Tyler (1973) used an underwater television system to study the fish assemblage associated with a Bahama reef. The frequency of species occurrence over three extensive

observation periods in June and December, 1970, and June, 1971, was compared by using an "index of resemblance". They found little variation in species composition of "benthic residents" (analogous to the Patch Reef Assemblage); however, there was marked seasonal variation in "suprabenthic nomads". Smith and Tyler concluded [that it is] ... "our subjective impression from limited observations during the past eight years that the population levels of these species are quite stable and that long-term changes in relative abundance are far less than short-term annual or seasonal fluctuations due to seasonal movements, time of recruitment, etc." A study of the successional and seasonal changes in the fish fauna of a new jetty at East Pass, Choctawhatchee Bay, Florida, over a period of two and a half years showed profound seasonal changes in species composition and number of individuals (Hastings, 1972). This more temperate region did also undergo marked seasonal climatic changes.

The temporal variations in species composition and number of individuals of the Enewetak patch reefs contrasts with the constant systems described by Smith and Tyler (1973) and Wass (1967). This may be due to environmental variations at Enewetak or more likely, is an effect of the small size of the populations monitored and the detail in which they were studied. A series of devastating typhoons struck Enewetak a year before reef censusing began and destroyed many fragile table corals and transported considerable amounts of sand. Changes in current flow through the atoll or in surrounding water masses could also have had major effects on the availability of fish larvae, zooplankton, and nutrients. Since Enewetak is at the northern most

edge of the North Equatorial Current, slight changes in velocity or direction of flow may significantly influence the availability of fish larvae to lagoon patch reefs (major shifts in the position of the North Equatorial Current were observed by Professor John Isaacs of Scripps Institution at Bikini Atoll in 1946, pers. com.). Flow patterns within the atoll may have significant effects on the residence times of lagoon zooplankton, nutrients, and fish larvae. Recirculating currents may prevent these items from being swept over the leeward reef of the atoll and thus lost to the system. In summary, the environment of the study area is subjected to variations in water flow, turbidity, and even wave surge and sand transport upon occasion.

Another explanation of reef faunal variability may be a function of the small size of resident fish populations and the isolated nature of the study reefs. Small reefs (with correspondingly small fish numbers) may suffer the same deficiencies as small statistical samples--i.e., larger reefs may not be as sensitive to temporal or spatial patchiness in the availability of post-larval fish recruits. In addition, stochastic processes will necessarily have a more profound effect on small reefs in that the replacement of a local species extinction may be less predictable for a small reef sample area than a larger reef. Predation, competition, or natural aging mortality will more rapidly decimate a species line on reefs where they are only present in small numbers. The time necessary for re-invasion may be quite variable due to environmental fluctuations and stochastic events during recruitment. Coral reefs, like streams, are unique systems because successful reproduction in one locale does not insure perpetuity

of the species on that reef. The continuation of a species on a particular reef is a function of the breeding activities of conspecifics upstream.

PART II

Colonization Patterns

INTRODUCTION

This study deals with the colonization pattern of fishes to defaunated patch reefs in the lagoon of Enewetak Atoll. The mechanisms of colonization have been of interest for many years beginning with the eruption of the Islands of Karakatau in 1883, which provided the first opportunity for scientists to follow and document the re-colonization of the flora and fauna of a completely devastated island (Dammermann, 1948; Docters van Leeuuen, 1936). Colonization studies gained popularity with the synthesis provided by MacArthur and Wilson (1967) who delineated several questions of importance ot the theory of colonization that pertain to this study: (1) Do the reciprocal processes of immigration and extinction result in an equilibrium number of species? (2) What is the relationship between successful colonization and the sequence and time of species invasion, i.e., are certain reefs "closed communities" to some species if a competing species is already present? (3) Does environmental diversity determine equilibrium species diversity?

Several studies have been performed that relied upon the provision of artificial "islands" or the defaunation of existing "islands". Ruth Patrick (in MacArthur and Wilson, 1967) allowed diatoms to colonize glass slides; Wass (1967) removed the fish population of a large patch reef in Kaneohe Bay, Hawaii, and followed its re-colonization; Randall (1963) followed the colonization of fishes on a concrete block reef in the West Indies; Cairns et al. (1969, 1970) placed artificial habitats in freshwater streams and followed the colonization patterns of protozoans. In a project specifically designed to investigate the equilibrium dynamics of island colonization, Wilson and

Simberloff 1969; Simberloff and Wilson, 1969, 1970; Simberloff, 1969. defaunated several small, mangrove islands at various distances from propagule sources and monitored repopulation throughout two years of periodic observations. Successful emigrants consisted predominantly of ants, spiders, and other insects that probably arrived through air borne dispersal. They concluded that MacArthur and Wilson's equilibrium model satisfactorily predicted the early stages of colonization; however, it did not take into account interactions between species. The non-interactive equilibrium theory is based upon constant immigration and extinction rates. In the interactive model, populations of "key species" eventually reach levels where presumably predation or competition eliminated other species. Exclusions on mangrove reefs seem to correlate with the increase in ant populations at about 300 days post defaunation. Simberloff and Wilson offer lines of evidence in support of an interactive equilibrium distinct from a non-interactive equilibrium: control mangrove islands of the same size and distance from source of propagules had similar numbers of species; "... one would expect intuitively that interactions on these Rhizophora islands would reduce the number of species." (argument based on intuition); the presence of an apparent overshoot followed by a decline to the original number of species. In summarizing, they say, "We can thus predict that on all islands but the most distant (E1) the colonization curves will first arrive according to the non-interactive model above the original interactive S, then decline gradually to the more enduring S."

Simberloff (1969) attempted a computer simulation using mangrove island colonization data and fixed immigration and extinction rates at

levels similar to those derived experimentally. Variance of these values caused the confidence limits of expected colonization curves to be so large that nearly any observed data would easily fit. However, using the values of 18-day average immigration and extinction rates, Simberloff was able satisfactorily to simulate early colonization, "the most important implication of the colonization runs is that the general equation for S vs. t cannot be intuited from [these] experimental islands." In an early paper, Simberloff and Wilson (1969) point out the necessity for experimental manipulations to gather empirical data in order to test the basis of the equilibirum theory, "For no island, however, is the course of colonization by even a large fraction of the inhabitants known."

Schoener (1974 a,b) installed plastic sponges in algal beds in the Bahamas and analyzed fouling plate data in an attempt to test the equilibrium theory. She found that the colonization curve of invertebrates on sponge "islands" was adequately described by the MacArthur Wilson model; however, isolated planar surfaces, "... often fail to exhibit convincing evidence that an equilibrium number of species is approached during colonization."

Fishes inhabiting the small patch reefs along the windward edge of Enewetak lagoon are very much isolated island members of the entire Patch Reef Assemblage. A colonization study necessarily produces many other types of ecological information because the attributes that enable a species to survive on a particular reef may also be those that determine its success in colonization. These questions are of key

significance in the attempt to understand resource partitioning on reefs and the maintenance of these systems of high species diversity.

METHODS

Natural reefs were defaunated and the recovery of their fish populations monitored using the same census techniques described in Part I. Simberloff (1969) clearly pointed out two of the important sources of error that result when censuses are used to determine invasion and extinction rates: species undetected during census; and error due to species that immigrate or go extinct between census periods. The former error is believed to be relatively contained at Enewetak (precision and accuracy of method described in Part I). Simberloff (1969) used a simulation model to determine the magnitude of the second type of error and concluded, "It is apparent from either estimate, then, that the error in the observed immigration and extinction rates is so large as to render them useless as a measure of true immigration or extinction rates, except possibly for order of magnitude ..." Without continuous monitoring of immigration and extinction, the only method of analyzing colonization is by plotting the number of species (or H_S) present at successive time periods.

Simberloff (1969) defined the terminology of colonization as a basis for his model of insular colonization. However, the ecology of reef fishes is such that the meaning of some of Simberloff's terms must be revised. For example, he defines a propagule as, "The minimum number of individuals of a species capable of breeding and population increase ..." It follows that the arrival of a reproductive pair of ants into a favorable habitat on an uninhabited mangrove island may result in eventual colonization by ants. However, an analogous arrival

of most species of reef fishes on a defaunated reef will not directly result in the propagation of that species on that reef because progeny are released into the water column. On the other hand, the arrival of a pair of Chromis caerulea into a lagoon deficient in that species would be a case of "propagule" introduction as defined by Simberloff. Since the marine environment has so many widely dispersing larvae, the term propagule should be defined more freely. In this study, it will be qualified to mean the first arrival of juvenile fishes of a given species to a particular reef. Simberloff's (1969) convention for the use of "immigration" (the rate of arrival of new species on a particular island) and "invasion" (the rate of arrival of new propagules of a given species on a particular island) will be used.

The natural patch reefs differed slightly in size and the amount and type of shelter available (Table 1) (e.g., some reefs were cavernous and some lacked Pocillopora heads); nine, standardized artificial reefs were installed on bare sand regions between natural study reefs (Plate 1B). Each artificial reef consisted of 20 modules, which were constructed of 7.6 cm (3" I.P.) plastic perforated drain pipe imbedded in cement. Each module consisted of three 1 m long pipes inserted at right angles to each other into each face of a concrete cube 26 cm long on a side. This gave the module a "jack" shape (reminiscent of the children's game). Twenty modules were stacked together to form a reef with a mean height and width of 1.6 m. These reefs provide a great range in the size of shelter holes--from small spaces inside the tubes to the larger interstices at the base and within the reef (Nolan, 1975).

Modules were formed by pouring cement into 1 cu. ft. cardboard boxes in which the pipes had been inserted through pre-cut holes. The modules can conveniently be cast in number by packing the pipe-box units together and supporting them with two parallel boards (Plate 2A). Modules retained their integrity even when 30-40% of their volume consisted of filler (e.g., beer bottles). The cardboard forms disintegrate within a month, freeing bare concrete surface which are rapidly colonized by algae and invertebrates. The modules were easily transported by a small skiff, dumped overboard and arranged into a reef with the help of a single assistant.

Module costs were moderately expensive as a result of using high-quality plastic pipe. A less expensive substitute for the plastic pipe would lower the costs considerably; however, plastic pipe has the attributes of being rapidly colonized by benthic organisms and fishes and of being extremely resilient. Enewetak jack reefs have withstood large typhoon-generated wave surge on a number of occasions with little dispersion. Nearby natural reefs, however, suffered extensive damage to fragile Acropora heads.

Table 16 summarizes the history of manipulations of natural and artificial reefs described in Part II.

RESULTS AND DISCUSSION

Patterns of Colonization

Three major questions can be asked regarding the patterns of colonization of defaunated reefs; i.e., does the fauna ever return to the pre-defaunation state; if so, how long does it take to reach climax condition, and what are the patterns of species invasions and extinctions which characterize reef colonization? The colonization curves of fishes to reef Nos. 3, 5, and 8 following defaunation are shown in Figures 5 and 6. In these curves, the time course of species addition and loss are plotted. To properly describe and predict the repopulation of defaunated reefs, the natural variability in the system must be considered.

It was not possible to census reef Nos. 3, 5, and 8 until 100 days after defaunation. Within this period, reefs No. 5 and No. 8 both attained about the same number of census species that they would have 16 months later (App. 1,2,3; Fig. 5). It appears that reefs No. 3 and No. 8 reached species equilibrium after 100 days and subsequently oscillated about that value. When reef No. 8 was defaunated a second time at 544 days, it had 45% of the original species present (66% of the original number) at the first defaunation. Reef No. 5 reached apparent equilibrium much later than reefs No. 3 and No. 8--at around 400 days. However, it had a much higher percentage (96%) of the original species number when defaunated 619 days later. Reef No. 8 was censused 88 days after the second defaunation and attained 22 species as opposed to 23 species after a similar time period following initial defaunation in September, 1972.

Colonization in terms of number of individuals is shown in Figure 6. At 100 days, reefs No. 3 and No. 8 had 429 and 537 individuals while reef No. 5 lagged behind with 311. Reef No. 5 did, however, exceed populations on other reefs at 300 days when it harbored 2,948 individuals. This large increase was due to the settling of about 2,000 unidentified larvae (Appendix Table 2). It did exceed reefs No. 3 and No. 8 in number of fishes even if larvae were not included, largely due to the presence of 150 Chromis caerulea and 530 Pomacentrus pavo.

None of the experimentally defaunated reefs ever achieved the exact pre-defaunation state in terms of number of species, species composition, or number of individuals. The faunal composition after 600 days did show species in common with the baseline pre-defaunation state (30% original species for reef No. 3, 45% for reef No. 5, 45% for reef No. 8--all based on census species). Strictly in terms of numbers of species present, the reefs showed better recovery. Reef No. 3 attained 81%, reef No. 5, 96%, and reef No. 8, 66% (based on census species at 600 days). The species composition of defaunated reefs at successive intervals in the time course of colonization are shown in Tables 17, 18, and 19 and Appendix Tables 1, 2, and 3. Four families comprise the majority of invaders at 94 days. Ranked in order of number of species represented per family, labrids were the most frequent colonizers followed by pomacentrids, chaetodontids and holocentrids (Table 20).

Reef No. 8 provides two opportunities to determine the compositional changes following defaunation (defaunated September,

1972, and May, 1974, Table 19). Ten species were common to both colonizations and 43% of the species that invaded following the initial defaunation also invaded following the second. Mean invasion rates were very similar following first and second defaunations (.24 species per day and .25 species per day). The first species that invaded reef No. 8 (Chromis caerulea, Pomacentrus pavo, P. vaiuli, and Paramia quinquelineata) were those that most frequently invaded other defaunated natural and artificial reefs.

Throughout the period of observation, there were many temporary invasions and extinctions on reef No. 8. Control reefs also were seen to undergo changes in species composition. Variability in number of species throughout the observation period did not differ significantly between control and experimentally defaunated reefs (CV= 21.1% control, 15.7% defaunated--based on census species). The mean number of species invading defaunated reefs after a period of 95 days was greater but not significantly so ($p \geq .05$) than that invading control reefs. The mean number of species invading per 100-day (approximate) census intervals on control reefs was 5.1 and 9.9 for experimental reefs.

The patterns of invasion, extinction, and species persistence 100 days after defaunation are essentially inditinguishable from the background fluctuations characteristic of control reefs. Within a few months after all fishes were removed, about the same number of species had recolonized. In terms of absolute number of species, reef No. 5 had nearly the same number of species when collected after 545 days as originally. It may be, however, that a "climax" condition may have arisen prior to this sampling period. Since assemblage recovery is

rapid, an experimental regime was designed that repeatedly and frequently removed fishes from three natural reefs (Nos. 9, 13, and 17) and three artificial reefs (Nos. 16, 19, and 20), Table 16. The artificial reefs were installed to control variability in quantity and quality of shelter inherent in natural reefs and will be discussed in detail in a later section.

Reef Nos. 9, 13, and 17 were repeatedly defaunated at approximately 100-day intervals (Table 16); and in many cases, short-term observations were made of initial invasions and extinctions. Figures 7, 8, and 9 present colonization curves derived from Tables 21, 22, and 23. The purpose of multiple defaunations was to determine the predictability of species invasions. Seasonal differences in recruitment were also noted and will be discussed in a special section. The number of species achieved on subsequent defaunations was remarkedly constant (reef No. 17, 16 to 17 species, Fig. 9; reef No. 13, 28 to 30 species, Fig. 8); however, reef No. 9 ranged from 15 to 28 species on subsequent collections over comparable colonization intervals. Numbers of individuals varied considerably during subsequent colonizations (Figs. 7, 8, and 9).

The species composition of multiple defaunation reefs is shown in Tables 21, 22, and 23. Trends in early invasion and persistence can be seen in these tables. Seventeen species were reliably seen to appear on reefs within 12 days of defaunation (eight sample periods on three reefs), Table 24. Four species, Pomacentrus pavo, P. vaiuli, P. quinquelineata, and Apogon novaeguineae were the most frequent early colonizers while eight other species invaded with a frequency of

25 to 38%. The persistence of early colonizers can also be seen in Table 24. The first four consistent invaders also show high persistence after a census period ranging from 67 to 123 days following defaunation (sample size of ten). Is persistence of these species on a particular reef a matter of survivorship of early settlers or continuous replacement via high recruitment rates? Although size data will not be presented in detail here, pomacentrids and labrids first appearing on the reefs were small individuals. On later observations (at about 100 days), adults were present along with juveniles. Apogonids were often initially represented by adults along with juveniles indicating plasticity in their nocturnal homing behavior and possibly suggesting that suitable daytime habitat for these species is non-limiting.

The survivorship of Chromis caerulea, Pomacentrus pavo, and P. albofasciatus was determined by daily censusing of specific heads added to artificial reefs. These data are presented in a latter section.

The general scheme of colonization to small Enewetak patch reefs based on multiple and single defaunations consists of 17 species that invade within 12 days. Of these, six species can be expected to persist after 100 days. Many other species will invade and become locally extinct within a few months. The fluctuation of control reefs around a mean of about ten censusable species results from the interrelationship between availability of propagules and their survivorship on small isolated reefs where space ultimately limits populations.

Reef Habitat Complexity and Colonization Patterns

Control and defaunated natural reefs demonstrate considerable variability in species composition and in number of species present at census periods. Variability might result from differential recruitment to natural reefs or might be a result of differential survival on those reefs. Observations on study reefs and other lagoon reefs have shown very stringent substrate requirements (shelter or feeding) for most members of the Patch Reef Assemblage. The fine structure of available shelter and type of coral substrate varied from reef to reef (Table 1) and may explain the presence or absence of certain species. To control substrate variability and the quality and quantity of shelter available, artificial reefs were placed on bare sand areas between study reefs. Artificial reefs provided a standardized amount of shelter along with a uniform substrate. The attributes of artificial reefs as compared with natural reefs are described elsewhere (Nolan, 1975).

Artificial reefs are of interest not only in that they provide standardized replicates, but in that they are simple, less complicated units of shelter. Diamond (1973) and MacArthur (1972) describe many situations in which species diversity is found to increase with habitat diversity. Similar relationships exist at Enewetak and will be reported elsewhere. MacArthur and Wilson (1967) predict higher species equilibrium values on larger islands than on small islands of the same distance from propagule source. This relationship is summarized in the concept of "species-area" curves in which an equation ($S = CA^{Z}$) satisfactorily predicts species diversity for a variety of island sizes. The biological factors determining species diversity in a given area

are not merely island dimension or carrying capacity, but also environmental heterogeneity. Larger islands support more species (lower rate of extinction species curve) because more species find favorable habitats.

At Enewetak, I have placed nine artificial reefs roughly approximating the size and shape of natural study reefs but lacking the diversity of coral substrates characteristic of natural patch reefs (artificial reefs do offer a wide variety of shelter configurations and sizes in the tubes but are notably deficient in large caverns). The experiments described here permit a direct test of MacArthur and Wilson's (1967) prediction for the colonization pattern for low vs high habitat diversity islands. Equilibrium theory predicts that simple systems will support fewer species than complex (or large) islands, due to a higher species extinction rate. It follows that the addition of different habitats to simple artificial reefs would be expected to increase species equilibrium value.

Nine artificial reefs were installed in two series; May, 1972 (Nos. 2, 4, 6, and 16), and September, 1972 (Nos. 18, 19, 20, 21, and 22). Reef Nos. 2, 4, 6, 18, 21, and 22 were replicates designed to determine colonization patterns to reefs uniformly less complex in habitat. Reef Nos. 16, 19, and 20 were sampled approximately at 100-day intervals to investigate any possible temporal patterns in fish recruitment (Table 16).

Artificial reefs reached apparent species equilibrium number between 100 and 200 days, as did natural reefs (Figs. 10 and 11). However, the colonization pattern on artificial reefs differed in

several aspects from that of defaunated natural reefs (Nos. 3, 5, and 8; Figs. 5 and 6). Tables 25 and 26 show some parameters that characterized artificial reef colonization. Reef Nos. 18, 21, and 22 had a mean of 9.8 species per 100-day census interval; and reefs Nos. 2, 4, and 6 had a similar mean of 9.3 species/census. Artificial reefs which generally had fewer species and individuals showed larger fluctuations than natural reefs in terms of number of species after 100 days. The coefficient of variation between successive censuses on artificial reefs was high for number of species ($\bar{X}$ = 33%) as compared to that of natural reefs ($\bar{X}$ = 8%), Table 25. This suggests that small populations living in conditions of limited habitat diversity have higher average turnover rates than those of complex natural reefs. The number of individuals varied considerably less than on recovering natural reefs (Figs. 12 and 13), probably reflecting the lower carrying capacity of the simpler reefs.

The first species immigrating to artificial reefs were those that characterized the early invasion of natural reefs. Pomacentrus pavo, Paramia quinquelineata, Labridae sp. No. 1, Acanthuridae sp. No. 1, Pomacentrus vaiuli, and P. albofasciatus were the dominant species on artificial reef Nos. 16, 19, and 20 at 100 days (Appendix Part A and B of 7, 8, 9, 10, 11, and 12). With the exception of Labridae sp. 1, these species persisted on the reefs and were present on most reefs at 200 days (Table 27).

Multiple defaunations of artificial reef Nos. 16, 19, and 20 at 100-day intervals have permitted comparison of number of species and species composition at subsequent, replicate periods of colonization.

The effect of plant and invertebrate succession on the colonization patterns of fishes is not known. It is of interest that the number of species from defaunations at 100 days post installation was always higher than at 200 days for reef Nos. 16, 19, and 20 (Table 28; Figs. 14, 15, and 16). As before, certain species persist that are also common colonizers on artificial reefs. The incomplete recovery of artificial reefs upon repetitive defaunations suggest that stochastic events may determine which species are available. The succession of substrate organisms on artificial reefs was not quantitatively monitored, but filamentous algae had attached to the concrete module faces within 30 days of placement. The interiors of the plastic pipes were colonized by polychaete worms, ascidians, and pearl oysters by 100 days; and by 200 days, they had completely occluded the openings of most of the pipes (Plate 2A). There is no obvious correlation between reef substrate development and fish species diversity. Certain species, however, were seen to appear only after the formation of the luxurious algal mat on the reef. The blenny Ecsenius bicolor always was a late invader on artificial reefs--it was present on reef No. 2 only after 108 days, reef No. 4 after 423 days, reef No. 6 after 606 days, reef No. 21 after 517 days, and reef No. 22 after 531 days ($\bar{X}$ - 437 days post installation). This animal browses on filamentous algae, and its survival may be dependent upon algal abundance. Ecsenius was observed in pre-defaunation surveys of natural reef Nos. 3, 5, and 8, but never successfully re-invaded the reefs. Epinephelus merra was an early colonizer of artificial reefs--nearly every newly installed or defaunated reef was

rapidly colonized by it and Pomacentrus pavo. The possible effects of these early invaders upon the developing reef assemblage will be discussed in a subsequent section.

Artificial reefs defaunated at intervals of 100 days allowed further opportunities to examine reef recovery and the fine structure of short-term colonization. It can be predicted from Table 29 that immediately following reef placement or defaunation, nine species will invade (Figs. 14, 15, and 16). These early invaders have usually been juveniles when first observed. For example, reef No. 19, at 202 days (7 days post defaunation) was colonized by 48 Paramia quinquelineata, 1 cm long; reef No. 20 at 338 days was colonized by seven 1 to 2 cm and one 6 cm P. quinquelineata 14 days after defaunation. The number of species per census remained at about four for the first two weeks then increased significantly at 83-96 days. Total number of species present on all three reefs increased monotonically (except three to seven days) from nine species at one to two days to 30 species at 83-96 days (Table 28). The species added throughout colonization were rare species with a frequency of occurrence less than or equal to 25% as shown in Table 29.

Of the nine species characterizing short-term invasion, six persist at nearly the same or higher frequency at 83-96 days (Appendix 4, 5, and 6). Here, as on natural reefs, it appears that the first species to invade the reef also persist. This is probably due to the continuous replacement of individuals by new recruits from the plankton. Pomacentrus pavo dominated artificial reef assemblages throughout the two and one half years of observations. Labridae sp. 1,

which appears immediately, occurred sporadically but was found in 50% of the reefs censused at 83-96 days.

The absence of appropriate shelter sites makes some species more vulnerable to predation or interspecific competition. The dominant species on artificial reefs are adapted to take shelter in rubble or dead coral habitats. For example, Pomacentrus pavo is a characteristic inhabitant of rubble and cobble regions. This species, unlike Chromis caerulea, seeks shelter in any available crack or crevice when threatened. It is also opportunistic in its feeding behavior, picking at suspended material in mid water or browsing on coral substrates for benthic attached algae.

Enewetak reefs provide a case where habitat diversity seems to limit species diversity. In an attempt to shape artificial reef assemblage structures to a state more similar to that of natural reefs, small heads of Pocillopora veruccosa ($\bar{X}$ = 25 cm^3) were added to the reefs. These were cemented into couplers (normally used by contractors to connect the plastic drain pipes together). This allowed them to be easily installed or removed from the ends of appropriate reef pipes (Plate 3A). Coral heads were added to artificial reef Nos. 2, 4, 21, 22, 16, 19, and 20 and also to natural reef Nos. 5, 7, 12, 15, and 17 and controls (Table 16). The heads had a significant effect on the species composition of artificial reefs in that new species were added but had little effect on the composition of natural reefs. Table 30 shows the qualitative effects of the addition of coral heads to the artificial reefs. Chromis caerulea, Dascyllus aruanus, and D. reticulatus are species closely tied to their resident coral heads.

The shelter seeking responses of pomacentrids has been described by Swerdloff (1970). It is clear that the addition of appropriate substrates had very predictable effects on the species composition of artificial reefs.

An experiment designed to analyze the effects of predation upon colonization patterns had interesting results pertaining to reef complexity and colonization studies. Two natural and two artificial reefs (Nos. 9 and 13; Nos. 19 and 20) were defaunated, installed, and immediately caged in August, 1972 (Plate 3B). The cages consisted of 1" diameter reinforcing steel rod as a cage form to which 1 1/2" stretch mesh nylon netting was sewn and the base sealed by a heavy chain (Fig. 23). In September, large typhoon-generated wave surge breaking in the study area for an extended period of two weeks destroyed the cages; and unfortunately, no predator exclusion data were obatined. The cages were then removed and other manipulations performed. In February, 1973, another attempt was made to cage a natural reef (No. 13). This cage was more successful and has remained intact since installation--a period of over 600 days, often in very rough weather. At 100 days, the cage had been overgrown by filamentous algae (Hormothamnion sp.) which grew luxuriously on the netting and frame. The census periods in October and February, 1973, were characterized by lush algal growth on the cage to the extent that the neeting was nearly occluded by an algal mat. In May, 1974, this coverage had diminished to a very sparse growth on the netting and so remained when last viewed in October, 1974.

Figure 8 and Table 22 show the remarkable changes that took place upon enclosure of reef No. 13. Diversity in terms of number of

species reached a reef history high of 24 census species within 113 days of caging. Ten of these had not previously been seen on the reef. Of these ten, only three persisted for 456 days more. Most notable was the large population of the goatfish, Mulloidichthys auriflamma. These were first seen on the reef as juveniles and 30 survived to adult size. Thirteen other new species had invaded the reef by 456 days with varying degrees of persistence. The reef always had a large number of individuals, and usually this number was substantially greater than on other natural reefs.

The caging experiments were designed to follow up similar studies in the intertidal region of Washington by Dayton (1973) who found that predator exclusion cages effected a significant decrease in diversity as competitive dominants were released from natural predation pressure. In contrast, the caging of reef No. 13 clearly resulted both in an increase in diversity and also in the number of individuals (i.e., the carrying capacity was increased). Species not normally present, such as Mulloidichthys auriflamma and Lutjanus kasmira, became abundant and other common species, such as Pomacentrus pavo and Apogon novaeguineae, achieved high populations. Although these experiments should be repeated, it seems evident that variables other than the expected release of competitive dominants were at work. Caged reef No. 13 was a very productive environment due to a large standing crop of algae associated with the net. Hormothamnion has been shown to be very efficient in the fixation of dissolved nitrogen (W. Wiebe and R. Johannes, University of Georgia, pers. com.). The cage became an expansive surface with a large area exposed to sunlight and perhaps

effectively "raining" nutrients down onto the reef below. Biomass is known to be positively correlated with productivity. It would be of interest to determine how a caged artificial reef might compare in diversity and population with an uncaged reef. The survival and success of the reef No. 13 enclosure testifies that large exclusion cages of this nature are feasible.

Seasonal Patterns of Breeding and Colonization

This project was not specifically designed to examine the availability of reef fish propagules on a seasonal basis. To answer such questions would require standardized plankton net tows made in the study reef vicinity and a detailed gonad sampling program of resident fishes with collections at various times throughout the year. My observations and experiments indicate the seasonal availability of fish recruits since the presence of juveniles was recorded on every census. In a similar manner, the species composition of reefs defaunated several times can be used to check for seasonal patterns in colonization. Finally, the breeding coloration or spawning activity of fishes was recorded whenever possible. Examples of such relevant observations might include the cardinalfishes in which the males brood the eggs orally, thus allowing for simple evaluation. Apogon novaeguineae and Paramia quinquelineata which were observed frequently with very extended buccal cavities clearly carrying eggs, and Pomacentrus pavo and Chromis caerulea in breeding colors were clear indicators of reproductive activity in these species.

Artificial reef data were chosen for the seasonal recruitment study because of the uniform, standardized stustrates they initially presented for fish invasion. Table 31 depicts the percent frequency of occurrence of juvenile fishes on artificial reefs at different seasons. The species tabulated are those which characteristically invaded artificial reefs as newly settled larvae. It is evident that if all species are combined, recruits were available at all times of the year in that there is no significant departure from an even distribution by season (Friedman's rank test in two way classification, $W = .036$, $p \geq .01$). Within the group there may be some periodicity of settling in certain species. Aspidontus taeniatus, for example, appeared only during summer months and juveniles of Thalassoma amblycephalus were observed only in winter or spring. This may be an error in sampling due to the rarity of both species (this also applies to Pterocaesio tricolor). Apogon novaeguineae was not a rare species, but juveniles were never observed on an artificial reef in the summer. Juveniles of this species were noted at all other seasons. Although, on natural reefs, they did sporadically occur during the summer, it is suspected that there may be less availability of young during the summer. This might be a result of decreased reproductive activity or alterations in the circulatory pattern of windward lagoon currents.

Data from natural reefs does show the presence of recently settled juveniles throughout the year. In summary, nearly all of the selected 16 species of Table 34 are available throughout all seasons of the year. Further insight into seasonality can be derived from the species composition of artificial reef Nos. 16, 19, and 20 which were

repeatedly defaunated at approximately 100-day intervals. Table 32 shows the seasonal frequency of species occurrence on multiply defaunated artificial reefs. The procedure for selecting the appropriate seasonal category to monitor for the colonization of a species will be illustrated by example. Reef No. 20 was defaunated in December, 1972, and again in February, 1973. The species present in the February collection necessarily invaded the reef since December and were placed in the "winter" category. The presence of species for the group selected in Table 32 did not vary significantly between seasons ($W = 0.139$, $p > .01$), although some species occurred less regularly than others. Species missing from seasonal samples were those normally found in small populations (both rare and more susceptible to local extinction), with the exception of gobies which were often numerous. Analyzing the frequency of the species of the family Gobiidae separately (Table 32), we find that their year-round distribution differs significantly from expected values ($W = .52$, $p \geq .05$) in that they are less frequent than expected in the fall and spring and more abundant than expected in the summer and winter. To further explore possible seasonality in the occurrence of gobiids, the frequencies of occurrence for this family were collated from multiply defaunated natural reef Nos. 9, 13, and 17 (Table 33). On these natural reefs, more species were present and most occurred in all seasons, except spring ($W = 0.9$,

$X^2 = 7.02$; therefore, significantly different at $p \geq .05$.[1] In summary, gobies show a seasonality in their presence both on artificial and natural reefs defaunated throughout the study period.

Reproductive coloration and spawning activities were evident year-round in some species. Male Apogon novaeguineae and Paramia quinquelineata were observed brooding eggs in October, February, May, and July. Pomacentrus pavo and Chromis caerulea were frequently observed spawning in every season on study reefs and other nearby reefs. The brightly colored males of Pomacentrus pavo defended territories and courted females in all seasons.

These data provide indirect evidence that potential propagules of many species of the Patch Reef Assemblage are available throughout the year. In terms of MacArthur and Wilson's (1967) theory, year-round propagule invasion reduces the scatter inherent in the immigration rate curve of a particular reef. Perhaps of more significance is that propagule resources are large and the slopes of immigration curves therefore steep.

[1]Randall (1961) demonstrated that the exclusion of herbivores from reef areas elicted a marked increase in algal standing crop. Accordingly, it might be expected that the removal of resident patch reef herbivores might result in a build up of plant food materials which might influence subsequent colonization rates or patterns. No gross changes in algal growth were detected on defaunated reefs--probably because of the browsing activities of roving herbivores (surgeonfishes, parrot fishes). Small changes would most effect very small herbivores that were not accountable by census techniques.

Reef Size and Colonization Patterns

The "species-area" curve predicts higher species numbers on larger islands, because larger islands usually have greater habitat diversity than small ones and larger populations per species with lower times to extinction. To test this at Enewetak, a reef roughly three times the mean volume of the natural study reefs and an artificial reef roughly two times the mean volume of the artificial reefs were defaunated/installed. Reef No. 31 is a natural reef occupying a volume of 47.2 m^3 with a high diversity of coral and shelter types. Artificial reef No. 6-18 consisted of 40 standard modules and was a result of transplanting and combining reef No. 6 with No. 18 after both had beed defaunated.

Reef No. 31 was defaunated on 8 July 1973 when 92 species were collected, of which 55 were species normally observable by census techniques. Nine days post defaunation, reef No. 31 had ten species and at 18 days had 17 species. When finally defaunated on 18 February 1974 (225 days after initial defaunation), it yielded 66 species of which 45 were census species. It is probable that this reef had not yet reached species equilibrium by 225 days; alternately, it is possible that the equilibrium value had been attained and the second defaunation represented a low point in oscillation about the equilibrium value. Using the 225 day recovery value, reef No. 31 had a minimum invasion rate of 1.00 species/day which was much higher than that of smaller defaunated natural reefs (Nos. 3, 5, and 8) which had a mean rate of 0.09 species/day measured over the same time interval.

In order to control the effects of increased substrate diversity with increasing reef size, two standard artificial reefs were combined.

Both reefs No. 6 and No. 18 were defaunated and then reef No. 6 modules were transported and added to those of reef No. 18 (both on top and around the periphery). The number of species and individuals following reef combination can be seen in Figures 11 and 13, and changes is species composition in Table 34. Table 5 is a distillation of these data and depicts the effects of reef combination. By 87 days, reef No. 6-18 supported 15 species which was higher than either reef ever attained before combination. Twelve of these species were new additions to both reef assemblages prior to combination. At 242 days, reef No. 6-18 harbored a very large school of juvenile Apogon gracilis. This species was seen sporadically on natural study reefs, but not in numbers this large. Apogon gracilis was uncommon on standard 20-module artificial reefs. A minimum invasion rate at 87 days was calculated at .17 species/day which is slightly greater than that of standard artificial reefs ($\bar{X}$ = .10 species/day).

As theory predicts, larger reefs were colonized more rapidly (had higher successful invasion rates) than smaller, but otherwise comparable reefs. Temporal and geographic variables that might affect the availability of recruits can be discounted since the two reef regimes were identical temporally and in location. Do more post-larval fishes invade larger reefs because the reef presents more quantitative or more appropriate qualitative stimuli to settle? Or perhaps, the effect is merely due to the larger sampling surface (in terms of the amount of water containing potential propagules passing over the reef) than small reefs. It might be that recruitment rates do not significantly differ from small to large reefs. A higher successful rate of

colonization would then be a result of differential survivorship in that more individuals of different species are able to survive on larger reefs.

In discussing the strategy of colonization, MacArthur and Wilson (1967) clearly establish that the expected survival time of a population is a function of the carrying capacity of the island for a particular species. A species with a given λ/μ (λ = per capita birth rate, μ = per capita death rate) will have T_1 (time to extinction) of about ten units of time with an equilibrium population size (K) of one. Increasing K to ten individuals increases T_1 to over 10^9 units. In their words, "... as K increases there is a rather sharp increase in T_1 (...), so that for small values of K, T_1 is short, while for increasing values of K it soon becomes prodigiously long."

Populations of selected species on small and large natural reefs can be seen in Table 35. Generally, the large reef had more individuals (463) than small reefs, although the values for small reefs varied considerably (range 102-426, $\bar{X}$ = 202.0, CV = 80%). Looking at the population of selected species, there appears to be no difference between large and small reefs. Observations on other reefs similar in size to No. 31 (i.e., much larger than study reefs) show diversity in number of species to be high; however, most large reefs did not harbor remarkably large populations of single species. Smaller reefs often supported equally large populations of single species--if appropriate habitat was available. Reef No. 12 possessed several ramose coral heads suitable for Chromis caerulea. A large reef that was endowed with similar heads characteristically would have high populations of

C. caerulea (a linear regression for population size of Chromis and amount of appropriate shelter available will be presented elsewhere). The presence of these heads and the substantial turnover (invasion rate/death rate) accounts for the extreme variability in number of individuals on control and defaunated reefs.

Table 37 shows the effect of coral head addition on number of individuals inhabiting artificial reefs. Population values are known to be notoriously variable; however, it is clear that in every case the addition of either five or ten Pocillopora heads resulted in positive increase in resident reef fish populations. These additions were due to schooling damselfishes (Chromis caerulea, Dascyllus aruanus, and D. reticulatus) that rapidly colonized empty heads. The distinction between the addition of five as compared to ten heads is obscured by variability.

The colonization of Enewetak reefs differs from that occurring on isolated islands. Survivorship and persistence (T_1) of a particular species on a specific reef may be related to the equilibrial population size (K) in a manner very different from that recognized by MacArthur and Wilson. The reproductive activities of most species result in the liberation of gametes, zygotes and eventually a free-swimming pelagic larvae. The probability that the same individuals will return to their native reef is miniscule. Recycling currents may, however, return them to nearby reefs or at least keep them in the lagoon population so that the cumulative K values taken for all windward lagoon reefs may determine T_1. For these reasons, it is not appropriate to test the effect of distance from propagule source upon invasion and extinction

rates. Most reefs are more or less subjected to the same invasion pressure due to widespread dispersal of propagules. The presence or absence of a species may be a result to selective settlement or differential survival upon settlement, or order of species settlement. Thus, the value of K may directly determine the T_1 of a species on a particular reef. The presence of a threshold number of residents of a given species might enhance settlement or increase the post settlement survivorship of juvenile conspecifics.

Mechanisms of Colonization

The great dependence of Chromis caerulea, Dascyllus aruanus, and D. reticulatus upon small Pocillopora heads for shelter is obvious to the most casual observer. The fish/shelter relationship is sufficiently strong that an entire colony of Chromis or Dascyllus may easily be collected by placing a plastic bag over the resident coral head and freeing the head from the reef with hammer and chisel. The head and its residents may then be transplanted to another site or the fish removed for experimentation. The shelter-seeking response of damsels has permitted a series of manipulations designed to gain insight into the actual mechanism of reef colonization. The order in which these experiments are described here is not necessarily the chronological order of their execution. In some cases, only qualitative results will be presented because many of these manipulations more exactly pertain to resource partitioning and will be dealt with elsewhere.

The substrate requirements of Chromis caerulea, Dascyllus aruanus, and D. reticulatus are not specific to coral species; but

these fishes do require small, dense coral heads that provide a quantity and variety of shelter interstices between coral fingers. They cannot survive at Enewetak withough the availability of such shelter because of the presence of large piscivores that cruise between isolated reefs (jacks, snappers, scombrids, sharks). In Hawaii, where piscivores are less common and less diverse, Chromis verater, Thalassoma duperryi, and the butterfly fishes, Chaetodon miliaris and Hemitaurichthys zoster, range freely in midwater with little association to coral shelter. In one series of experiments in the study area at Enewetak, Chromis caerulea were released 10 to 20 m from the nearest reef. Invariably, most of the released individuals were captured by Lutjanus bohar, Caranx melampygus, Aphareus furcatus, Epinephelus clathratas, E. macrospilos, or Aprion virescens. The individuals that survived the initial onslaught of predators sometimes reached a reef that was already inhabited by conspecifics. In those situations, the displaced individuals were sometimes excluded from the reef by intraspecific aggression from residents. Predators persisted in the area and were repeatedly seen to pick off stray individuals which were displaced from the sanctuary of the reef. Another series of experiments involved the addition of Chromis and Dascyllus to artificial reefs which had reached equilibrium with large established populations of Pomacentrus pavo but lacked appropriate shelter heads. Eighteen 1 cm C. caerulea were added to reef No. 20 on 14 October 1973. Two days later, all had perished; and at this time, six 4 cm C. caerulea, two 4 cm Dascyllus aruanus, and three 4 cm D. reticulatus were introduced. The following day only one C. caerulea had survived. These experiments indicate the absolute

dependence of Chromis and Dascyllus upon proper shelter substrate for survival. If they are displaced from the security of their resident heads, they become accessible to predation. Individuals of these species, however, will range back and forth between nearby coral heads; but adults and juveniles have never been seen to swim between reefs separated by as small a distance as 2 to 3 m. It is likely that heads to which juveniles initially settle from the plankton are the ones on which they will spend the duration of their lives. Joel Sohn (pers. comm.) has suggested that the correlation between the size of shelter available on Red Sea coral heads and the size of resident damselfishes indicates that small individuals must move to larger heads as they mature. However, this apparent movement could be the result of differential survival determined by a threshold value of the ratio of shelter to size of fish. As a juvenile increases in size on a small coral head, it will have increasing difficulty avoiding predators by darting back into the head and may be more vulnerable both to daytime predators and nocturnally feeding morays. An example of what happens to maturing Dascyllus reticulatus was indicated by observations made on study reef No. 30. In March, 1973, this reef supported two Dascyllus reticulatus, one 6 cm and one 4 cm in total length, and both inhabited two small Pocillopora verrucosa heads. By May, 1974 (nearly 400 days later), many individuals of this species had invaded and perished, but the reef still supported five 1 cm, eight 3 cm, one 6 cm and six 10 cm individuals. The largest specimens no longer inhabited the small coral heads, but took shelter at the base of nearby corals or in the many cracks of reef No. 30. Large D. reticulatus normally inhabit large,

wide-branched coral heads, e.g., Pocillopora eydouxi. There are numerous colonies of large Dascyllus inhabiting P. eydouxi heads in the vicinity of a cement barge grounded on a reef bordering the deep channel on the windward side of Enewetak. Here single heads frequently harbor hundreds of individuals, suggesting that these are a more optimal habitat for the species. The survival of Dascyllus on reef No. 30 is a fortuitous case where the fishes were able to adapt to an adjacent shelter type when they outgrew their native coral heads. They apparently did not opt to leave this marginal habitat to seek more optimal shelter in a reef (No. 8) only 20 m away which had a very large Pocillopora eydouxi head (this head supported about 800 Chromis caerulea, the adults of which were some of the largest seen). Furthermore, pomacentrids that seek shelter in coral heads (Dascyllus aruanus, D. reticulatus, and Chromis caerulea) were never seen to range between reefs at day or night. For these reasons, the selection of a proper settling site is of major importance both in short-term survival and in survival to maturation.

In October, 1973, populations of Chromis caerulea and their resident coral heads were added to reefs No. 19 and No. 22 (defaunated). This was accomplished by collecting a head with resident fishes and separating (followed by counting and measuring) them in the lab. The head was then attached with construction grade cement to a pipe coupler. The coupler and head were added to artificial reefs with the same group of fishes that originally inhabited the head (Plate 3A). Five fish/coral head units with 25, 5 cm, Chromis caerulea adults were added to reef No. 22 (newly defaunated) on the 22nd of October 1973. Within

ten minutes, the Chromis had begun to feed in midwater above their resident head. Within two days, all of the Chromis except for two individuals had disappeared; but these persisted for the duration of the observation period (seven days).

Unexpectedly, eight newly settled transparent Chromis caerulea were present at two days, and 12 at four days after head addition. After seven days, there were nearly 24 newly settled C. caerulea along with the originally introduced Dascyllus aruanus and D. reticulatus and a newly invaded 5 cm Zebrasoma veliferum and two 1 cm Pomacentrus albofasciatus. All of these new recruits were closely associated with the introduced heads, darting in between coral branches when approached. Juvenile C. caerulea also settled on reef No. 19 where two heads with C. caerulea, D. aruanus, and D. reticulatus had been introduced. However, this reef was in the equilibrium state (100 days since last defaunation) with a large population of resident fishes numerically dominated by 49 adult and juvenile Pomacentrus pavo. Ten days after head introduction, the first juvenile recruits were detected. These consisted of 1 to 2 cm total length Chromis caerulea (two), Abudefduf curacao (one), Pomacentrus albofasciatus (one), and P. pavo (18). After 15 days, C. caerulea recruits totaled 18 and P. pavo, 40. Plate 3A shows recently settled juveniles on a coral head attached to an artificial reef.

As a control, five coral heads that lacked resident fishes were added to reef No. 16 (reef No. 16 had been defaunated) and reef No. 21 (which was in equilibrium condition 430 days since installation) in October, 1973. It was not possible to perform daily censuses on these

reefs; however, no C. caerulea had invaded after seven days although juvenile P. pavo did appear on both reefs within this period. However, 100 days later (February, 1974), C. caerulea had invaded both reefs (App. 4 and 11). These experiments confirm the hypothesis that the presence of appropriate coral shelter heads determines the occurrence of Chromis caerulea, Dascyllus aruanus, and D. reticulatus. Experimental reefs in which fish were introduced with the shelter coral units were rapidly invaded by juveniles, while reefs that lacked adult innoculates were colonized more slowly. The larvae of Chromis could have been preferentially attracted to reefs with resident adults; juveniles settling on these reefs might have enjoyed a higher rate of survival. Reef No. 22, defaunated beforehand with adult C. caerulea introduced with the heads, provided an empty environment for Chromis and Dascyllus propagules to invade. The best invader or best survivor between censuses was Chromis caerulea. Reef No. 19 possessed a resident population of P. pavo (and other species); and here, also, C. caerulea juveniles invaded. Pomacentrus pavo juveniles also made appearances on the reef. The juveniles of P. pavo do not associate quite as intimately with coral heads as do juvenile C. caerulea and frequently seek shelter among the interstices of the artificial reef modules. Pomacentrus pavo juveniles were fairly large ($\bar{X}$ = about 15 mm) and also appeared on the reefs only in the pigmented adult coloration. Chromis caerulea recruits were smaller ($\bar{X}$ = 7.5 to 10 mm) and occasionally were first seen as transparent larvae with silvery abdomens. Transformation to the adult pigmentation occurred within 12 hours of settling in some individuals. The fact that some C. caerulea were first observed on the reef in the

adult coloration state and others in the larval state indicates flexibility in time of settlement. Individuals with the adult coloration presumably were older (since they were larger) and may have delayed their descent to benthic existence until a suitable habitat was encountered.

These initial experiments suffered several deficiencies. Of primary concern was the perturbation introduced by the use of dead corals. However, the Chromis line persisted on many of these initial corals long after their initial introduction to the reef (reef No. 19 had 30 individuals and reef No. 16, 83, 190 days after head installation). The luxurious growth of algae that eventually plugged the spaces between coral branches probably made the heads unsuitable for Chromis habitation.

Another problem with this first regime was that observation periods were few and spaced at an interval of two days. Many invasions and extinctions may have occurred during these periods without detection. For these reasons, it was not possible to isolate the relative contributions of invasion or extinction to the overall rate of successful colonization.

A year later, in October, 1974, experiments were enacted to distinguish between the processes of invasion and extinction and to evaluate the effect of the presence or absence of adults upon successful colonization by C. caerulea juvenile conspecifics.

Living coral heads were added to artificial reefs under four different experimental regimes:

a. Two living heads with resident Chromis caerulea were added to a reef that had just been defaunated (reef No. 20).

b. Two living heads without resident Chromis (specimens previously removed from head) were added to reef that had just previously been defaunated (Reef No. 21).

c. Two living coral heads with resident C. caerulea were added to the reef at equilibirum (reef No. 4).

d. Two living coral heads without resident Chromis were added to reef at equilibrium (reef No. 2).

The following diagram is a summary of the above regime:

	Reef defaunated	Reef at Equilibrium
Chromis absent	No. 21	No. 2
Chromis present	No. 20	No. 4

Living heads were attached to the artificial reefs by sliding aluminum tube receptacles into the module pipes. The Pocillopora heads were supported by stainless rods that radiated from the central tube. A coral head with its resident fish population could be bagged, detached, transplanted and installed into the receptacles within a matter of minutes.

Four control reefs (no heads added and reef at equilibrium) were also monitored daily (Table 38). These reefs had the following attributes:

a. Artificial reef with Chromis caerulea already present on preplaced heads from October, 1973 (reef No. 19).

b. Artificial reef lacking C. caerulea (reef No. 22).

c. Natural reef with C. caerulea resident (reef No. 5).

d. Natural reef that lacked C. caerulea substrate and also lacking C. caerulea (reef No. 11).

Both experimental and control reefs were monitored daily (except for the 8th day).

Invasion and extinction of newly settled juveniles on experimental and control reefs is depticted in Table 38. The effect of adult Chromis resident on introduced heads upon the settling rate of juvenile C. caerulea will be considered first. Reef No. 20 and reef No. 4 (both with introduced C. caerulea) were invaded by juvenile Chromis by the third and fourth days respectively. Reef Nos. 21 and 2 (lacking adults) were not colonized until seven to nine days. The number of juveniles present differed between the two types of reefs; after nine days, reef No. 20 and reef No. 4 jointly supported 190 individuals and reefs No. 21 and No. 2 had a joint population of 17 Chromis juveniles.

The same trends are found in the colonization of control reefs. Artificial reef No. 19 (with pre-existing C. caerulea) was successfully invaded by one Chromis caerulea juvenile on day five and supported 18 juveniles by day nine. Reef No. 22 which lacked suitable substrate was never seen to be inhabited by Chromis juveniles. Natural reef No. 5 (with Chromis) was invaded by one Dascyllus reticulatus on day nine and 22 C. caerulea on day ten. Natural reef No. 11 (lacking Chromis) was unsuccessfully invaded by 18 C. caerulea on day ten. In summary, artificial and natural reefs with adult Chromis were colonized successfully at a faster rate and supported larger populations of juveniles at the end of ten days than reefs lacking Chromis adults.

The colonization of juvenile Chromis caerulea to reefs at equilibrium and reefs that were defaunated are described next. The purpose of these experiments was to determine whether the presence of

species such as Pomacentrus pavo has any effect on the settling pattern of juvenile C. caerulea. The colonization of reef No. 4 (at equilibrium, C. caerulea adults were introduced) was very similar to that of reef No. 20 (defaunated with C. caerulea adults present). Both had been successfully invaded by juvenile Chromis after five days and by the evening of day ten supported similar numbers of individuals (158 juveniles for reef No. 20 and 152 for reef No. 4). There appears to be no significant difference in the colonization by C. caerulea juveniles between artificial reefs at equilibrium (No. 2) and those defaunated (No. 21). Both received their first successful immigrants by days seven to nine; and by the evening of day ten, the reefs were similar both in number and species of juveniles present (Table 37). This indicates that the presence of other species like P. pavo on the reef has little effect as long as adult C. caerulea are present. The availability of shelter habitat followed by presence of adults in the corals are the major factors determining the success of colonization. Since empty heads are eventually colonized by Chromis, why are heads with adults colonized more rapidly? Do recruits preferentially select heads with established populations of adults, or do they survive better on heads with adults? A clue to this situation is found in time of day that the pelagic larvae descend to the reefs.

Observations on days nine and ten indicate that considerable settling of C. caerulea juveniles occurred at night between 1700 hours (dusk) and 0630 hours (dawn). Populations on reefs No. 20 and No. 4 increased by 230 C. caerulea, 1 D. reticulatus, and 1 P. albofasciatus throughout the night of 22 October. On one occasion, an actual invasion

was witnessed. This was at dusk at reef No. 6-18 in which one lone, transparent C. caerulea larva attempted to gain access to the heads that had just been placed at the top of the reef. Since no adult C. caerulea had been introduced to the heads, the propagule was chased from the reef after being vigorously attacked by four large male P. pavo. By invading the reefs at night, juvenile C. caerulea are able to avoid the abundant diurnal midwater feeding piscivores (the nocturnal midwater reef fauna is not nearly as abundant or diverse) and also the threat of interspecific aggression from other reef residents. The detection of suitable reef substrates should not pose any special problems except on the darkest, cloud-bound nights. Normally, the stars or moon provide ample illumination to easily resolve the highly contrasting reefs and light sand background.[2] It is likely that nocturnal settling is primarily a response to suitable physical shelter and not to the presence of adult conspecifics wedged among the branches of coral heads. Reefs with adults colonized sooner and supported larger juvenile populations than reefs without adults. This probably is the result of differential survivorship, not preferential settlement.

[2]A lagoon vs an ocean source of propagules might provide an alternate explanation for the different rates of invasion throughout the nighttime and daytime of days nine and ten. However, within these periods, both ebb (from the lagoon) and flood (from the outer ocean) tides occurred. For example, during the night of day nine, the tide ebbed from a high (5.0') at 1700 hrs to a low of (0.5') at 2300 hrs and flooded again to a high at 0500 hrs. During the daylight period of day ten, the tide ebbed from a high at 0500 hrs to a low at 1200 hrs and returned to a high at 1800 hrs. In each case, the tide ranged from high to low and back to high; presumably conveying potential propagules in a similar fashion during light or darkness.

Table 38 supports the hypothesis that survivorship of a given invader is increased when adults are present. Reefs No. 22 and No. 2 show the loss of C. caerulea juveniles during the day of October 22. These were individuals that were present in the morning but absent in the evening of day ten. Support of the widespread nocturnal settlement of C. caerulea juveniles is found in the colonization history of reef No. 11. The 19 C. caerulea juveniles that invaded this reef were not associated with Pocillopora heads (none were available), but ranged freely over the reef. By evening they were gone--presumably taken by predators.

Reef Nos. 4, 5, 19, and 20 (with C. caerulea adults present) did show increased survival of Chromis juveniles throughout the observation period. No extinctions were detected on day ten from dawn to dusk; however, the accuracy of censuses conducted on large populations is such that it was not possible to resolve losses of the magnitude of those of reefs No. 22 and No. 2.

The limited experiments performed indicate that the settling of Chromis caerulea, Dascyllus aruanus, D. reticulatus, and Pomacentrus albofasciatus occurs predominantly at night. The sudden appearance of juveniles on many reefs on the evening of day ten may signify short-term, temporal patchiness in the availability of larvae; but it does confirm the reality that fishes are capable of invading reefs at night. The number of individuals invading reefs No. 4 and No. 20 (without adults) is not known exactly because they were not censused until about an hour after first light, and predators might have dispersed them by that time. It is of interest that all C. caerulea juveniles observed on the

morning of 22 October were very small--about 7.5 mm and transparent. In most cases, newly settled groups of C. caerulea or P. pavo were of uniform size, suggesting that larvae may school as plankton.

Using the data at hand and with the application of Occam's razor, it seems most likely that settling larvae have the capability of detecting favorable shelter substrates, but not to preferentially pick those with adults. The adults breed year-round and the larvae seem to be continuously available. Behavioral observations of juvenile Chromis caerulea on heads with adults and on heads lacking adults suggests some possible explanations for differential survivorship.

Juveniles on heads with adults fed above the coral head but remained in a very cohesive and responsive school. They were sensitive to escape and alarm movements of the adults overhead (adults and juveniles invariably stratified during feeding with the adults foraging up to 1.5 m vertically above the head the juveniles usually up to 10 cm above the head). Juveniles on heads lacking adults gathered in loose schools with considerable disorder in their feeding height and attitude to the reef. They characteristically ranged between the coral heads, and some individuals were observed feeding solitarily up to 50 cm above the heads. These juveniles would seem to become vulnerable to predators or to displacement by interspecific aggression. The adults may serve as an early warning system to the juveniles. The approach of a predator causes the adults to rapidly dart back into the reef and the juveniles appear to key on this movement. This would permit the juveniles to capitalize on the better vantage points of the overhead adults.

The larger schools of juveniles were more cohesive and responsive. This may be due to social facilitation that occurs in group situations in a variety of animals; e.g., groups of carp are better at avoiding a net than conspecifics trained in isolation (Hunter and Wisby, 1964). Rapid learning of predator avoidance behavior is a necessary attribute in the dense piscivore environment of a coral reef. Young Chromis on coral heads with adults may derive some protection from interspecific aggression between adult C. caerulea and other species. There is clear foraging height partitioning between P. pavo and C. caerulea (C. caerulea usually feed higher above the reef while P. pavo feed up to the base of the Chromis school and extend laterally in the upcurrent direction). Agonistic behavior between adults of the two species was only rarely encountered; but on one occasion, P. pavo adults were seen to attack and drive away an incoming C. caerulea larva. The presence of actively feeding C. caerulea may provide a window of access from upper waters to the reef that provides immunity from P. pavo aggression. This may account for the successful daytime invasion of reefs No. 4 and No. 19.

Juvenile survivorship is higher on heads with adult conspecifics but there must be some limit as the carrying capacity of head is approached. Intraspecific competition for feeding space and shelter must increase with the number and size of the individuals to a point where new invaders are not successful. Reef No. 21 shows an instance of this saturation when 150 new juveniles arrived on the morning of day ten and about 150 juveniles were already present. By the evening of day ten, only half of the immigrants persisted.

species and the extinction of existing species. Like untreated mangrove islands, control reefs had a limited range in number of species when initially observed or defaunated, although the species composition did vary considerably. The number of species originally present on control reefs also did not change significantly throughout the 500 days of observation. However, oscillations about an equilibrium species number did occur. The period of oscillation and the equilibrial of species varied more on natural reefs (that characteristically had a greater amount of shelter and coral substrate diversity) than on the more uniform artificial reefs. Natural defaunated reefs were seen to have recovered approximately their original number of species when they were defaunated 500 days later. Further support is the high rate of species turnover.

The non-interactive equilibrium model predicts that the rate of species acquisition will follow a simple rate formula; $\frac{dS}{dt} = \lambda_A (PS) - \mu_{AS}$ where λ_A equals the average immigration rate of new species per species when S species are present; therefore, total immigration rate = $\lambda_A (P-S)$ where P equals number of species available for colonization and S equals number of species already present and λ_A equals the average extinction rate per species (total extinction rate equals $\lambda_A S$), as summarized from Wilson and Bossert (1971). Solving this equation results in

$$S = \frac{\lambda_A P}{\lambda_A + \mu_A} (1 - e^{-(\lambda_A + \mu_A)t})$$

and this reduces to $\hat{S} = \frac{\lambda_A P}{\lambda_A + \mu_A}$ as t becomes large and permits the deriviation of the "turnover equation" ($t_{.90} = \frac{1.2\hat{S}}{\mu_{\hat{S}}}$, $\hat{S}$ = equilibrium species number, where $\lambda_A = \mu_A$). This allows the prediction of the time necessary to achieve 90% of equilibrium value. Using these basic equations, it is possible to compare predicted $\hat{S}$, $t_{.90}$, and turnover rates with measured values on natural and artificial reefs. Assuming $\lambda_A = \mu_A$, the total extinction rate at equilibrium equals $(\mu_{\hat{S}}) = \frac{1.2\hat{S}}{t_{.90}}$.

Artificial reef Nos. 2, 4, 6, 18, and 21 reached equilibrium in about 200 to 300 days with a $\hat{S} = 8.6$ resulting in a predicted $\mu_{\hat{S}}$ of .03 species/day (based on 300 days). The measured $\mu_{\hat{S}}$ was also .03 species/day. Similar treatment of natural reef Nos. 3, 5, and 8 for $t_{.90}$ of 200 days and $\hat{S} = 21$ results in a predicted $\mu_{\hat{S}}$ of .13 species/day. This contrasts with a mean measured rate of .04 species/day. The agreement between measured and predicted rates on artificial reefs is remarkable, but it sould be noted that measured extinction rates are necessarily minimums. Natural reefs had measured $\mu_{\hat{S}}$ rates that were somewhat lower than expected. It does follow from the turnover equation that reefs with a large $\hat{S}$ will have a greater total extinction rate than reefs with a small $\hat{S}$ (if both have similar $t_{.90}$). But, if the $\mu_{\hat{S}}$ of natural reefs is comparable to that of the less speciose artificial reef, the average turnover may be less than expected on natural reefs because of the high diversity of coral substrates and shelter

types. Enewetak turnover rates interestingly enough, do fall within the $\mu_{\hat{S}}$ values of mangrove islands which uniformly had a higher value of $\hat{S}$ than patch reefs, but similar $t_{.90}$ values.

The equilibrium number of species ($\hat{S}$) can be calculated from the basic colonization rate equation if the average immigration rate and the average extinction rates are known. Multiply defaunated reefs furnish short-term immigration and extinction rates that allow the computation of a predicted $\hat{S}$. One such calculation had been made for the seasonal artificial and natural reefs; however, more are possible from the available data. The calculation of predicted $\hat{S}$ will be described in detail for natural reef No. 9 (Table 21). This reef was defaunated a second time in February, 1973, 193 days following the first defaunation. Censuses were conducted at 5 days, 7 days, and 11 days (n will stand for sample size in this discussion, i.e., n = 3) after the last defaunation. λ_A (average immigration rate) equals the total immigration rate/number of species not yet invaded the reef (P somewhat arbitrarily set at 100 species). By day 11, seven total immigrations had occurred (therefore, λ_A = .007). The average extinction rate (μ_A) equals the total extinction rate divided by the number of species already present on the reef. Since there were two successful invasions, μ_A = .036. Using the equation, we obtain a solution of 16.28 species. One hundred and eight days later, reef No. 9 did have 16 species (countable by census techniques). In this case and in some of the others that follow, it was possible to very accurately predict $\hat{S}$ by analyzing early colonization success. Natural reef No. 13 was censused on days six and ten after defaunation in February, 1973 (Table 23),

and $\lambda_A = .009$, $\mu_A = .029$, $\hat{S} = 23.69$. One hundred thirteen days later, it supported 25 species (census). The reef had been caged on day ten; however, this did not seem to effect turnover rate to equilibrium, although species composition did differ fron non-caged reefs. Natural reef No. 17 was monitored three times in 12 days following a February, 1973, defaunation. In this case, however, all early invaders persisted; therefore, $\hat{S}$ was predicted at 100 species ($\lambda_A = .003$, $\mu_A = 0.0$).

The predictive value of the equilibrium equation was lower for artificial reefs. Reef No. 20 at ten days (n = 3, February, 1973; $\lambda_A = .014$, $\mu_A = .063$, $\hat{S} = 18.18$. Seventy-three days later, $\hat{S}$ = 6 species (census). Reef No. 16, 12 days following February defaunation (n = 3) $\lambda_A = .008$, $\mu_A = .024$, S = 25.00. One hundred seventeen days later, the reef supported 14 species (census; 20-absolute). Reef No. 19 (July, 1973, 14 days, n = 3) $\lambda_A = .005$, $\mu_A = .054$, $\hat{S} = 8.48$. Eighty-two days later, $\hat{S} = 10$. In this case, the low $\hat{S}$ of reef No. 19 was predicted by the slow initial rate of successful immigration.

$\hat{S}$ of natural reefs can be predicted by the early dynamics of colonization, but artificial reefs are not as predictable as natural reefs. However, the turnover rates of natural reefs were shown to be lower than expected using the same parent equation. The explanation of this may be found in the relative diversities of habitat available on natural as compared to artificial reefs. The higher percent turnover rates on artificial reefs may reflect the smaller populations which are more vulnerable to stochastic extinctions of resident fishes; this would also explain the lower certainty of determination of $\hat{S}$. In

general, it seems that the basic non-interactive equilibrium theory adequately models with high predictive power the colonization rates of fishes to Enewetak patch reefs.

Simberloff and Wilson have presented several arugments that the non-interactive equilibrium model is insufficient--based on intuitive thinking and supported by their experimental findings. Their results point out not only the basic differences between mangrove island and patch reef ecosystems, but also the different physical dimensions involved. Lack of an interactive equilibrium preceded by overshoot on patch reefs may be a result of scalar processes. Mangrove islands in terms of percentage of species are, like patch reefs, colonized predominantly by transients; however, on mangrove islands, ants (denoted "ecological dominants" by Simberloff) were late to immigrate and slow to increase in numbers. Simberloff (1969) stresses the community wide importance of ants, "... all direct observations of interaction in this experiment have involved ants, and almost all these have been near the end of the experiment as densities were rising noticeably."

Based on frequency of interaction and persistence from early invasion throughout the observation period, damselfishes (particularly Pomacentrus pavo and Chromis caerulea) constitute the ecological dominants of the patch reef assemblage. They are the first species to invade the reefs and rapidly increase in size and numbers. Relative to the size of their "island", these species are much larger than ants compared to mangrove islands. They also may defend territories encompassing much or all of the reef. For these reasons, colonizing individuals may interact strongly with any potential propagule attempting

reef immigrations. Even small-sized damsels may be very aggressive, so intense interactions between species occur immediately upon the arrival of the first propagule. Daily existence on patch reef is rigorous and demanding due to the high risk of predation that threatens reef fishes at every stage of their life cycle from egg to maturity.

Experimental manipulations which even slightly perturb the relationship between prey and shelter often result in their demise to predators. For these reasons, competition for daytime or nighttime shelter is intense; and for many species, it seems that shelter is more immediately limiting than food. No indication of the type of interactive equilibrium described by Simberloff and Wilson was observed throughout the time course of colonization on Enewetak patch reefs; i.e., there was no marked overshoot of number of species followed by an increase in number of ecological dominants and accompanied by the exclusion of other species. Interactions between species must occur on patch reefs from the first day of colonization. The effects of adult presence on the survivorship of young Chromis definitely indicates the importance of interactions between species in the process of colonization. Extinction rates certainly are not constants determined by stochastic events, but complex variables that depend upon the milieu of physical and biological environment.

In these ways, the species and individuals present on a reef may shape the ensuing structure and composition of the developing assemblage. Smith and Tyler (1973) summarize that:

> ... because the organisms of coral reef communities have effective dispersal mechanisms (planktonic eggs and larvae or wandering adults) there will invariably be new species coming into the habitat. Most of these are unable to become established, hence the community is restricted by rejection of unacceptable colonizers. The only newcomers that can become part of the community are those that have specialized adaptations that allow them to utilize the available resources without competition with species that are already established members of the community.

It is clear that these natural systems of co-occurrence are highly tuned systems, selected for survival. In Florida, Arthur Myberg, of the University of Miami (pers. comm.), suggested that the non-selective aggressive response of some reef fishes might be a possible means of maintaining community homeostasis. For example, Eupomacentrus planiforms excludes species of sponge-feeding fishes more aggressively than species that have food habits similar to its own. This would be considered misdirected intraspecific aggression according to Lorenz (1963) but actually may be an essential means of protecting the environment of Eupomacentrus planiforms from disturbance. Fine adjustment in foraging height of midwater feeding pomacentrids may also be an important means of maintaining assemblage homeostasis on Enewetak patch reefs.

Patch Reef Colonization as a Test of Equilibrium Theory

The number of species of patch reef fishes on a particular reef is clearly in dynamic equilibrium with the process of immigration of new

SUMMARY AND CONCLUSIONS

1. Small patch reefs share many of the attributes of atolls; for example, the component organisms are generally space limited and rely upon pelagic larval stages for dispersal. The problems of progeny dispersal and successful colonization of new habitats by patch reef fishes are much like those faced by most atoll species whether they be hermatypic corals or calcareous algae.
2. The fishes of the patch reef assemblage are very diverse and most are restricted to the immediate proximity of the reef. Fishes belonging to other lagoon assemblages also seek shelter in patch reefs when quiescent at night. Many members of the patch reef assemblage obtain their nutrition from advected food resources passing over the reef that are derived from the productivity of the outer reef and algal ridge.
3. The species composition of the patch reef assemblage varied considerably about an equilibrial value over an observation period of two and a half years. Likewise, the variability found in defaunation collections of comparable reefs was found to be high. The sources of variability are believed to result from stochastic events that influence the availability of propagules and, also, the availability of appropriate types of shelter as interspecific and intraspecific competition, predation, and natural mortality free niche sites for potential colonists.
4. The colonization of defaunated natural reefs was characterized by the early invasion and persistence of 17 species--of which

Pomacentrus pavo, P. vaiuli, Paramia quinquelineata, and Apogon novaeguineae were the most frequent. No defaunated reef ever achieved the exact pre-defaunation composition; and in many cases, the species composition at 600 days differed markedly from that of the baseline condition. The reefs did, however, attain a species number comparable to the original state. The characteristic oscillation about a value of about 22 species (accountable by census) following defaunation, supports the equilibrium theory of island colonization (MacArthur and Wilson, 1967). The basic theoretical equation describing the equilibrium species value nicely models the colonization of the patch reef assemblage. Short-term rates of immigration that were measured within ten days of defaunation adequately predicted the equilibrium number of species found after 100 to 200 days.

5. Equilibrium theory predicts that small islands or islands depauperate in habitat diversity will achieve a lower species equilibrium than that of large or habitat diverse islands. In this study, a larger reef was found to have a higher species equilibrium while artificial reefs that lacked habitat diversity had fewer species. The first invaders of artificial reefs were the same species that successfully colonized natural reefs. The assemblage structure of artificial reefs can be shaped by providing dense Pocillopora heads. These were rapidly colonized by Chromis caerulea, Dascyllus aruanus, and D. reticulatus. It is clear that an increase in artificial reef habitat diversity was accompanied by an increase in equilibrium species number.

6. Pocillopora coral heads added to artificial reefs and which contained transplanted adults were successfully colonized at a higher rate and supported a larger population of juveniles than heads that lacked adults. This, along with the observation that Chromis caerulea juveniles are capable (and may preferentially) settle on reefs at night, indicate the high pressure that midwater feeding fishes and inter-reef predators apply to potential reef colonists. The presence of adult conspecifics may open a window of access to immigrating juveniles wherein they are immune to the daytime agonistic attacks of other fishes. In this way, established reef residents may regulate the homeostasis of the reef by selectively permitting or denying the invasion of certain species.
   Juveniles living on heads with adults may also utilize an early warning system in that they seem to cue upon the shelter seeking response of adults. These advantages enhance the survival of juveniles on heads with adults. Social facilitation of schooling behavior might also contribute to juvenile survival.
7. The recovery following perturbation of the patch reef assemblage proceded very rapidly, and this must have been due to the nearby proximity and abundance of colonizing propagules. It is apparent, however, that the sequence of invasions had repercussions throughout the history of patch reef colonization. The recovery of an atoll ecosystem after large scale disturbance will also be expected to be determined by both stochastic and predictable invasion events; but in this case, the source of propagules is orders of

magnitude removed and the time required to reach species equilibrium is predicted to be proportionally great.

PLATE 1A

Photograph of Natural Study Reef. Small Fishes are Apogon gracilis.

PLATE 1B

Photograph of 40-Module Artificial Reef.





PLATE 2A

Photograph Demonstrating Method of Artificial Reef Module Construction.

PLATE 2B

Photograph of a Typical Module Pipe at 200 Days Showing Ascidians, Soft and Hard Corals.





PLATE 3A

Photograph of Pocillopora Head Attached to Artificial Reef. Fishes that Invaded the Head were Chromis caerulea, Dascyllus aruanus and Thalassoma amblycephalus.

PLATE 3B

Photograph of Artificial Reef Surrounded by Nylon Net Exclusion Cage.



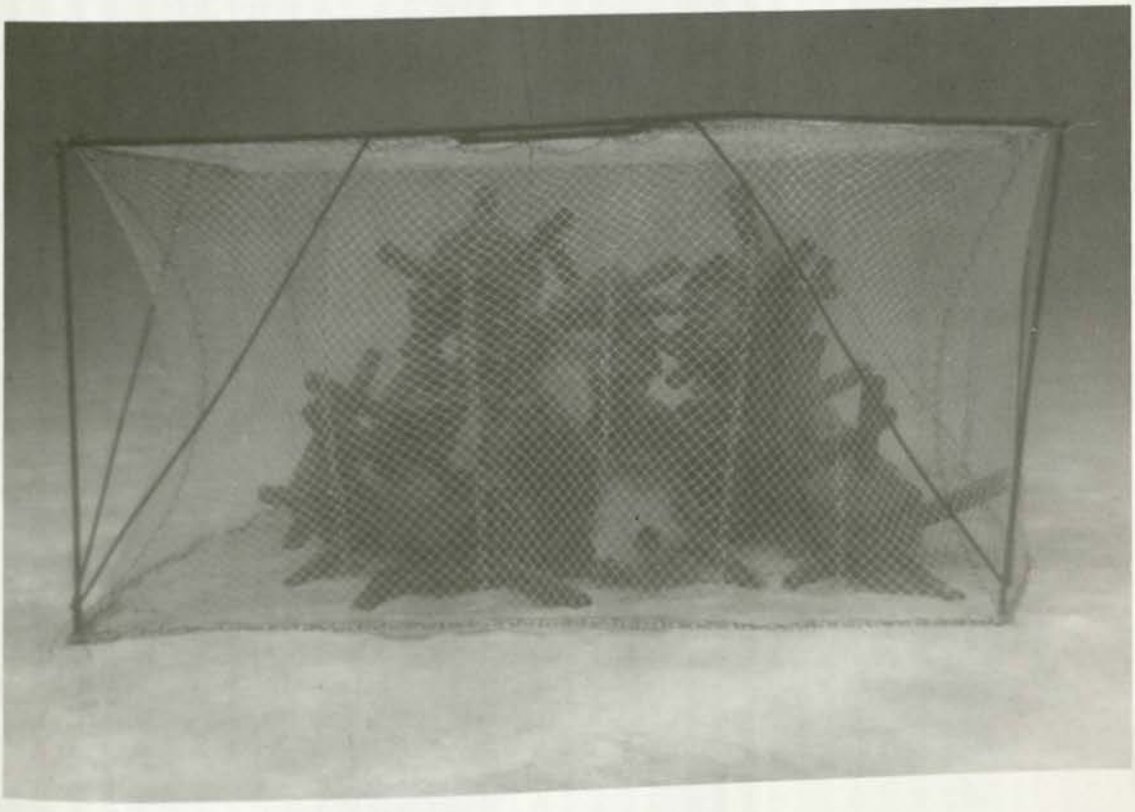


FIGURE 1

Map of Enewetak Atoll, Marshall Islands showing the study region along the windward side of the atoll. The hatching indicates the limits of the seaward reef.

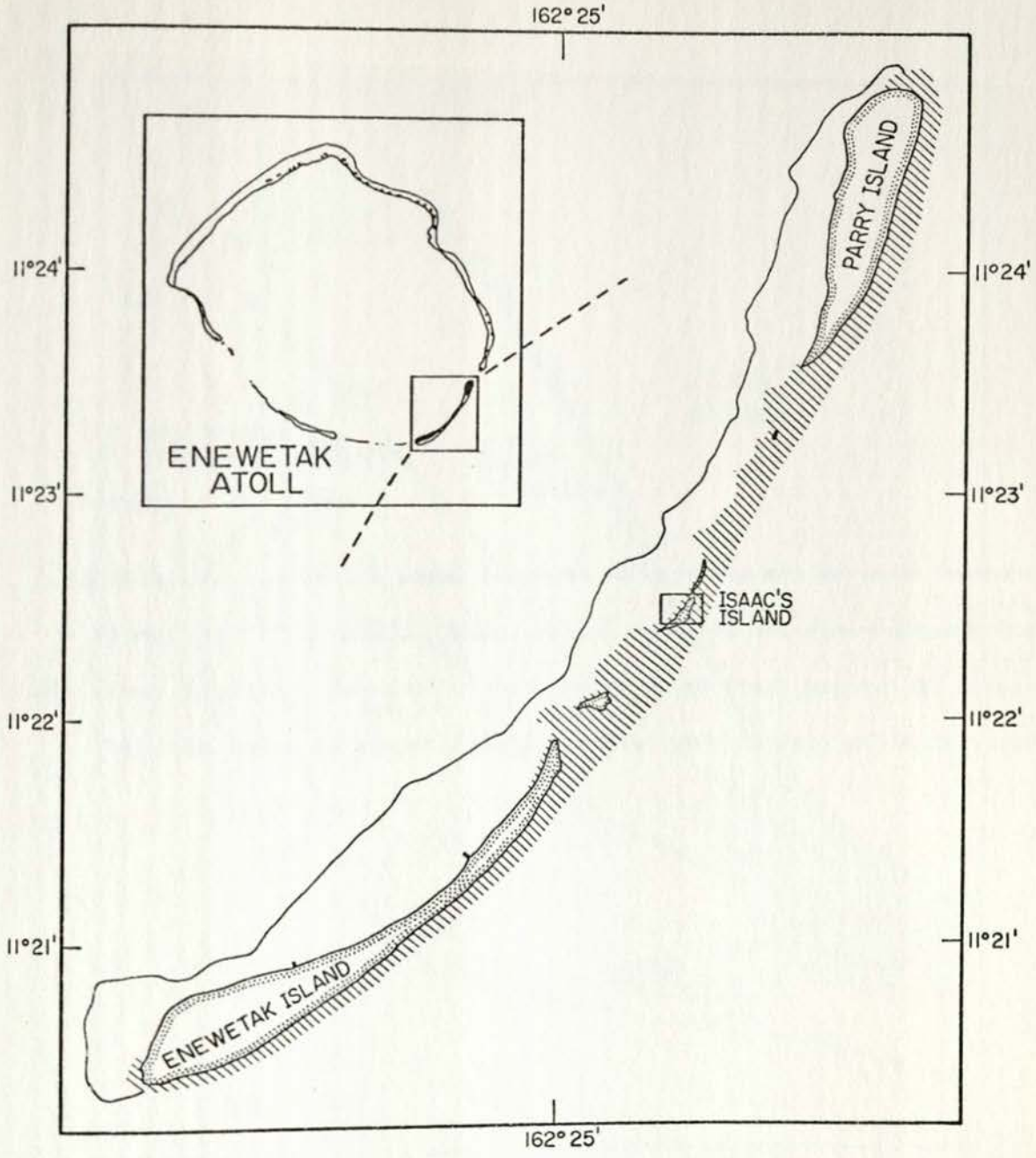

162° 25'
11°24'
11°23'
11°22'
11°21'
ENEWETAK ATOLL
PARRY ISLAND
ISAAC'S ISLAND
ENEWETAK ISLAND

FIGURE 2

Detailed view of the study site expanded from Figure 1. Experimental and control reefs are located in the lagoon directly in the lee of a small, low island (here designated Isaac's Island). Natural reefs are represented by open circles and artificial reefs by solid circles.

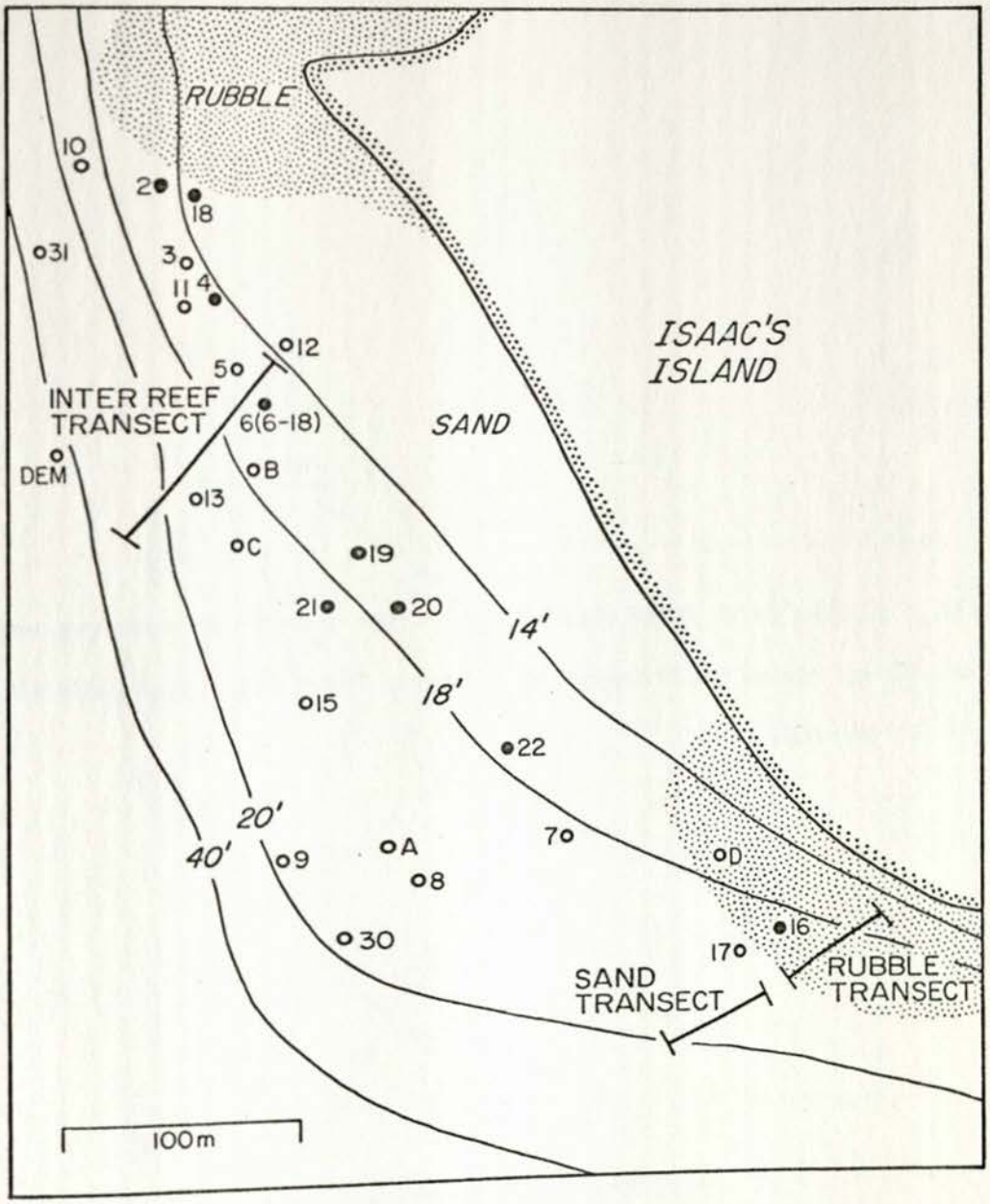

RUBBLE
ISAAC'S
ISLAND
SAND
INTER REEF
TRANSECT
6(6-18)
DEM
14'
18'
20'
40'
SAND
TRANSECT
RUBBLE
TRANSECT
100m

FIGURE 3

Stability of the Patch Reef Assemblage. The number of species was determined by visual techniques on control (undisturbed) reefs over a period of 526 days.

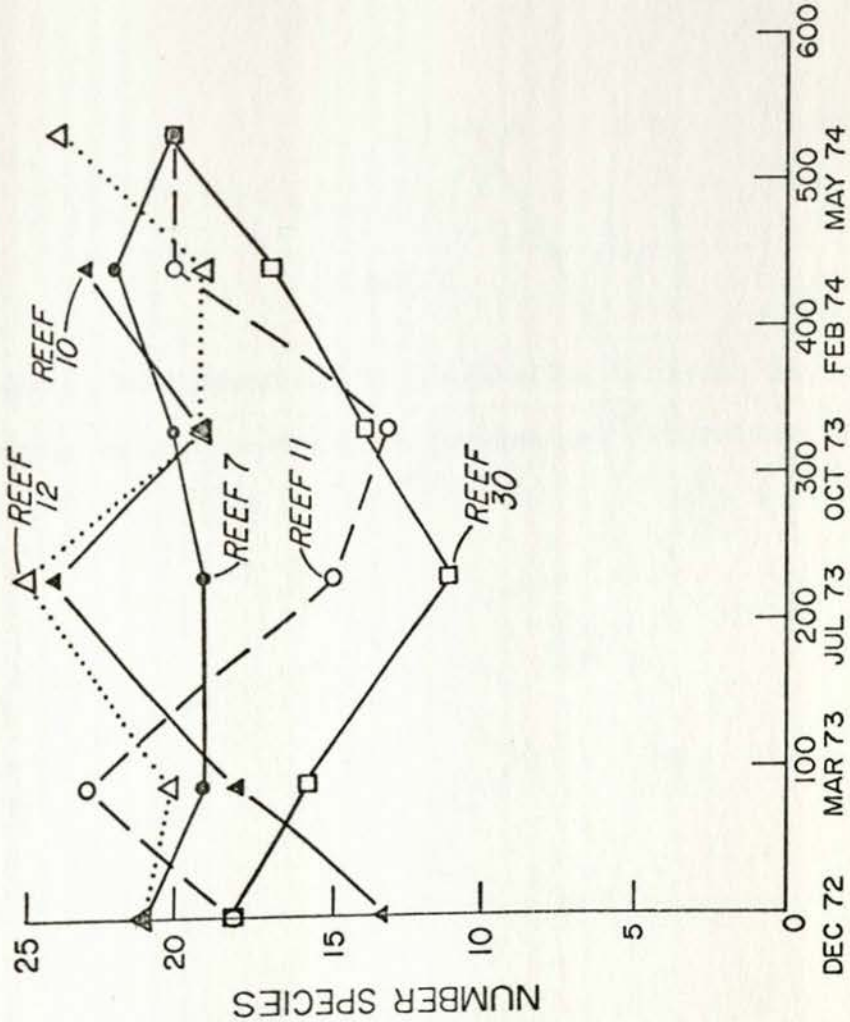

NUMBER SPECIES
25
20
15
10
5
0
DEC 72
100
MAR 73
200
JUL 73
300
OCT 73
400
FEB 74
500
MAY 74
600
DAYS SINCE INITIAL OBSERVATION
REEF 12
REEF 10
REEF 7
REEF 11
REEF 30

FIGURE 4

Stability of number of individuals of the Patch Reef Assemblage. The number of individuals was determined by visual census techniques over a period of 526 days.

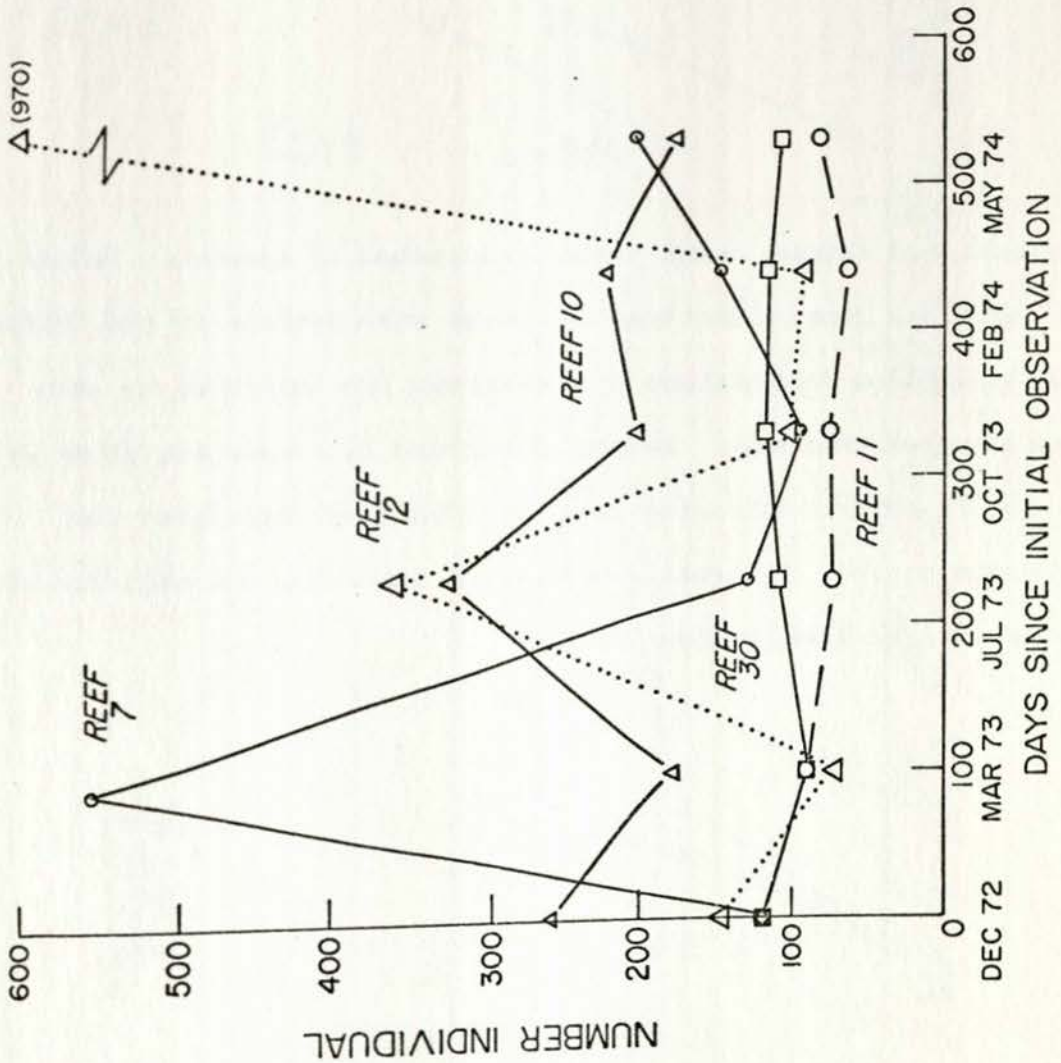

NUMBER INDIVIDUAL
600
500
400
300
200
100
0
△(970)
REEF 7
REEF 12
REEF 10
REEF 30
REEF 11
DEC 72
100
MAR 73
200
JUL 73
300
OCT 73
400
FEB 74
500
MAY 74
600
DAYS SINCE INITIAL OBSERVATION

FIGURE 5

Colonization of natural reefs based upon number of species. Values that were determined from collections are shown with symbols at the initial and at subsequent defaunations (defaunations are indicated by open arrows directed downward). Values determined by census are shown by the same symbols, but in this case they are connected throughout the observation period. The small solid arrow indicates the addition of five empty coral heads to reef No. 5.

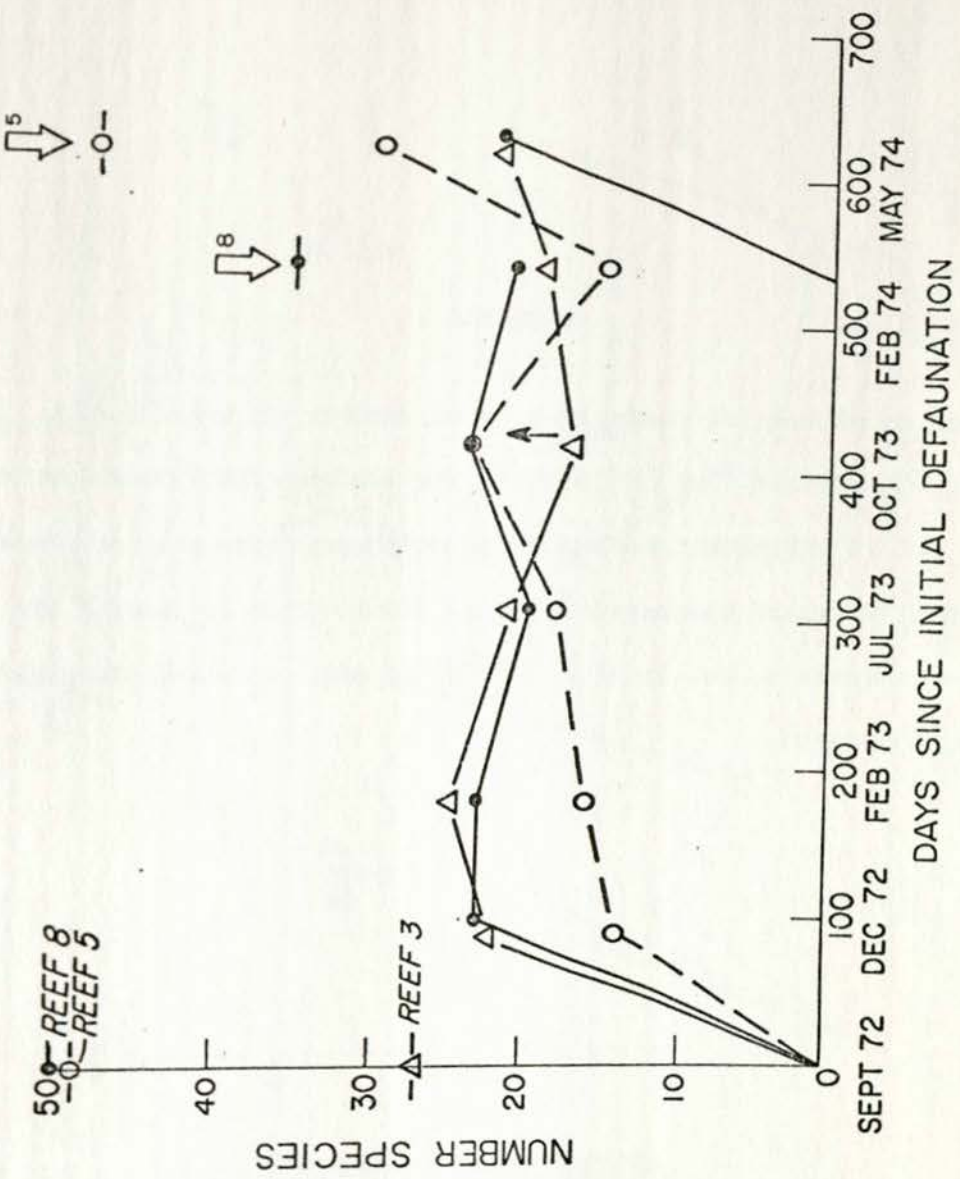

REEF 8
REEF 5
REEF 3
NUMBER SPECIES
DAYS SINCE INITIAL DEFAUNATION
SEPT 72
DEC 72
FEB 73
JUL 73
OCT 73
FEB 74
MAY 74

FIGURE 6

Colonization of natural reefs based upon number of individuals. Values that were determined from collections are shown with symbols at the initial and at subsequent defaunations (defaunations are indicated by open arrows directed downward). Values determined by census are shown by the same symbols, but in this case they are connected throughout the observation period.

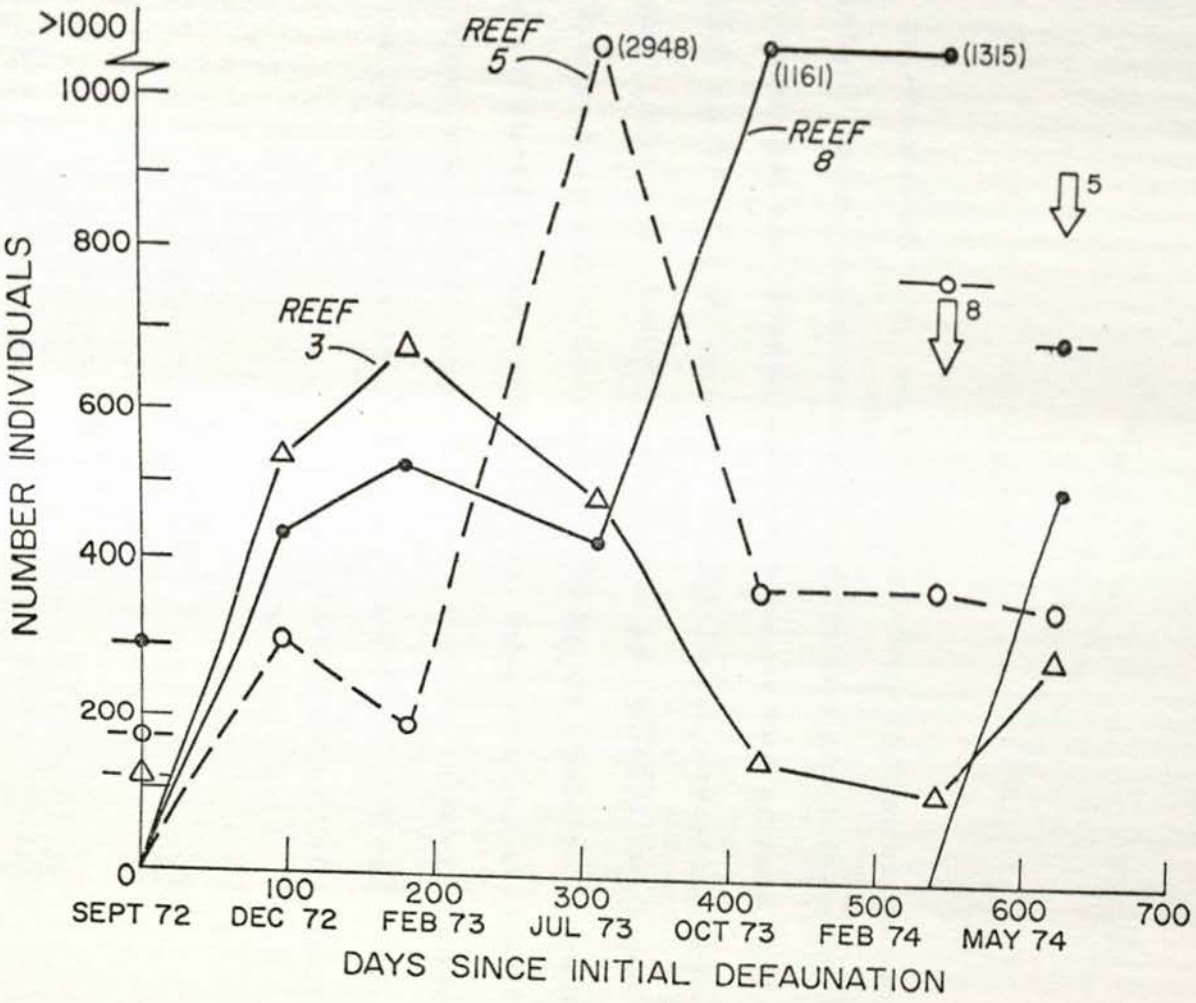

>1000
1000
800
600
400
200
0
NUMBER INDIVIDUALS
REEF 5
(2948)
(1161)
(1315)
REEF 8
REEF 3
5
8
100
200
300
400
500
600
700
SEPT 72
DEC 72
FEB 73
JUL 73
OCT 73
FEB 74
MAY 74
DAYS SINCE INITIAL DEFAUNATION

FIGURE 7

Short-term colonization of natural Reef No. 9. The numbers of species and individuals were determined by defaunation or census (defaunations are indicated by open arrows directed downward, and the value determined by defaunation by a symbol specific to each reef). Values determined by census are shown by the same symbols; but in this case, they are connected throughout the observation period. This graph portrays five defaunations and subsequent recolonization over intervals ranging from about 100 to about 200 days. In some instances censuses were conducted within a few days following defaunation; these are plotted on an expanded time abscissa (Scale A).

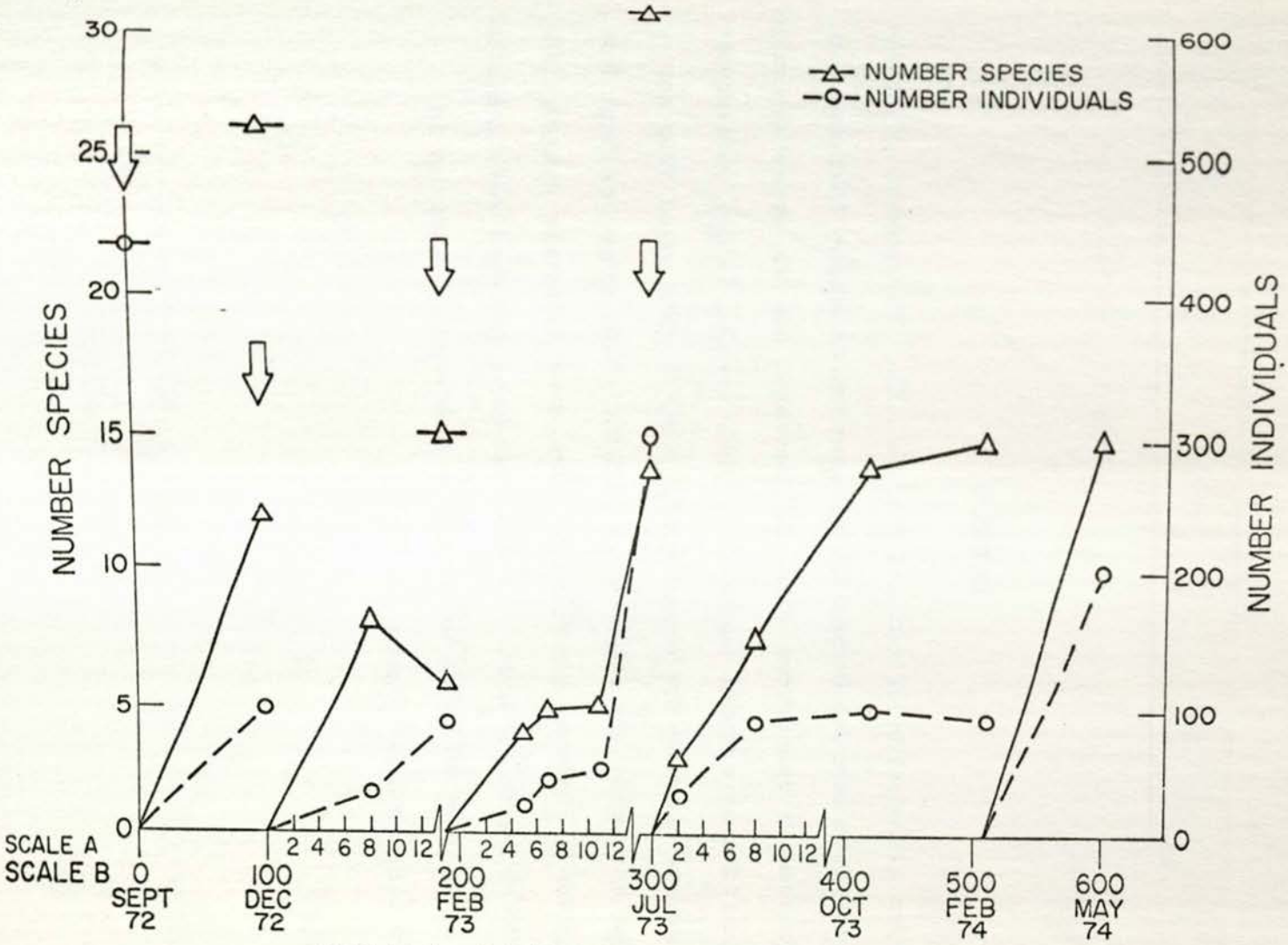

NUMBER SPECIES
NUMBER INDIVIDUALS
30
25
20
15
10
5
0
600
500
400
300
200
100
0
SCALE A
SCALE B
0 SEPT 72
100 DEC 72
200 FEB 73
300 JUL 73
400 OCT 73
500 FEB 74
600 MAY 74
2 4 6 8 10 12
SCALE A - DAYS SINCE LAST DEFAUNATION
SCALE B - DAYS SINCE INSTALLATION

FIGURE 8

Short-term colonization of natural Reef No. 13. The numbers of species and individuals were determined by defaunation or census (defaunations are indicated by open arrows directed downward, and the value determined by defaunation by a symbol specific to each reef). Values determined by census are shown by the same symbols; but in this case, they are connected throughout the observation period. This graph portrays four defaunations and subsequent recolonization over intervals ranging from about 100 to about 200 days. In some instances censuses were conducted within a few days following defaunation; these are plotted on an expanded time abscissa (Scale A).

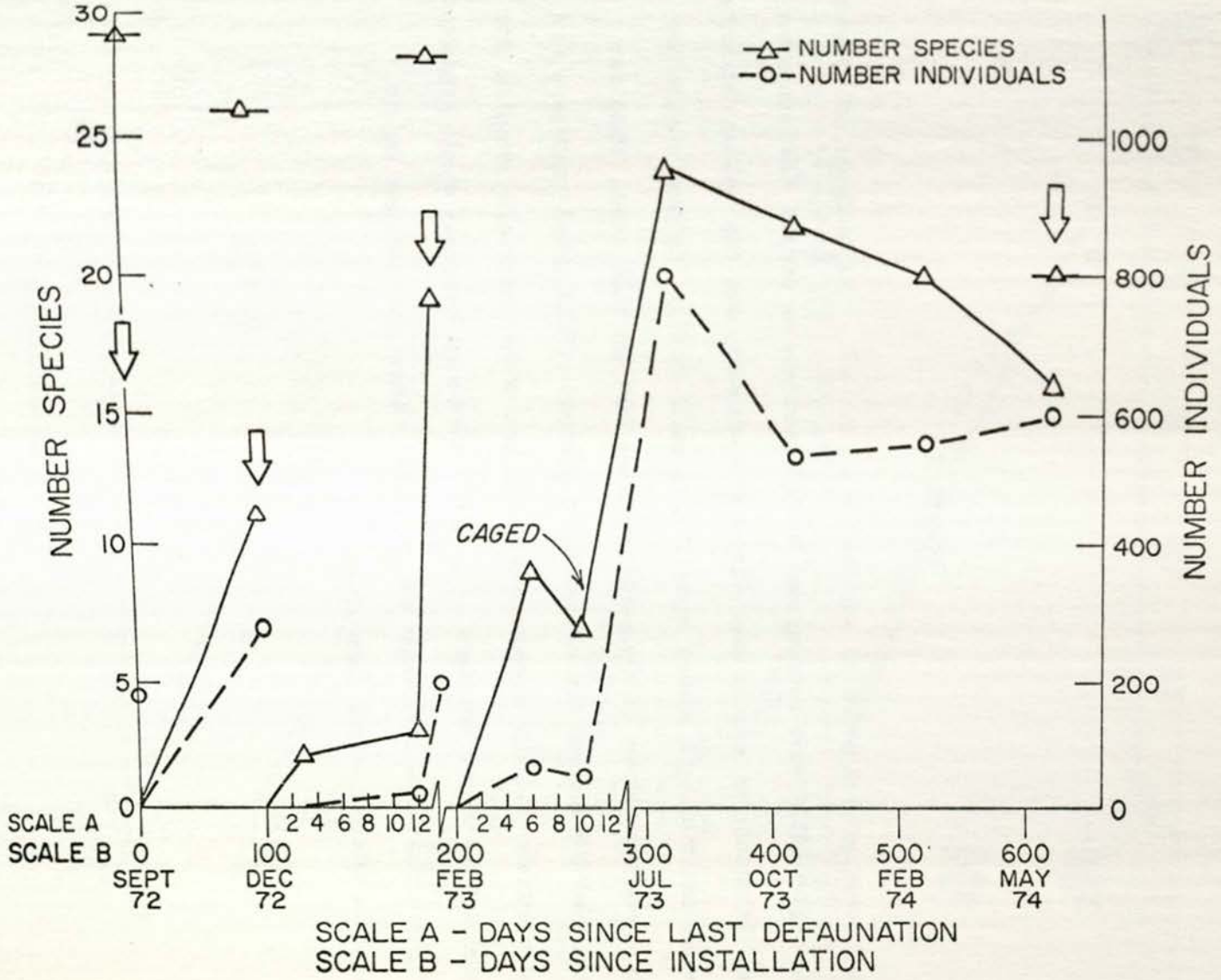

NUMBER SPECIES
NUMBER INDIVIDUALS
NUMBER SPECIES
NUMBER INDIVIDUALS
30
25
20
15
10
5
0
1000
800
600
400
200
0
CAGED
SCALE A
SCALE B
0
SEPT 72
100
DEC 72
200
FEB 73
300
JUL 73
400
OCT 73
500
FEB 74
600
MAY 74
2 4 6 8 10 12
2 4 6 8 10 12
SCALE A - DAYS SINCE LAST DEFAUNATION
SCALE B - DAYS SINCE INSTALLATION

FIGURE 9

Short-term colonization of natural Reef No. 17. The numbers of species and individuals were determined by defaunation or census (defaunations are indicated by open arrows directed downward, and the value determined by defaunation by a symbol specific to each reef). Values determined by census are shown by the same symbols; but in this case, they are connected throughout the observation period. This graph portrays four defaunations and subsequent recolonization over intervals ranging from about 100 to about 200 days. In some instances censuses were conducted within a few days following defaunation; these are plotted on an expanded time abscissa (Scale A).

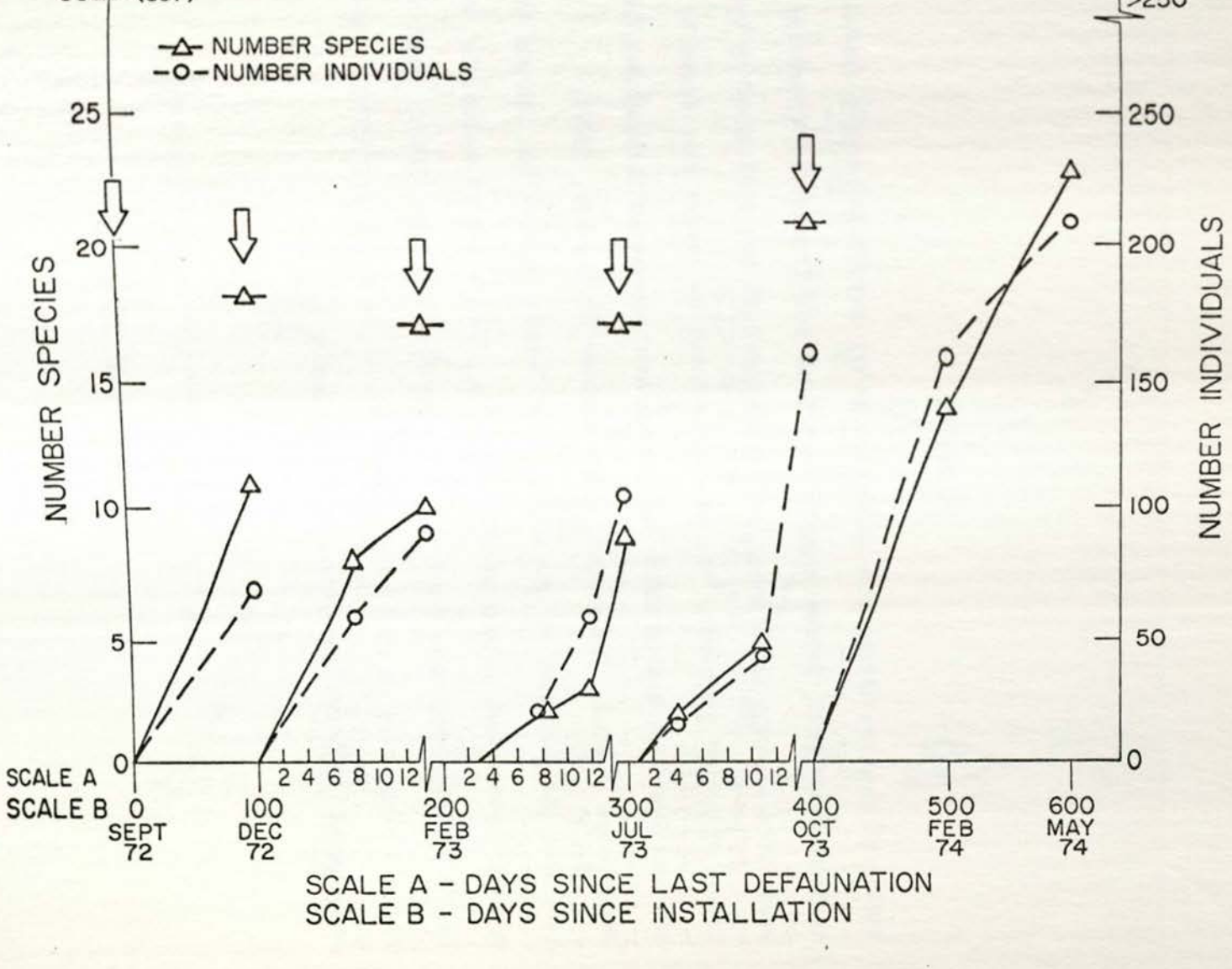

30
(397)
NUMBER SPECIES
NUMBER INDIVIDUALS
25
20
15
10
5
0
NUMBER SPECIES
>250
250
200
150
100
50
0
NUMBER INDIVIDUALS
SCALE A
SCALE B
2 4 6 8 10 12
0
SEPT 72
100
DEC 72
200
FEB 73
300
JUL 73
400
OCT 73
500
FEB 74
600
MAY 74
SCALE A - DAYS SINCE LAST DEFAUNATION
SCALE B - DAYS SINCE INSTALLATION

FIGURE 10

Number of species during the colonization of artificial reefs installed in September 1972. Values that were determined from collections are shown with symbols at defaunations (defaunations are indicated by open arrows directed downward). Values determined by census are shown by the same symbols; but in this case, they are connected throughout the observation period. The small, solid arrows at October, 1973, indicates the addition of ten empty coral heads to Reef No. 21 and five heads with resident fishes to Reef No. 22. The break in values of Reef No. 22 signify that this reef was not censused in July, 1973. Reef No. 18 was transported to the site of Reef No. 6 in February, 1974. Later censuses at 750 days have been added for Reef No. 21.

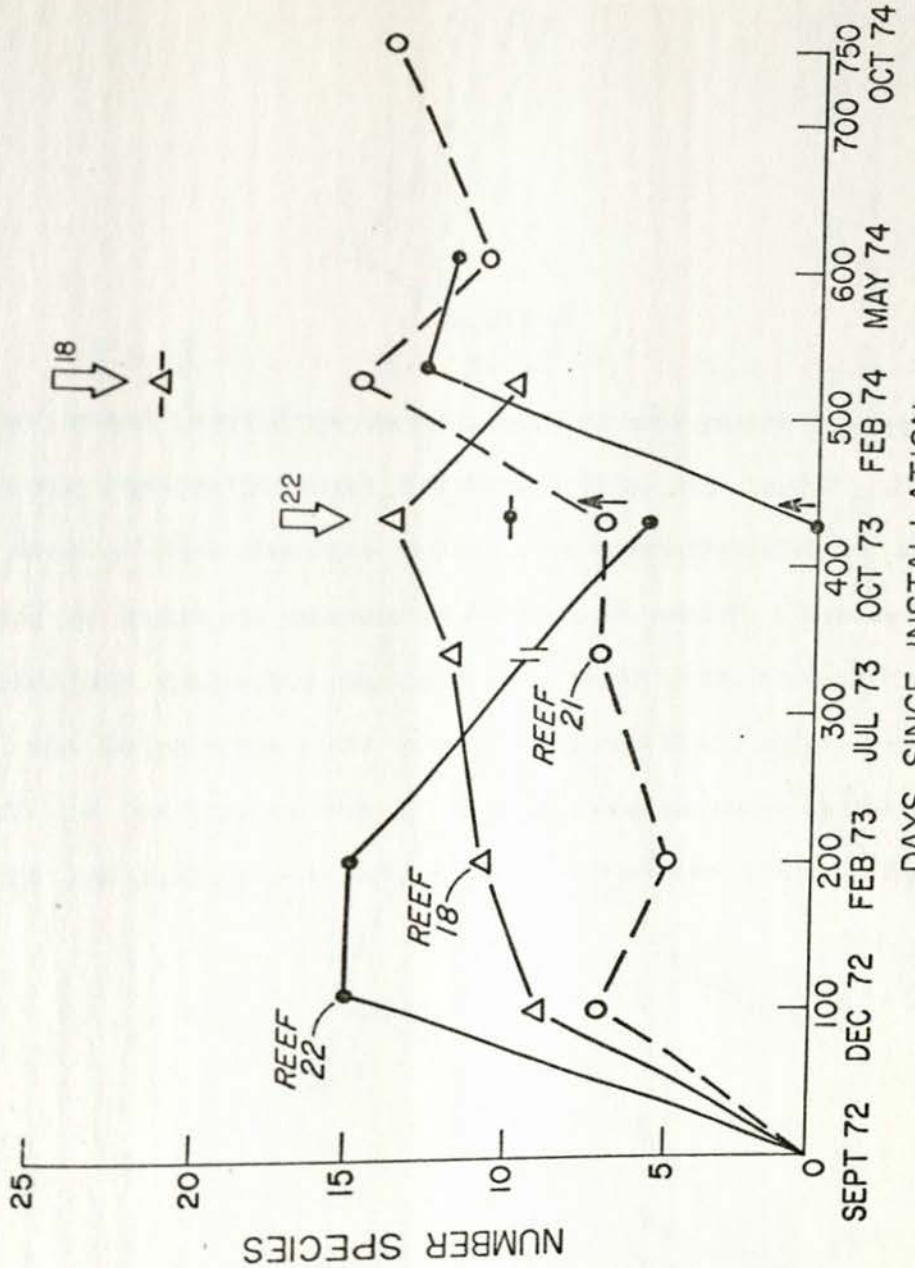

NUMBER SPECIES
25
20
15
10
5
0
SEPT 72
DEC 72
100
FEB 73
200
JUL 73
300
OCT 73
400
FEB 74
500
MAY 74
600
OCT 74
700 750
DAYS SINCE INSTALLATION
REEF 22
REEF 18
REEF 21
22
18

FIGURE 11

Number of species during the colonization of artificial reefs installed in May, 1972. Values that were determined from collections are shown with symbols at defaunations (defaunations are indicated by open arrows directed downward). Values determined by census are shown by the same symbols; but in this case, they are connected throughout the observation period. The single, solid arrows indicate the addition of ten uninhabited coral heads to both Reef No. 2 and to Reef No. 4. The twin, solid arrows show the combination of Reef No. 6 with Reef No. 18.

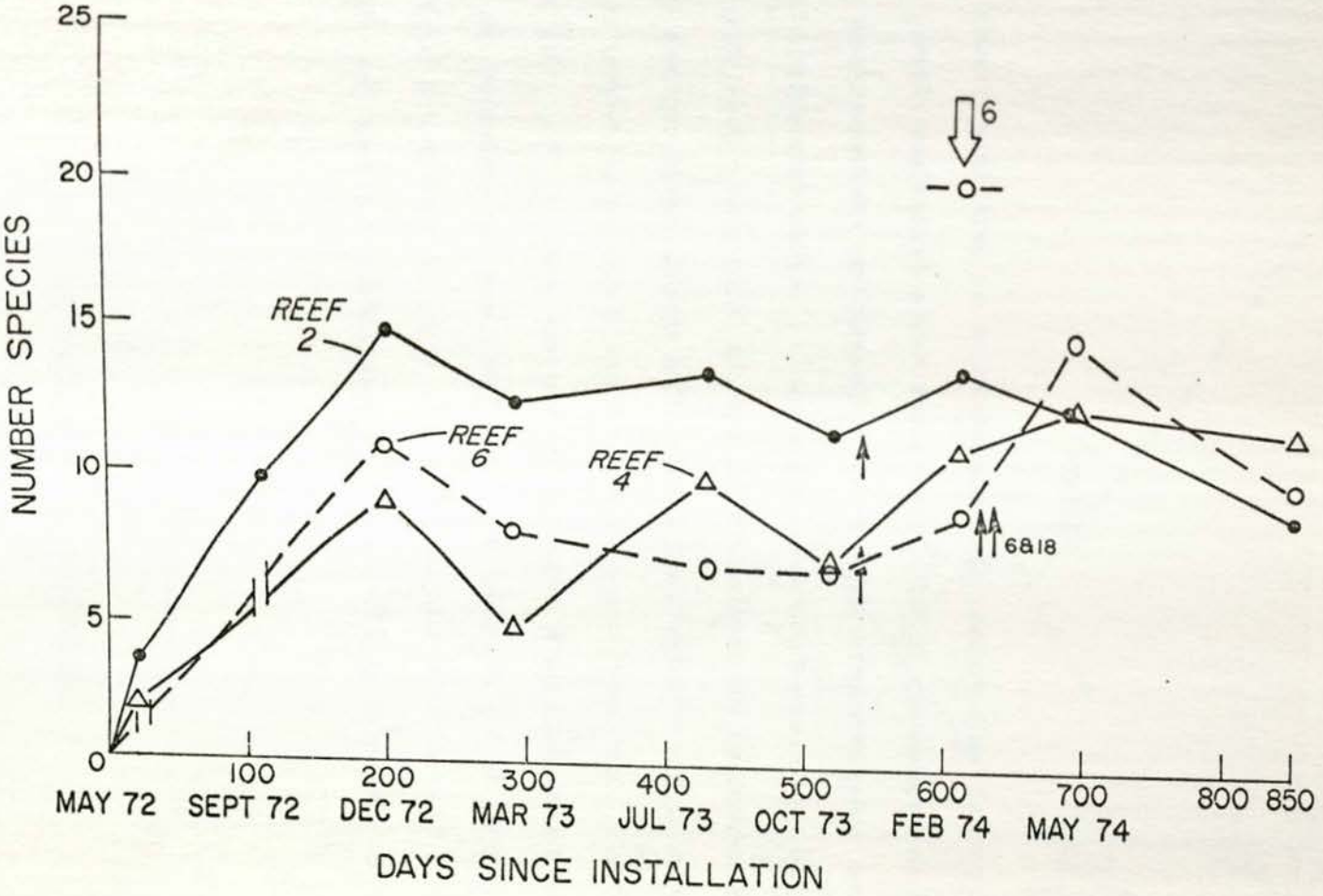

NUMBER SPECIES
25
20
15
10
5
0
6
REEF 2
REEF 6
REEF 4
6&18
100
200
300
400
500
600
700
800
850
MAY 72
SEPT 72
DEC 72
MAR 73
JUL 73
OCT 73
FEB 74
MAY 74
DAYS SINCE INSTALLATION

FIGURE 12

Number of individuals during the colonization of artificial reefs installed in September, 1972. Values that were determined from collections are shown with symbols at defaunations (defaunations are indicated by open arrows directed downward). Values determined by census are shown by the same symbols; but in this case, they are connected throughout the observation period. The small, solid arrows at October, 1973, indicates the addition of ten empty coral heads to Reef No. 21 and five heads with resident fishes to Reef No. 22. The break in values of Reef No. 22 signify that this reef was not censused in July, 1973. Reef No. 18 was transported to the site of Reef No. 6 in February, 1974. Later censuses at 750 days have been added for Reef No. 21.

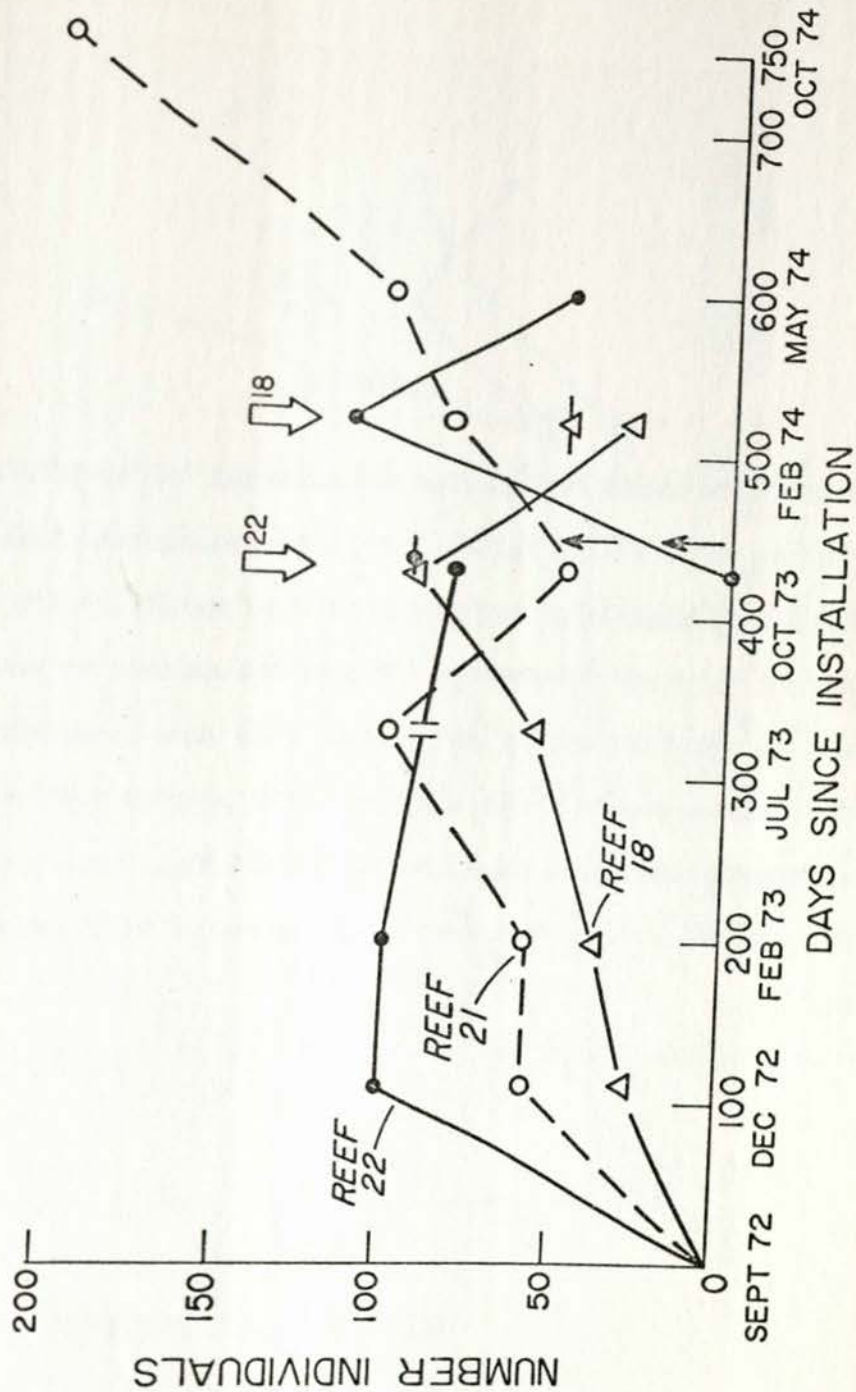

NUMBER INDIVIDUALS
200
150
100
50
0
REEF 22
REEF 21
REEF 18
22
18
SEPT 72
DEC 72
FEB 73
JUL 73
OCT 73
FEB 74
MAY 74
OCT 74
100
200
300
400
500
600
700
750
DAYS SINCE INSTALLATION

FIGURE 13

Number of individuals during the colonization of artificial reefs installed in May, 1972. Values that were determined from collections are shown with symbols at defaunations (defaunations are indicated by open arrows directed downward). Values determined by census are shown by the same symbols; but in this case, they are connected throughout the observation period. The single, solid arrows indicate the addition of ten uninhabited coral heads to both Reef No. 2 and to Reef No. 4. The twin, solid arrows show the combination of Reef No. 6 with Reef No. 18.

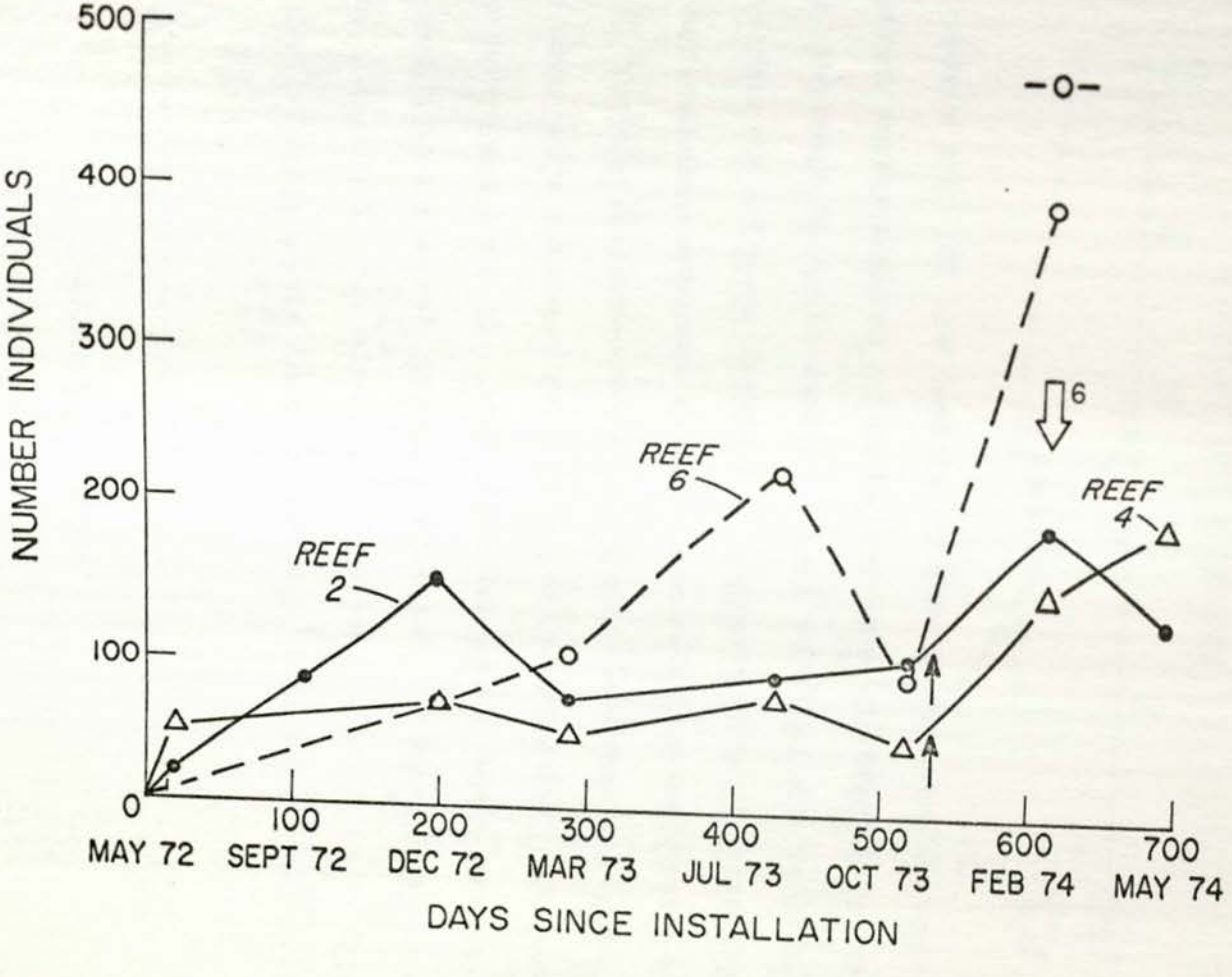

NUMBER INDIVIDUALS
500
400
300
200
100
0
-o-
6
REEF 6
REEF 2
REEF 4
100
200
300
400
500
600
700
MAY 72
SEPT 72
DEC 72
MAR 73
JUL 73
OCT 73
FEB 74
MAY 74
DAYS SINCE INSTALLATION

FIGURE 14

Short-term colonization of artificial Reef No. 16. The numbers of species and individuals were determined by defaunation or census (defaunations are indicated by open arrows directed downward, and the value determined by defaunation by a symbol specific to each reef). Values determined by census are shown by the same symbols; but in this case, they are connected throughout the observation period. This graph portrays five defaunations and subsequent recolonization over intervals ranging from about 100 to about 200 days. In some instances censuses were conducted within a few days following defaunation; these are plotted on an expanded time abscissa (Scale A). The small, solid arrow indicates the addition of five empty coral heads added at 541 days.

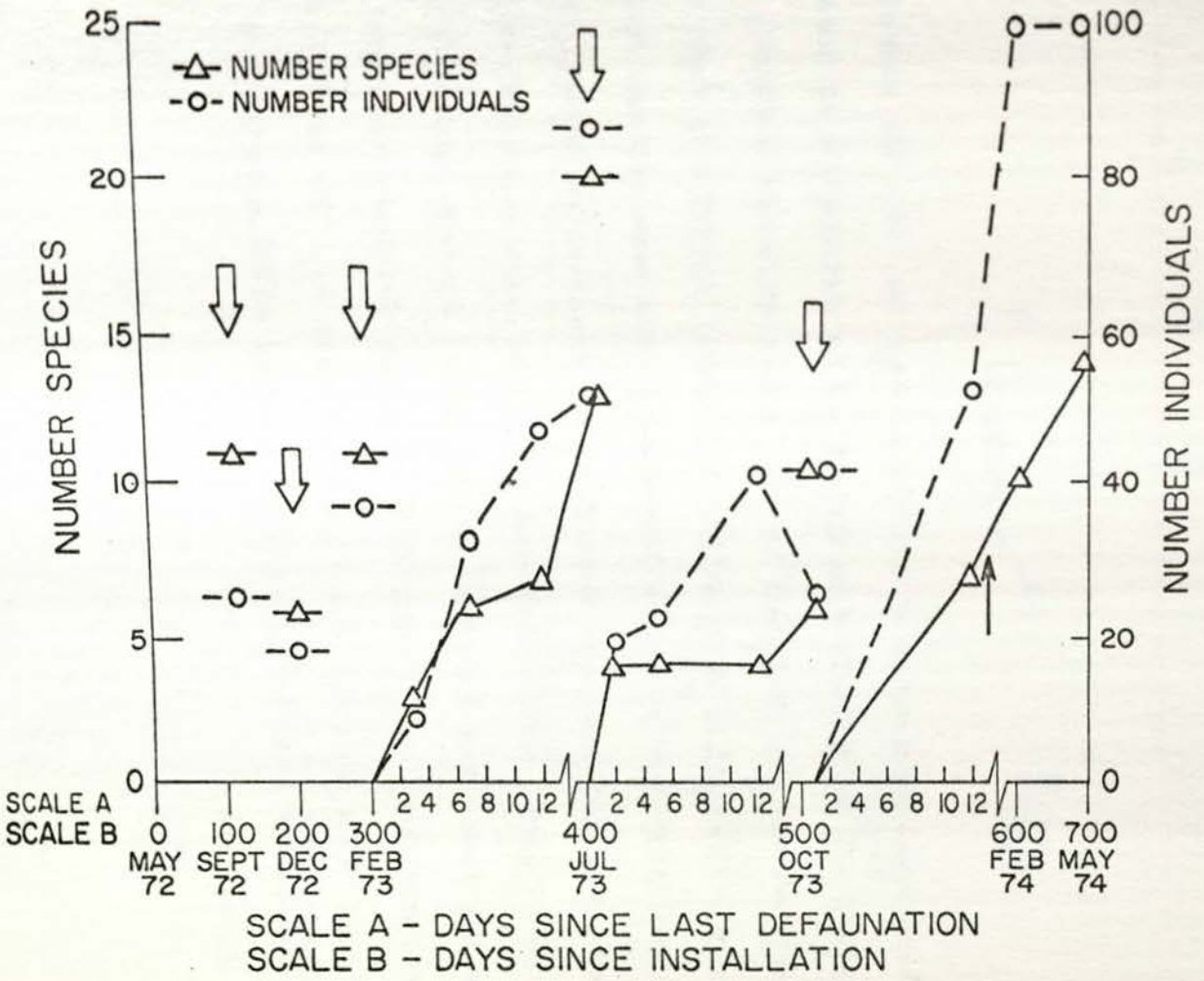

NUMBER SPECIES
NUMBER INDIVIDUALS
NUMBER SPECIES
NUMBER INDIVIDUALS
25
20
15
10
5
0
100
80
60
40
20
0
SCALE A
SCALE B
0
MAY 72
100
SEPT 72
200
DEC 72
300
FEB 73
400
JUL 73
500
OCT 73
600
FEB 74
700
MAY 74
2 4 6 8 10 12
SCALE A - DAYS SINCE LAST DEFAUNATION
SCALE B - DAYS SINCE INSTALLATION

FIGURE 15

Short-term colonization of artificial Reef No. 19. The numbers of species and individuals were determined by defaunation or census (defaunations are indicated by open arrows directed downward, and the value determined by defaunation by a symbol specific to each reef). Values determined by census are shown by the same symbols; but in this case, they are connected throughout the observation period. This graph portrays three defaunations and subsequent recolonization over intervals ranging from about 100 to about 200 days. In some instances censuses were conducted within a few days following defaunation; these are plotted on an expanded time abscissa (Scale A). The small, solid arrow indicates the addition of five coral heads with resident fish in October, 1973.

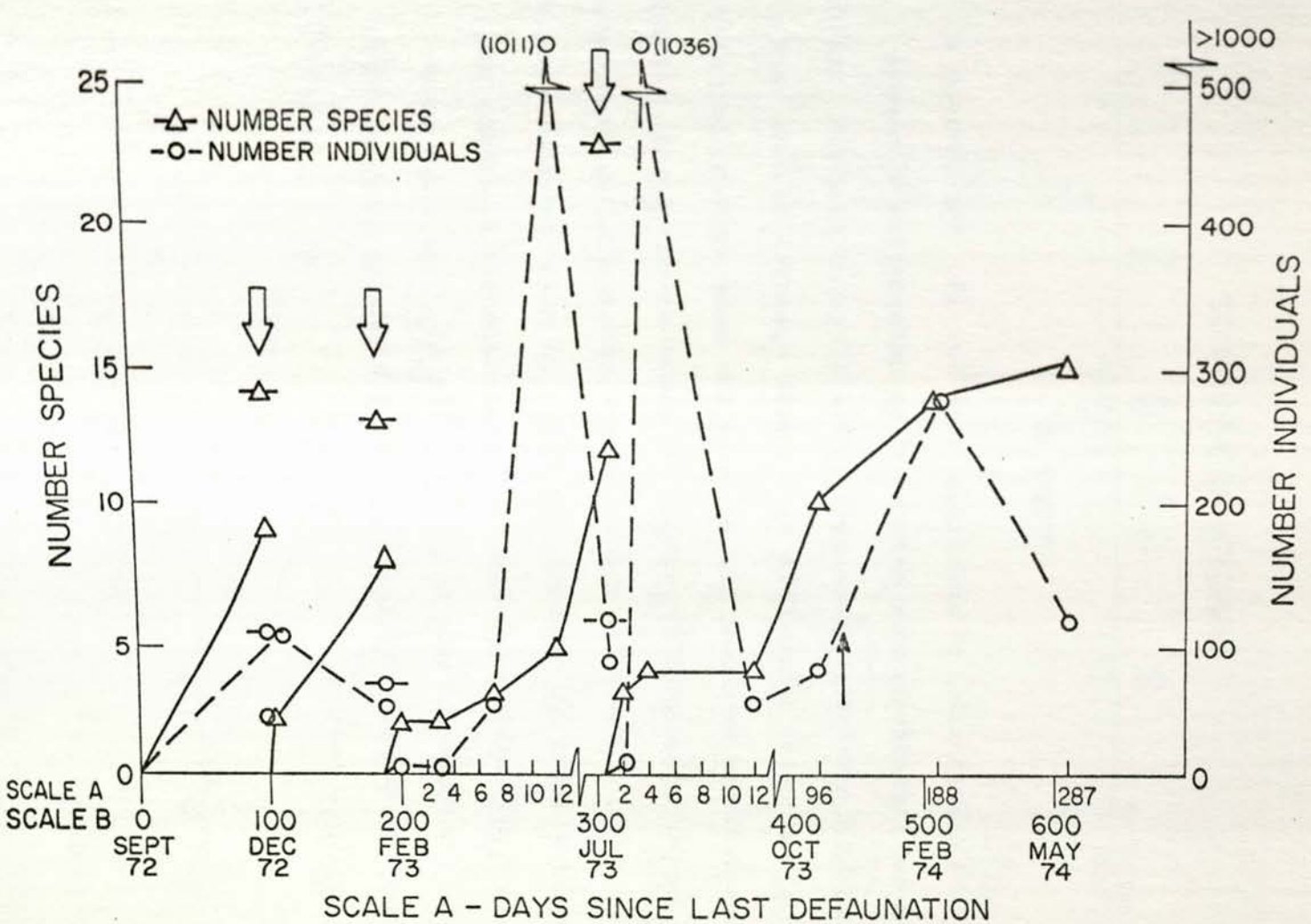

(1011)
(1036)
>1000
500
400
300
200
100
0
25
20
15
10
5
0
NUMBER SPECIES
NUMBER INDIVIDUALS
NUMBER SPECIES
NUMBER INDIVIDUALS
SCALE A
SCALE B
0
SEPT
72
100
DEC
72
200
FEB
73
300
JUL
73
400
OCT
73
500
FEB
74
600
MAY
74
2 4 6 8 10 12
2 4 6 8 10 12
96
188
287
SCALE A - DAYS SINCE LAST DEFAUNATION
SCALE B - DAYS SINCE INSTALLATION

FIGURE 16

Short-term colonization of artificial Reef No. 20. The numbers of species and individuals were determined by defaunation or census (defaunations are indicated by open arrows directed downward, and the value determined by defaunation by a symbol specific to each reef). Values determined by census are shown by the same symbols; but in this case, they are connected throughout the observations period. This graph portrays three defaunations and subsequent recolonization over intervals ranging from about 100 to about 200 days. In some instances censuses were conducted within a few days following defaunation; these are plotted on an expanded time abscissa (Scale A). The solid arrow indicates the addition of five empty coral heads in October, 1973.

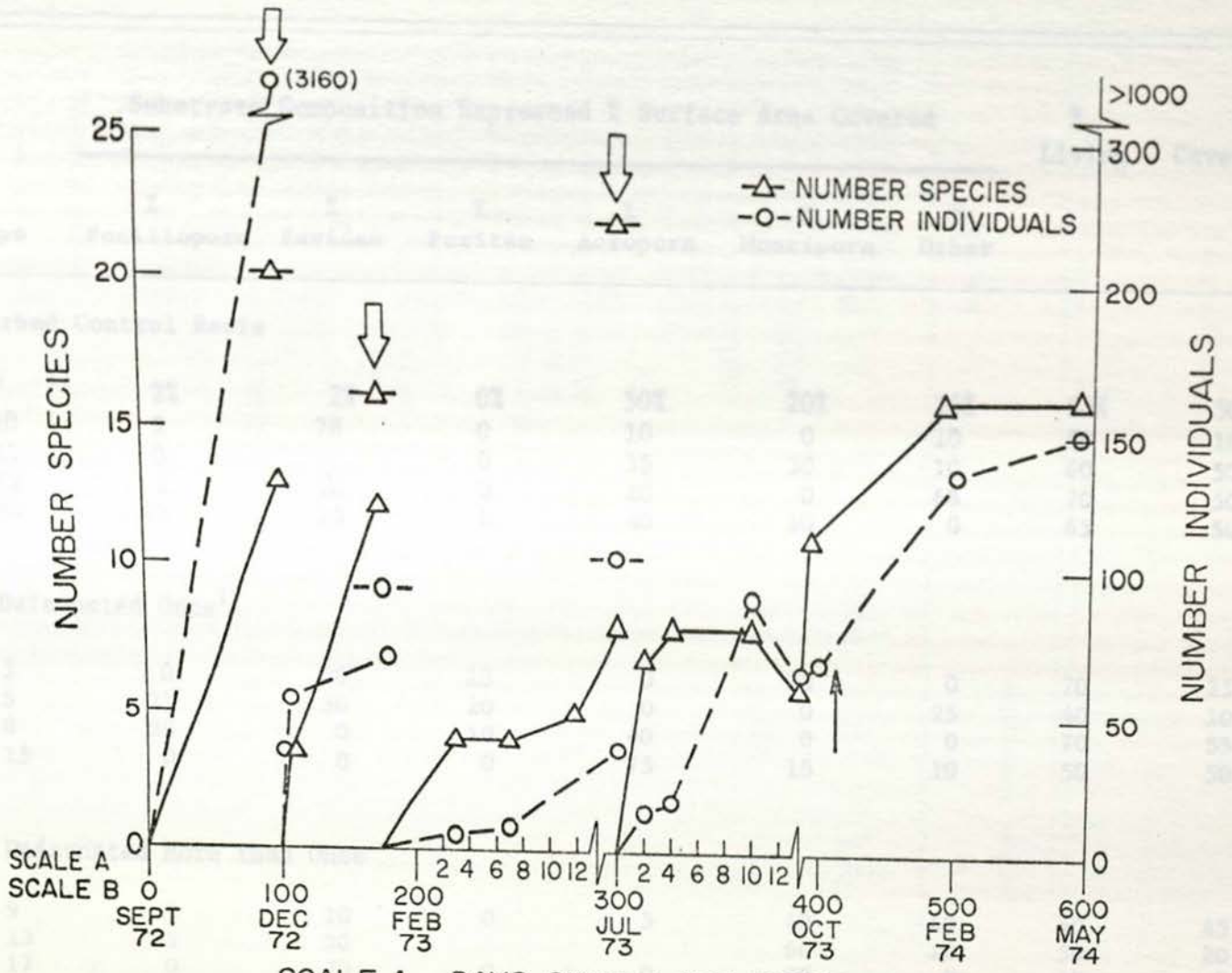

(3160)
>1000
NUMBER SPECIES
NUMBER INDIVIDUALS
NUMBER SPECIES
NUMBER INDIVIDUALS
25
20
15
10
5
0
300
200
150
100
50
0
SCALE A
SCALE B
0
2 4 6 8 10 12
2 4 6 8 10 12
0
100
200
300
400
500
600
SEPT 72
DEC 72
FEB 73
JUL 73
OCT 73
FEB 74
MAY 74
SCALE A - DAYS SINCE LAST DEFAUNATION
SCALE B - DAYS SINCE INSTALLATION

Table 1. Physiography of Natural Reefs

Reef Type	Substrate Composition Expressed % Surface Area Covered						% Living	% Cavernous	Reef Volume in M^3
	% Pocillopora	% Favidae	% Porites	% Acropora	% Montipora	% Other			
Undisturbed Control Reefs									
No. 7	2%	2%	0%	50%	20%	26%	65%	50%	22.3
No. 10	2	78	0	10	0	10	50	10	18.2
No. 11	0		0	35	30	10	60	50	20.5
No. 12	2	10	0	20	0	68	70	50	25.4
No. 30	40	10	0	40	10	0	65	50	--
Reefs Defaunated Once[1]									
No. 3	0	20	10	0	70	0	70	25	15.8
No. 5	25	30	20	0	0	25	40	10	17.4
No. 8	50	0	10	40	0	0	70	55	24.1
No. 15	0	0	0	75	15	10	50	50	12.7
Reefs Defaunated More than Once									
No. 9	5	10	0	5	40	40	40	45	15.3
No. 13	5	30			60	10	50	20	15.0
No. 17	0	20	0	0	80	0	40	0	15.3

[1]Reefs A, B, C, D were defaunated but their locations were lost when a typhoon carried away marker buoys.

Table 2. Precision of census technique. Values are numbers of individuals from replicate censuses on Reef No. 12. Censuses were conducted on 13,14,18, and 20 July 1973.

Species	Replicate Number 1	2	3	4
Abudefduf dicki	1	0	1	1
Chromis caerulea	230	210	230	250
Chromis agilis	2	2	2	1
Pomacentrus coelestis	1	1	1	1
Pomacentrus pavo	111	120	120	140
Pomacentrus nigricans	1	1	1	1
Pomacentrus vaiuli	5	6	6	7
Bodianus axillaris	0	0	1	0
Coris aygula	0	0	2	0
Gomphosus varius	2	2	3	2
Halichoeres hortulanis	1	1	1	1
Halichoeres marginatus	1	0	0	0
Halichoeres trimaculatus	4	6	1	5
Labridae sp.	8	8	8	6
Ecsenius bicolor	1	1	1	1
Apogon novaeguineae	1	6	3	2
Cheilodipterus macrodon	6	8	6	6
Paracirrhites arcatus	4	5	4	3
Flammeo sammara	1	1	0	1
Myripristis murdjan	2	1	2	0
Pterelotris tricolor	1	1	5	6
Oxymonacanthus longirostris	1	1	1	1
Naso lituratus	0	1	0	0
Centropyge flavissimus	2	2	2	2
Chaetodon ephippium	0	0	1	0
Zanclus canescens	0	0	0	1
Total Species	21	20	22	20

Table 3. Roving Fish Assemblage. Abundance of fishes occurring along a 100 m long x 20 m wide inter-reef transect (2000 m^2).

Species	Frequency[1]	Mean No. Individuals/Census with 95% Confidence Limits
BALISTIDAE		
Odonus niger	7	0.9 ± 0.4
CARANGIDAE		
Carangoides ferdau*	5	2.4 ± 2.4
Caranx melampygus*	4	0.8 ± 0.8
LABRIDAE		
Halichoeres trimaculatus	2	0.9 ± 1.7
SCOMBRIDAE		
Grammatorcynus bilineatus*	3	0.2 ± 0.5
LUTJANIDAE		
Aphareus furcatus*	1	0.1 ± 0.2
Pterocaesio tile	1	6.1 ± 3.4
MULLIDAE		
Parupeneus barberinus	8	3.3 ± 2.6
Parupeneus cyclostomus	1	0.6 ± 0.6
Parupeneus pleurostigma	1	0.4 ± 0.9
Parupeneus trifasciatus	1	0.3 ± 0.7
SERRANIDAE		
Epinephelus flavocoeruleus*	4	0.2 ± 0.5
Epinephelus macrospilos*	4	0.4 ± 0.5
CHAETODONTIDAE		
Chaetodon auriga	3	0.6 ± 0.7
SIGANIDAE		
Siganus rostratus	1	0.6 ± 1.4
ACANTHURIDAE		
Acanthurus nigricans	10	19.8 ± 7.0
Acanthurus olivaceous	1	0.1 ± 0.2
Ctenochaetus striatus	1	0.1 ± 0.2
SCARIDAE		
All spp.	6	1.5 ± 1.1

*Piscivores
[1]No. of transects that each species was found on.

Table 4. Rubble and Sand Assemblages. The first two columns represent the number of individuals present on two replicate censuses that were performed on both a rubble and a sand transect (each 50 m long and 10 m wide). The last two columns depict the mean number of individuals per 25 m^2 quadrat.

Species	Number of Individuals Per Census		Mean Number of Individuals Per Quadrat	
	Rubble	Sand	Rubble	Sand
GOBIIDAE				
Amblygobius albimaculatus	0-2	1-1	.002	.002
Eleotrid sp. (white)	4-10	0-15	.014	.015
Eleotroides strigatus	1-2	---	.003	---
Goby sp.	0-2	1-1	.002	.002
Pogonoculis sp. (white)	100-108	50-101	.208	.151
Pogonoculis zebra	20-39	---	.059	---
BRANCHIOSTEGIIDAE				
Malacanthus hoedti	---	0-1	---	.001
Malacanthus latovittatus	0-1	---	.001	---
Malacanthus sp.	24-32	---		.056
BALISTIDAE				
Odonus niger	---	0-1	---	.001
Rhinecanthus aculeatus	1-1	---	.002	---
Sufflamen chrysoptera	1-1	0-1	.002	.001
POMACENTRIDAE				
Abudefduf biocellatus	17-22	---	.039	---
Dascyllus reticulatus*	26-28	1-12	.054	.013
Pomacentrus albofasciatus	1-9	0-2	.010	.002
Pomacentrus coelestis	10-43	---	.053	---
Pomacentrus pavo*	8-8	40-82	.016	.123
Pomacentrus vaiuli	---	0-7	---	.007
BLENNIDAE				
Ecsenius bicolor	1-1	---	.002	---
Plagiotremus tapeinosome	0-3	---	.003	---
LABRIDAE				
Coris gaimard	2-20	---	.022	---
Cheilinus chlorourus	0-2	---	.002	---

Table 4, Cont'd.

Species	Number of Individuals Per Census		Mean Number of Individuals Per Quadrat	
	Rubble	Sand	Rubble	Sand
Cheilinus sp.	---	0-1	---	.001
Halichoeres hoeveni	0-1	---	.001	---
Halichoeres trimaculatus	43-52	19-34	.095	.053
Labroides dimidiatus	2-2	---	.004	---
Macropharyngodon sp.	0-1	---	.001	---
Stethojulis axillaris	15-24	0-1	.039	---
Thalassoma amblycephalus	2-7	---	.009	---
Thalassoma margaritaceous	5-6	---	.011	---
Xyrichthys taeniourus	1-2	---	.003	---
CHAETODONTIDAE				
Chaetodon citrinellus	2-2	---	.004	---
ACANTHURIDAE				
Acanthurus olivaceous	5-8	---	.013	---
Ctenochaetus sp. (white tail)	0-5	---	.005	---
Ctenochaetus striatus	11-12	2-3	.023	.005
PARAPERCIDAE				
Parapercis clathratas	0-3	---	.003	---
CARANGIDAE				
Caranx melampygus	0-2	---	.002	---
CIRRHITIDAE				
Paracirrhites arcatas*	0-3	---	.003	---
MULLIDAE				
Parupeneus cyclostomus	0-1	---	.001	---
Parupeneus pleurostigma	4-4	0-6	.008	.006
SCARIDAE				
All spp.	3-8	---	.011	---
SERRANIDAE				
Epinephelus macrospilos	---	0-1	---	.001
Epinephelus merra*	---	3-4	---	.007

Table 4, Cont'd.

Species	Number of Individuals Per Census		Mean Number of Individuals Per Quadrat	
	Rubble	Sand	Rubble	Sand
LUTJANIDAE				
Monotaxis grandoculis	---	0-1	---	.001
APOGONIDAE				
Apogon novaeguineae	---	200-200	---	.400
Total	---	---	---	---

*These species had individuals that were obviously associated with either dead or living coral heads within the transect. Only those clearly seeking shelter in rubble or sand substrates were computed into the total mean no. individuals/m^2.

Table 5. Patch Reef Assemblage. Frequency and abundance of fishes collected from twelve natural reefs.

Species	Frequency (out of 12 reefs)	$\bar{X}$ No. Ind./Sample (if present)	Abundance Range and Quartiles[1]	Relative Abundance[2] A	C	S
HOLOCENTRIDAE						
Adioryx spinifer	1	1.0	0-0-0-0-1	0	0	1
Flammeo sammara	3	1.7	0-0-0-0-2	0	0	1
Holocentrus diadema	2	1.5	0-0-0-0-2	0	0	1
Holocentrus microstomus	1	1.0	0-0-0-0-1	0	0	1
Holotrachys sp.	1	1.0	0-0-0-0-1	0	0	1
Myripristis argyromus	7	4.7	0-0-1-4-11	1	0	1
Myripristis murdjan	1	1.0	0-0-0-0-1	0	0	1
SYNGNATHIDAE						
Corythoichthys flavofasciatus	3	3.0	0-0-0-0-4	0	0	1
Corythoichthys nigripectis	6	1.7	0-0-0-0-3	0	0	3
Doryrhamphus melanopleura	6	2.0	0-0-0-1-4	0	0	3
SCORPAENIDAE						
Sebastipistes sp.	1	1.0	0-0-0-0-1	0	0	1
Scorpanodes guamensis	1	1.0	0-0-0-0-1	0	0	1
Scorpanodes hirsutus	4	1.0	0-0-0-1-2	0	0	1
Scorpanodes kellogi	4	1.3	0-0-0-1-2	0	0	1
Scorpanodes parvippinus	1	1.0	0-0-0-0-1	0	0	1
Taenionotus triacanthus	4	1.0	0-0-0-1-1	0	0	4
SOLEIDAE						
Aseraggodes sp. (cf. *smithi*)	1	1.0	0-0-0-0-1	0	0	1
SERRANIDAE						
Cephalopholis leopardus	3	2.0	0-0-0-0-3	0	0	1

Table 5, Cont'd.

Species	Frequency (out of 12 reefs)	$\bar{X}$ No. Ind./Sample (if present)	Abundance Range and Quartiles[1]	Relative Abundance[2] A	C	S
Cephalopholis urodelus	4	1.3	0-0-0-1-2	0	0	4
Epinephelus macrospilos	1	1.0	0-0-0-0-1	0	0	1
Epinephelus merra	2	1.0	0-0-0-0-1	0	0	1
APOGONIDAE						
Apogon erythrinus	10	3.1	0-1-2-4-8	0	2	1
Apogon exostigma	9	51.2	0-0-6-31-310	2	3	1
Apogon gracilis	7	328.9	0-0-0-255-824	4	0	1
Apogon novaeguineae	11	57.6	0-12-35-62-200	3	5	0
Apogon savayensis	2	1.5	0-0-0-0-2	0	0	1
Cheilodipterus macrodon	4	3.3	0-0-0-6-420	0	1	2
Paramia quinquelineata	4	1.5	0-0-0-1-2	0	1	2
Apogon robustus	1	1.0	0-0-0-0-1	0	0	1
CHAETODONTIDAE						
Chaetodon auriga	1	2.0	0-0-0-0-2	0	0	0
Chaetodon citrinellus	2	1.0	0-0-0-0-1	0	0	2
Chaetodon miliaris	1	1.0	0-0-0-0-1	0	0	1
Chaetodon trifasciatus	4	1.3	0-0-0-1-2	0	0	2
Chaetodon reticulatus	1	1.0	0-0-0-0-1	0	0	1
POMACANTHIDAE						
Centropyge flavissimus	6	2.2	0-0-0-1-5	0	1	1
Pygoplites diacanthus	1	1.0	0-0-0-0-1	0	0	1
POMACENTRIDAE						
Abudefduf curacao	1	3.0	0-0-0-0-3	0	0	0
Abudefduf dicki	2	1.5	0-0-0-0-2	0	0	1
Abudefduf leucozona	1	3.0	0-0-0-0-3	0	0	0

Table 5, Cont'd.

Species	Frequency (out of 12 reefs)	$\bar{X}$ No. Ind./Sample (if present)	Abundance Range and Quartiles[1]	Relative Abundance[2] A	C	S
Amphiprion melanopus	1	1.0	0-0-0-0-1	0	0	1
Chromis caerulea	10	16.8	0-3-12-19-54	2	2	0
Chromis dimidiatus	2	2.0	0-0-0-0-2	0	0	0
Chromis ternatensis	1	1.0	0-0-0-0-1	0	0	1
Dascyllus aruanus	3	5.0	0-0-0-1-10	1	0	1
Dascyllus reticulatus	8	3.3	0-0-1-3-8	1	0	1
Dascyllus trimaculatus	1	1.0	0-0-0-0-1	0	0	1
Pomacentrus coelestis	1	52.0	0-0-0-0-52	0	0	0
Pomacentrus nigricans	5	2.6	0-0-0-2-5	0	1	0
Pomacentrus pavo	12	33.5	0-6-20-35-71	6	0	1
Pomacentrus vaiuli	11	6.9	0-3-5-7-15	2	4	0
LABRIDAE						
Bodianus sp.	1	1.0	0-0-0-0-1	0	0	1
Cheilinus chlorourus	1	1.0	0-0-0-0-1	0	0	1
Cheilinus trilobatus	1	1.0	0-0-0-0-1	0	0	1
Coris variegata	2	1.0	0-0-0-0-1	0	0	2
Gomphosus varius	5	1.2	0-0-0-1-2	0	0	2
Halichoeres bimaculatus	1	1.0	0-0-0-0-1	0	0	1
Halichoeres trimaculatus	9	5.1	0-0-3-5-15	1	2	2
Pseudocheilinus hexataenia	2	1.5	0-0-0-0-2	0	0	1
Stethojulis axillaris	1	1.0	0-0-0-0-1	0	0	1
Thalassoma amblycephalus	3	7.0	0-0-0-0-19	0	1	2
Thalassoma lutescens	5	1.8	0-0-0-1-4	0	0	2
Wetmorella ocellata	3	1.0	0-0-0-0-1	0	0	3
BLENNIDAE						
Ecsenius bicolor	11	5.7	0-1-7-8-10	0	1	3

Table 5, Cont'd.

Species	Frequency (out of 12 reefs)	$\bar{X}$ No. Ind./Sample (if present)	Abundance Range and Quartiles[1]	Relative Abundance[2] A	C	S
Meiacanthus atrodorsalis	1	3.0	0-0-0-0-3	0	0	0
Plagiotremus tapeniosoma	2	1.0	0-0-0-0-1	0	0	1
ACANTHURIDAE						
Acanthurus elongatus	1	1.0	0-0-0-0-1	0	0	1
Acanthurus nigricans	1	1.0	0-0-0-0-1	0	0	1
Ctenochaetus binotatus	1	1.0	0-0-0-0-1	0	0	0
Ctenochaetus striatus	7	4.4	0-0-1-1-12	0	1	3
Naso lituratus	1	1.0	0-0-0-0-1	0	0	1
Zebrasoma veliferum	1	1.0	0-0-0-0-1	0	0	1
CANTHIGASTERIDAE						
Canthigaster solandri	3	1.0	0-0-0-0-1	0	0	3
GOBIIDAE						
Acentrogobius sp. (cf. *decoratus*)	6	2.2	0-0-0-1-6	0	0	3
Callogobius sp. 8 (cf. *sclateri*)	3	1.0	0-0-0-0-1	0	0	3
Eleotroides sp. 18	1	2.0	0-0-0-0-2	0	0	0
Eviota distigma	11	12.7	0-3-5-21-28	2	4	0
Eviota sebreii	10	6.7	0-1-2-8-23	0	1	2
Eviota smaragdus	8	10.3	0-0-2-6-31	1	1	0
Gnatholepis anjerensis	1	1.0	0-0-0-0-1	0	0	1
Gobiodon sp. A	4	3.3	0-0-0-2-6	0	1	0
Paragobiodon echinocephalus	9	6.1	0-0-3-5-14	1	2	1
Paragobiodon lacunicola	1	1.0	0-0-0-0-1	0	0	1
Paragobiodon xanthosoma	5	1.6	0-0-0-1-3	0	0	2
Paragobiodon sp. 17	5	2.0	0-0-0-1-3	0	0	2
Pterelotris tricolor	1	2.0	0-0-0-0-2	0	0	0
Trimma caesiura	6	4.0	0-0-0-4-8	1	1	1

Table 5, Cont'd.

Species	Frequency (out of 12 reefs)	$\bar{X}$ No. Ind./Sample (if present)	Abundance Range and Quartiles[1]	Relative Abundance[2] A	C	S
SYNODONTIDAE						
Synodus gracilis	1	2.0	0-0-0-0-2	0	0	1
Synodus variegatus	3	1.3	0-0-0-0-2	0	0	2
CALLIONYMIDAE						
Synchiropus sp.	5	2.2	0-0-0-1-5	0	0	2
CARACANTHIDAE						
Caracanthus unipinnus	4	1.5	0-0-0-1-2	0	0	2
BROTULIDAE						
Dienmatichthys iluocoetiodes	4	1.5	0-0-0-1-2	0	0	2
SCARIDAE						
Scarus unimaculatus	1	1.0	0-0-0-0-1	0	0	1
PLEURONECTIDAE						
Bothus mancus	1	1.0	0-0-0-0-1	0	0	1
Pleuronectid sp. 1	5	1.0	0-0-0-0-1	0	0	1
GERREIDAE						
Gerres elongatus	1	1.0	0-0-0-0-1	0	0	1
MULLIDAE						
Parupeneus barberinus	2	1.5	0-0-0-0-2	0	0	1
Parupeneus pleurostigma	2	1.0	0-0-0-0-1	0	0	2
PLATYCEPHALIDAE						
Thysanophrys arenicola	4	1.0	0-0-0-0-1	0	0	1
LUTJANIDAE						
Lethrinus variegatus	1	1.0	0-0-0-0-1	0	0	1

Table 5, Cont'd

Species	Frequency (out of 12 reefs)	$\bar{X}$ No. Ind./Sample (if present)	Abundance Range and Quartiles[1]	Relative Abundance[2] A	C	S
Trimma eviotops	2	2.0	0-0-0-0-2	0	0	0
Gobiodon sp. B	1	3.0	0-0-0-0-3	0	0	0
Eviota nebulosa	10	14.6	0-6-10-18-22	4	0	0
Gobiidae sp. 15	1	1.0	0-0-0-0-1	0	0	1
Gobiidae sp. 20	5	6.0	0-0-0-5-11	0	2	0
Gobiidae sp. 21	2	1.0	0-0-0-0-1	0	0	1
Gobiidae sp. 22	2	2.0	0-0-0-0-2	0	0	0
OPHICHTIDAE						
Leiuranus semicinctus	1	1.0	0-0-0-0-1	0	0	1
Callechelys marmoratus	1	1.0	0-0-0-0-1	0	0	1
ECHELIDAE						
Muraenichthys gymnotus	4	1.8	0-0-0-1-3	0	0	2
MURAENIDAE						
Enchelycore bayeri	2	1.0	0-0-0-0-1	0	0	2
Gymnothorax buroensis	7	2.0	0-0-12-2-4	0	1	3
Gymnothorax meleagris	2	1.0	0-0-0-0-1	0	0	1
Gymnothorax zonipectis	1	1.0	0-0-0-0-1	0	0	1
MORINGUIDAE						
Moringua sp.	2	1.5	0-0-0-0-2	0	0	1
Myrophis uropterus	1	1.0	0-0-0-0-1	0	0	1
GRAMMISTIDAE						
Grammistops ocellatus	10	2.7	0-1-1-3-7	0	1	4
CIRRHITIDAE						
Paracirrhites arcatas	6	2.3	0-0-0-2-6	1	0	2

Table 5, Cont'd.

Species	Frequency (out of 12 reefs)	$\bar{X}$ No. Ind./Sample (if present)	Abundance Range and Quartiles[1]	Relative Abundance[2] A	C	S
MONACANTHIDAE						
Oxymonacanthus longirostris	2	1.5	0-0-0-0-2	0	0	1
OSTRACIODONTIDAE						
Ostracion cubicus	1	1.0	0-0-0-0-1	0	0	1
MICRODESMIDAE						
Gunnelichthys unimaculatus	2	3.0	0-0-0-0-4	0	0	0
TRYPTERYGIIDAE						
Trypterygiidae sp. 1	11	3.9	0-2-3-4-6	0	0	1
Trypterygiidae sp. 2	10	2.3	0-1-2-4-5	0	0	1

[1]Values in the first and last columns represent the range in number of individuals collected on the twelve natural reef defaunations. The second column represents the 2nd quartile (25% of the samples contained fewer individuals than the value listed); the third column, the 3rd percentile; and the fourth column, the 4th percentile.

[2]Relative Abundance was scored by categories. In each of the 12 samples the species were listed in decreasing order by number of individuals until a sum equal to half the total was reached--these were then classified as Abundant (A). This process was continued until 75% of the total individuals were summed resulting in the category Common (C). Species occurring only as single individuals were termed Single (S).

Table 6. Patch Reef Assemblage Structure Based on Biomass of Poisoned Samples. Means and ranges of fish families are expressed as percent total wet biomass. The first column depicts the minimum weight; the second column the mean, and the third the maximum.

Family	Reef No. 3,5,8,9,13,15,17	Reefs B,C,D[1]	Mean All Reefs
Angulliforme	0-15.7-43	0-7.3-16	12.3
Labridae	0-6.7-15	0-0-0	4.0
Serranidae	0-16.8-34	0-8.0-16	13.3
Apogonidae	3-11.2-42	38-45.5-57	24.9
Pomacentridae	0-10.0-17	3-17.5-32	13.0
Scorpaenidae	0-0.3-2	0-0.8-3	0.5
Chaetodontidae	0-2.8-14	0-0.5-2	1.9
Pomacanthidae	0-3.0-9	0-2.0-7	2.6
Blennidae	0-0.7-3	0-1.3-2	0.9
Cirrhitidae	0-0.8-3	0-0-0	0.5
Holocentridae	3-13.3-32	0-9.3-23	11.7
Other	3-5.5-12	2-8.5-16	6.7
Total Mass in Grams	354-975.2-2248	486-1019.0-1593	992.7

[1]These reefs are treated separately because of the large numbers of juvenile Apogon gracilis they supported.

Table 7. Patch Reef Assemblage Structure Based on Family Biomass Rank. Data compiled from Table 6.

Rank	1-3	4-6	7-9	10-12	None Present
Anguilliforme	4	1	2	-	3
Labridae	1	4	-	-	5
Serranidae	6	1	1	-	2
Apogonidae	4	3	2	-	-
Pomacentridae	4	4	1	-	1
Scorpaenidae	-	1	1	-	8
Chaetodontidae	1	-	2	1	6
Pomacanthidae	-	2	3	1	4
Blennidae	-	2	2	2	4
Cirrhitidae	-	-	2	-	8
Holocentridae	5	4	-	-	1
Acanthuridae	2	-	-	-	8
Other	2	4	4	-	-

Table 8. Number of Species, Individuals, and Wet Biomass (in grams) of Twelve Natural Study Reefs. Ranks are shown in parentheses.

Reef	Number Species	Number Individuals	Biomass
9	26 (1)	597 (10)	398 (3)
13	29 (2)	179 (2)	210 (1)
3	31 (3.5)	138 (1)	800 (6)
15	31 (3.5)	185 (3)	354 (2)
17	32 (5)	397 (8)	429 (4)
10	40 (6)	247 (5)	- -
A	41 (7)	334 (7)	486 (5)
D	42 (8)	762 (11)	1593 (9)
B	43 (9)	1514 (12)	889 (7)
5	47 (10)	189 (4)	1622 (10)
C	48 (11)	568 (9)	1107 (8)
8	61 (12)	318 (6)	2248 (11)

Table 9. Nocturnal Fauna of the Patch Reef Assemblage. The frequency, range, and mean number of individuals is presented for nine nighttime reef censuses. Mean number of individuals is based only on samples in which the species was present. Asterisks denote species in which at least one individual was inactive when observed, and pluses indicate species known to feed at night.

Species	% Frequency of Occurrence	Range	Number of Individuals Mean
Acanthurus nigricans*	89	0-30	0.4
Adioryx microstomus+	11	0-1	1.0
Adioryx spinifer+	44	0-2	1.8
Flammeo opercularis+	33	0-1	1.0
Flammeo sammara+	11	0-1	1.0
Holocentrus diadema+	44	0-1	1.3
Myripristis murdjan+	66	0-50	2.3
Apogon exostigma+	22	0-6	2.7
Apogon novaeguineae+	11	0-50	50.0
Apogon savayensis+	33	0-2	2.0
Apogon sp.+	11	0-3	2.5
Cheilodipterus macrodon+	56	0-2	1.6
Paramia quinquelineata+	22	0-100	50.0
Carangoides ferdau	11	0-50	50.0
Aphareus furcatas	11	0-1	1.0
Lethrinus sp.	11	0-1	1.0
Pterecaesio tile*	11	0-3	3.0
Scarus sp. 1*	11	0-1	1.0
Scarus sp. 2*	11	0-1	1.0
Cheilinus chlorourus*	11	0-1	1.0
Chaetodon auriga	11	0-1	1.0
Chaetodon citrinellus	11	0-1	1.0
Ctenochaetus striatus	22	0-1	1.0
Epinephelus merra	22	0-1	1.0

TABLE 10

Invasions and Extinctions on Reef No. 7 (Control. (+) indicates the appearance of a species; (-) indicates its subsequent extinction. An arrow portrays the last date the species was recorded.

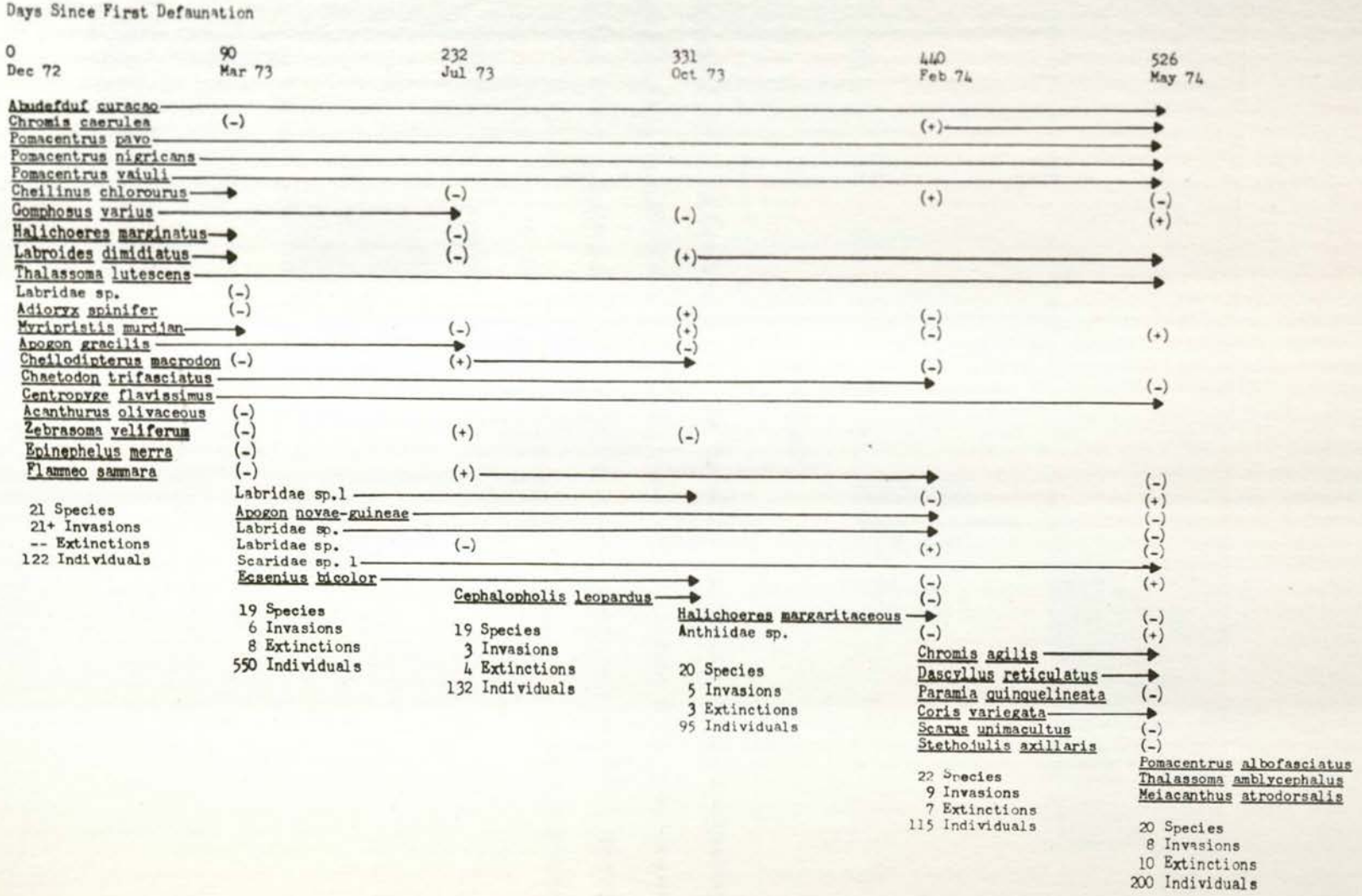

Days Since First Defaunation
0
Dec 72
90
Mar 73
232
Jul 73
331
Oct 73
440
Feb 74
526
May 74
Abudefduf curacao
Chromis caerulea
Pomacentrus pavo
Pomacentrus nigricans
Pomacentrus vaiuli
Cheilinus chlorourus
Gomphosus varius
Halichoeres marginatus
Labroides dimidiatus
Thalassoma lutescens
Labridae sp.
Adioryx spinifer
Myripristis murdjan
Apogon gracilis
Cheilodipterus macrodon
Chaetodon trifasciatus
Centropyge flavissimus
Acanthurus olivaceous
Zebrasoma veliferum
Epinephelus merra
Flammeo sammara
21 Species
21+ Invasions
-- Extinctions
122 Individuals
Labridae sp.1
Apogon novae-guineae
Labridae sp.
Labridae sp.
Scaridae sp. 1
Ecsenius bicolor
19 Species
6 Invasions
8 Extinctions
550 Individuals
Cephalopholis leopardus
19 Species
3 Invasions
4 Extinctions
132 Individuals
Halichoeres margaritaceous
Anthiidae sp.
20 Species
5 Invasions
3 Extinctions
95 Individuals
Chromis agilis
Dascyllus reticulatus
Paramia quinquelineata
Coris variegata
Scarus unimacultus
Stethojulis axillaris
22 Species
9 Invasions
7 Extinctions
115 Individuals
Pomacentrus albofasciatus
Thalassoma amblycephalus
Meiacanthus atrodorsalis
20 Species
8 Invasions
10 Extinctions
200 Individuals

TABLE 11

Invasions and Extinctions on Reef No. 10 (Control). (+) indicates the appearance of a species; (-) indicates its subsequent extinction. An arrow portrays the last date a species was recorded. An * indicates defaunation.

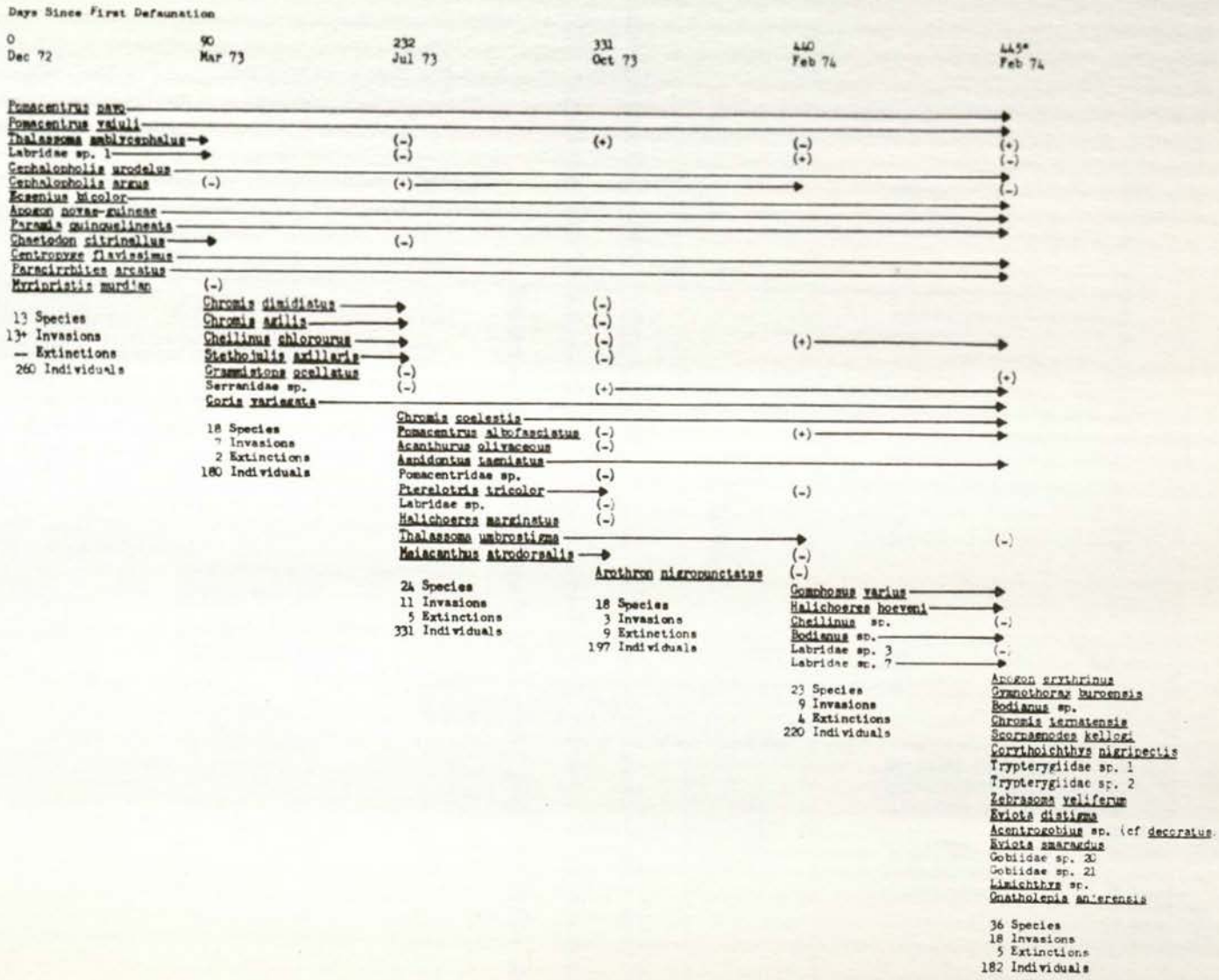

Days Since First Defaunation
0
Dec 72
90
Mar 73
232
Jul 73
331
Oct 73
440
Feb 74
445*
Feb 74
Pomacentrus nagu
Pomacentrus vaiuli
Thalassoma amblycephalus
Labridae sp. 1
Cephalopholis urodelus
Cephalopholis argus
Ecsenius bicolor
Apogon novae-guineae
Paramia quinquelineata
Chaetodon citrinellus
Centropyge flavissimus
Paracirrhites arcatus
Myripristis murdjan
13 Species
13+ Invasions
— Extinctions
260 Individuals
Chromis dimidiatus
Chromis agilis
Cheilinus chlorourus
Stethojulis axillaris
Grammistops ocellatus
Serranidae sp.
Coris variegata
18 Species
7 Invasions
2 Extinctions
180 Individuals
Chromis caerulea
Pomacentrus albofasciatus
Acanthurus olivaceous
Aspidontus taeniatus
Pomacentridae sp.
Pterelotris tricolor
Labridae sp.
Halichoeres marginatus
Thalassoma umbrostigma
Naiacanthus strodorsalis
Arothron nigropunctatus
24 Species
11 Invasions
5 Extinctions
331 Individuals
18 Species
3 Invasions
9 Extinctions
197 Individuals
Gomphosus varius
Halichoeres hoeveni
Cheilinus sp.
Bodianus sp.
Labridae sp. 3
Labridae sp. 7
23 Species
9 Invasions
4 Extinctions
220 Individuals
Apogon erythrinus
Gymnothorax buroensis
Bodianus sp.
Chromis iomatensis
Scorpaenodes kelloei
Corythoichthys nigripectis
Trypterygiidae sp. 1
Trypterygiidae sp. 2
Zebrasoma veliferum
Eviota distigma
Acentrogobius sp. (cf decoratus
Eviota smaragdus
Gobiidae sp. 20
Gobiidae sp. 21
Limnichthys sp.
Gnatholepis anderensis
36 Species
18 Invasions
5 Extinctions
182 Individuals

TABLE 12

Invasions and Extinctions on Reef No. 11 (Control). (+) indicates the appearance of a species; (-) indicates its subsequent extinction. An arrow portrays the last date a species was recorded.

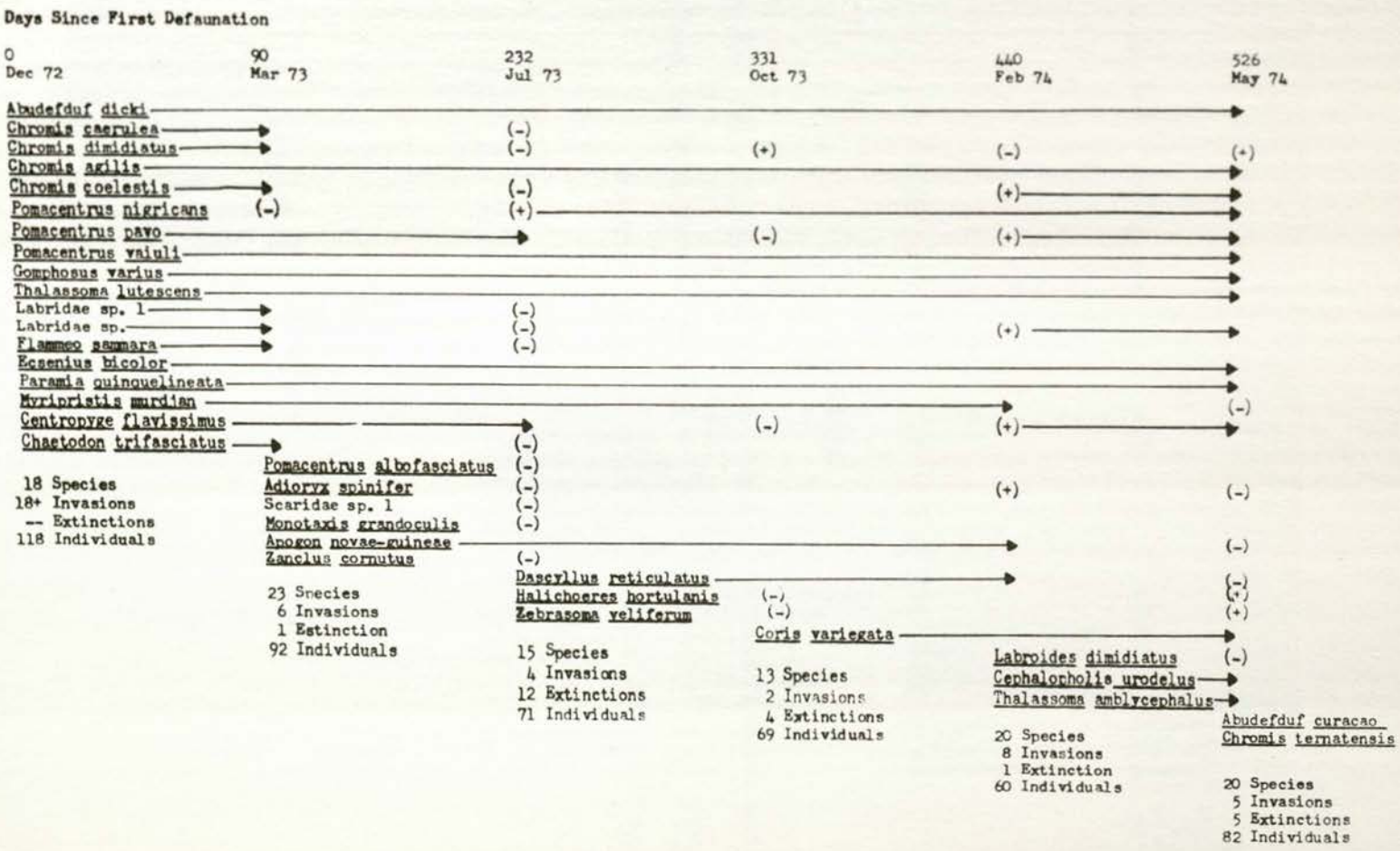

Days Since First Defaunation
0
Dec 72
90
Mar 73
232
Jul 73
331
Oct 73
440
Feb 74
526
May 74
Abudefduf dicki
Chromis caerulea
Chromis dimidiatus
Chromis agilis
Chromis coelestis
Pomacentrus nigricans
Pomacentrus pavo
Pomacentrus vaiuli
Gomphosus varius
Thalassoma lutescens
Labridae sp. 1
Labridae sp.
Flammeo sammara
Ecsenius bicolor
Paramia quinquelineata
Myripristis murdjan
Centropyge flavissimus
Chaetodon trifasciatus
18 Species
18+ Invasions
-- Extinctions
118 Individuals
Pomacentrus albofasciatus
Adioryx spinifer
Scaridae sp. 1
Monotaxis grandoculis
Anogon novae-guineae
Zanclus cornutus
23 Species
6 Invasions
1 Extinction
92 Individuals
Dascyllus reticulatus
Halichoeres hortulanis
Zebrasoma veliferum
15 Species
4 Invasions
12 Extinctions
71 Individuals
Coris variegata
13 Species
2 Invasions
4 Extinctions
69 Individuals
Labroides dimidiatus
Cephalopholis urodelus
Thalassoma amblycephalus
20 Species
8 Invasions
1 Extinction
60 Individuals
Abudefduf curacao
Chromis ternatensis
20 Species
5 Invasions
5 Extinctions
82 Individuals

TABLE 13

Invasions and Extinctions on Reef No. 12 (Control). (+) indicates the appearance of a species; (-) indicates its subsequent extinction. An arrow portrays the last date a species was recorded.

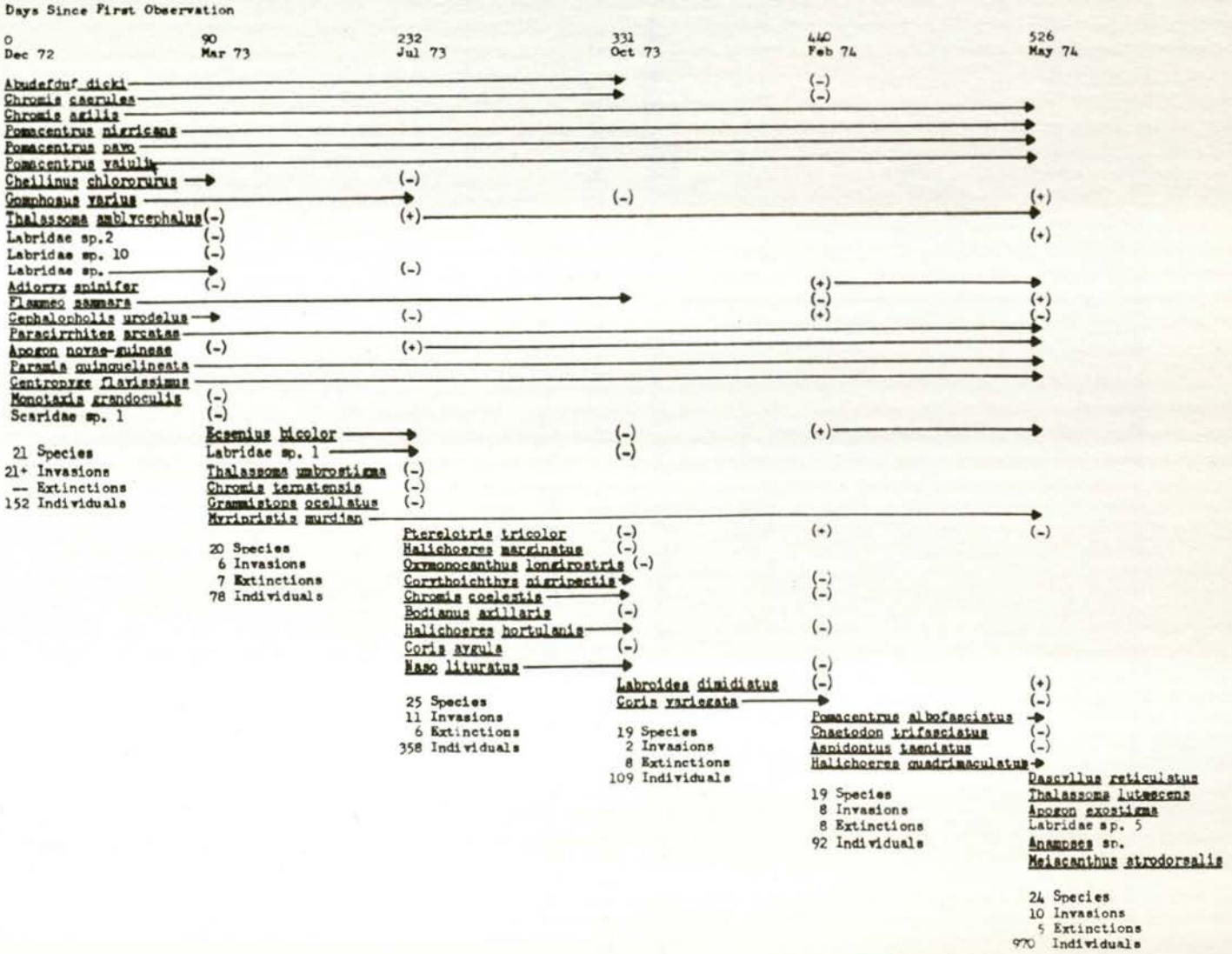

Days Since First Observation
0
Dec 72
90
Mar 73
232
Jul 73
331
Oct 73
440
Feb 74
526
May 74
Abudefduf dicki
Chromis caerulea
Chromis agilis
Pomacentrus nigricans
Pomacentrus pavo
Pomacentrus vaiuli
Cheilinus chlorourus
Gomphosus varius
Thalassoma amblycephalus
Labridae sp.2
Labridae sp. 10
Labridae sp.
Adiorrx spinifer
Flammeo sammara
Cephalopholis urodelus
Paracirrhites arcatus
Apogon novae-guineae
Paramia quinquelineata
Centropyge flavissimus
Monotaxis grandoculis
Scaridae sp. 1
21 Species
21+ Invasions
— Extinctions
152 Individuals
Scarus sordidus
Labridae sp. 1
Thalassoma umbrostigma
Chromis ternatensis
Grammistops ocellatus
Myripristis murdjan
20 Species
6 Invasions
7 Extinctions
78 Individuals
Pterelotris tricolor
Halichoeres margaritaceus
Oxymonocanthus longirostris
Corythoichthys nigripectis
Chromis coelestis
Bodianus axillaris
Halichoeres hortulanus
Coris aygula
Naso lituratus
25 Species
11 Invasions
6 Extinctions
358 Individuals
Labroides dimidiatus
Coris variegata
19 Species
2 Invasions
8 Extinctions
109 Individuals
Pomacentrus albofasciatus
Chaetodon trifasciatus
Aspidontus taeniatus
Halichoeres quadrimaculatus
19 Species
8 Invasions
8 Extinctions
92 Individuals
Dascyllus reticulatus
Thalassoma lutescens
Apogon exostigma
Labridae sp. 5
Anampses sp.
Meiacanthus atrodorsalis
24 Species
10 Invasions
5 Extinctions
970 Individuals

TABLE 14

Invasions and Extinctions on Reef No. 30 (Control). (+) indicates the appearance of a species; (-) indicates its subsequent extinction. An arrow portrays the last date a species was recorded.

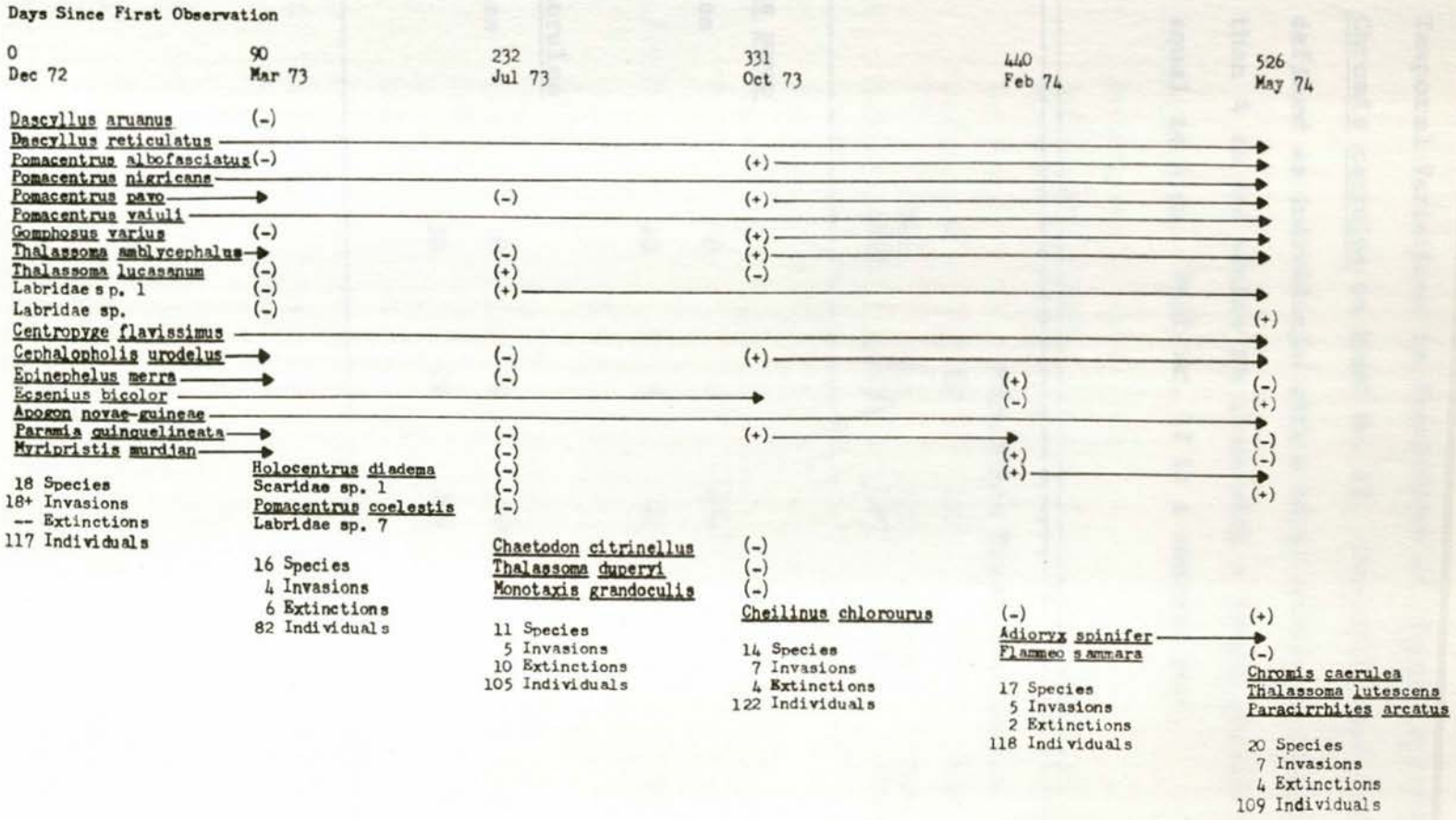

Days Since First Observation
0
Dec 72
90
Mar 73
232
Jul 73
331
Oct 73
440
Feb 74
526
May 74
Dascyllus aruanus
Dascyllus reticulatus
Pomacentrus albofasciatus
Pomacentrus nigricans
Pomacentrus pavo
Pomacentrus vaiuli
Gomphosus varius
Thalassoma amblycephalus
Thalassoma lucasanum
Labridae sp. 1
Labridae sp.
Centropyge flavissimus
Cephalopholis urodelus
Epinephelus merra
Ecsenius bicolor
Apogon novae-guineae
Paramia quinquelineata
Myripristis murdjan
18 Species
18+ Invasions
-- Extinctions
117 Individuals
Holocentrus diadema
Scaridae sp. 1
Pomacentrus coelestis
Labridae sp. 7
16 Species
4 Invasions
6 Extinctions
82 Individuals
Chaetodon citrinellus
Thalassoma duperyi
Monotaxis grandoculis
11 Species
5 Invasions
10 Extinctions
105 Individuals
Cheilinus chlorourus
14 Species
7 Invasions
4 Extinctions
122 Individuals
Adioryx spinifer
Flammeo sammara
17 Species
5 Invasions
2 Extinctions
118 Individuals
Chromis caerulea
Thalassoma lutescens
Paracirrhites arcatus
20 Species
7 Invasions
4 Extinctions
109 Individuals

Table 15. Temporal Variations in Populations of Pomacentrus pavo and Chromis caerulea on Reef No. 12. Juveniles were arbitrarily defined as individuals with a total estimated length less than 4 cm and adults as those with a length greater than or equal to 4 cm. Reef No. 12 is a control reef.

	Days Since First Observation					
	0	90	232	331	440	526
	Dec. 1972	Mar. 1973	Jul. 1973	Oct. 1973	Feb. 1974	May 1974
Pomacentrus pavo						
Juveniles	0	2	100	23	0	44
Adults	40	8	20	6	15	1
Chromis caerulea						
Juveniles	0	0	50	1	0	0
Adults	30	26	200	12	0	0

Table 16. Manipulations of Study Reefs. All reefs were censused (2 replicates) Sept., Dec. 72; Mar., Jul., Oct., 73; Feb., May, Oct., 74. Control reefs (No. 7,10,11,12,30), as well as natural defaunated and artificial reefs were censused.

Defaunated Natural Reefs

Reef No. 3	Defaunated 2 Sept. 1972.
Reef No. 5	Defaunated 2 Sept. 72 and 11 May 74; five heads with pedistals installed 29 Oct. 73.
Reef No. 8	Defaunated 2 Sept. 72 and 12 Feb. 74.
Reef No. 9	Defaunated 24 Aug. 72, 30 Nov. 72, 23 Feb. 73, 9 July 73, 15 Feb. 74.
Reef No. 13	Defaunated 25 Aug. 72, 30 Nov. 72, 23 Feb. 73, 11 May 74; caged 6 Mar. 73.
Reef No. 15	Defaunated 25 Aug. 72 and 9 July 73.
Reef No. 17	Defaunated 2 Sept. 72, 29 Nov. 72, 23 Feb. 73, 6 July 73, 6 Oct. 73.

Artificial Reefs

Reef No. 2	Installed 17 May 72; 10 uninhabited coral heads added 23 Oct. 73.
Reef No. 4	Installed 17 May 72; 10 uninhabited coral heads added 23 Oct. 73; of these seven remained until Feb. 74, four until May 74 and 2 until Oct. 74.
Reef No. 6	Installed 17 May 72. Defaunated 4 Feb. 74. Combined with Reef No. 18 (at the site of No. 16) on 5 Feb. 74.
Reef No. 16	Defaunated 2 Sept. 72, 23 Feb. 73, 6 Jul. 73, 6 Oct. 73.
Reef No. 18	Installed 22 Aug. 72, defaunated 4 Feb. 74. Combined with Reef No. 6 5 Feb. 74. Two living coral heads added 12 Oct. 74.
Reef No. 19	Installed 15 Aug. 72. Defaunated 29 Nov. 72, 23 Feb. 73, 7 July 73. Added two heads with fish 14 Oct. 73.
Reef No. 20	Installed 25 Aug. 73. Defaunated 29 Nov. 72, 23 Feb. 73, 7 July 73. Five empty heads added 29 Oct. 73.
Reef No. 21	Installed 23 Aug. 74. Defaunated 12 Oct. 74. Two living coral heads added 12 Oct. 74.
Reef No. 22	Installed 23 Aug. 72. Defaunated 19 Oct. 73. Five coral heads with resident fishes added 22 Oct. 73. 5 heads added 23 Oct. 73.

TABLE 17

Invasions and Extinctions on Reef No. 3 (Natural Defaunation Reef). (+) indicates the appearance of a species; (-) indicates its subsequent extinction. An arrow indicates the last date a species was recorded.

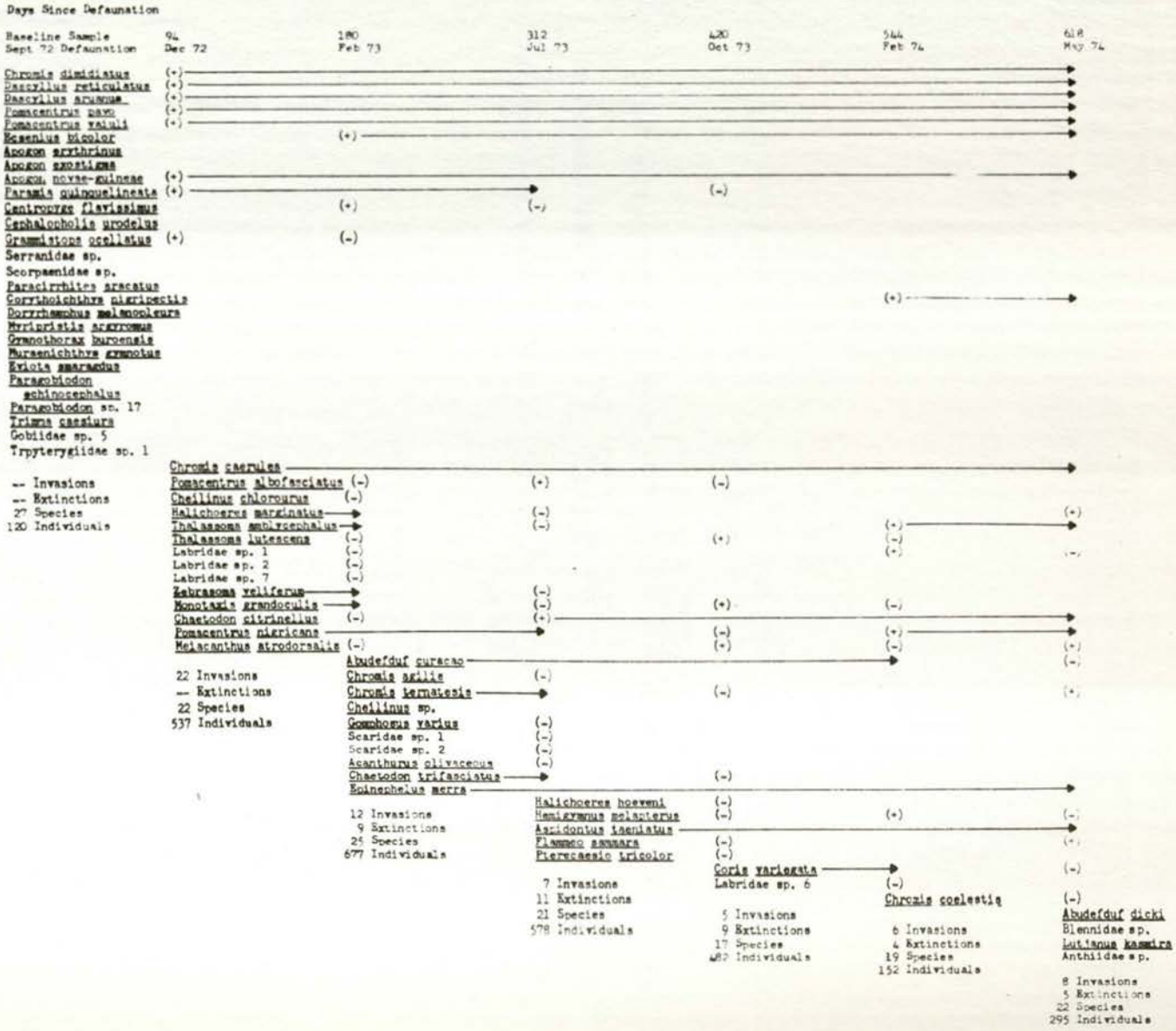

Days Since Defaunation
Baseline Sample
Sept 72 Defaunation
94
Dec 72
180
Feb 73
312
Jul 73
420
Oct 73
544
Feb 74
618
May 74
Chromis dimidiatus
Dascyllus reticulatus
Dascyllus aruanus
Pomacentrus pavo
Pomacentrus vaiuli
Acanthurus bicolor
Apogon erythrinus
Apogon exostigma
Apogon novae-guineae
Paramia quinquelineata
Centropyge flavissimus
Cephalopholis urodelus
Grammistops ocellatus
Serranidae sp.
Scorpaenidae sp.
Paraclinitis aracatus
Corythoichthys nigripectis
Dorrychamphus melanopleura
Myripristis argyromus
Ornonhorax barbensis
Murenichthys xanthotus
Exiqua amaranthus
Paragobiodon echinocephalus
Paragobiodon sp. 17
Trimma cassiura
Gobiidae sp. 5
Trpyterygiidae sp. 1
-- Invasions
-- Extinctions
27 Species
120 Individuals
Chromis caerulea
Pomacentrus albofasciatus
Cheilinus chlorourus
Halichoeres marginatus
Thalassoma amblycephalus
Thalassoma lutescens
Labridae sp. 1
Labridae sp. 2
Labridae sp. 7
Zebrasoma veliferum
Monotaxis grandoculis
Chaetodon citrinellus
Pomacentrus nigricans
Melacanthus atrodorsalis
Abudefduf curacao
Chromis agilis
Chromis ternatensis
Cheilinus sp.
Gomphosus varius
Scaridae sp. 1
Scaridae sp. 2
Acanthurus olivaceous
Chaetodon trifasciatus
Epinephelus merra
22 Invasions
-- Extinctions
22 Species
537 Individuals
Halichoeres hoeveni
Hemigymnus melapterus
Aaxidontus taeniatus
Flammeo sammara
Pterocaesio trilcolor
12 Invasions
9 Extinctions
25 Species
677 Individuals
Coris variegata
Labridae sp. 6
7 Invasions
11 Extinctions
21 Species
578 Individuals
Chromis coelestis
5 Invasions
9 Extinctions
17 Species
482 Individuals
Abudefduf dicki
Blennidae sp.
Lutianus kasmira
Anthiidae sp.
6 Invasions
4 Extinctions
19 Species
152 Individuals
8 Invasions
5 Extinctions
22 Species
295 Individuals

TABLE 18

Invasions and Extinctions on Reef No. 5 (Natural Defaunation Reef). (+) indicates the appearance of a species, (-) indicates its subsequent extinction. An arrow indicates the last date a species was recorded.

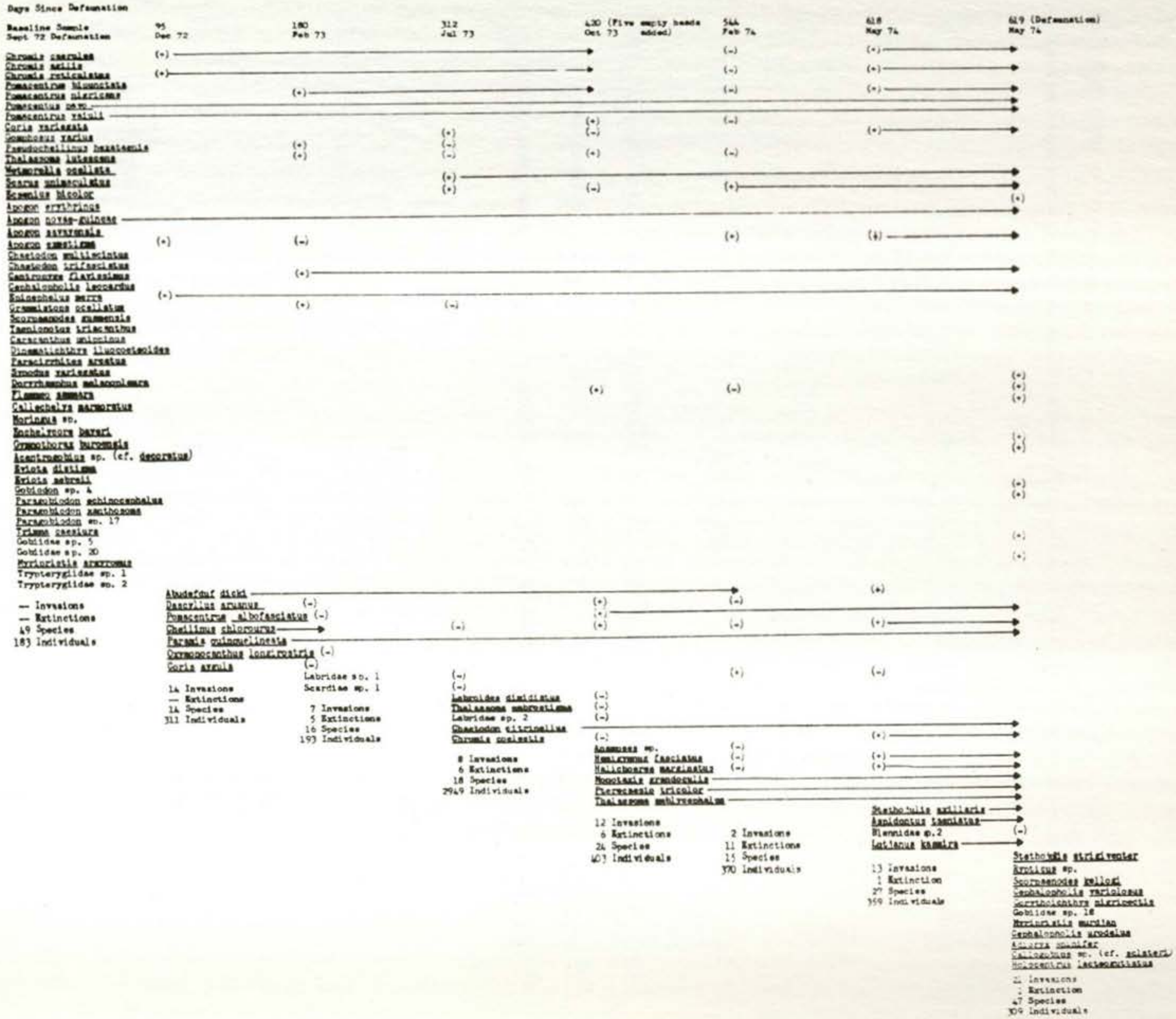

Days Since Defaunation
Baseline Sample
Sept 72 Defaunation
95
Dec 72
180
Feb 73
312
Jul 73
430 (Five empty heads added)
Oct 73
544
Feb 74
618
May 74
619 (Defaunation)
May 74
Chromis caeruleus
Chromis agilis
Chromis reticulatus
Pomacentrus bipunctata
Pomacentrus nigricans
Pomacentrus pavo
Pomacentrus vaiuli
Coris variegata
Gomphosus varius
Pseudocheilinus hexataenia
Thalassoma lutescens
Wetmorella ocellata
Scarus unimaculatus
Ecsenius bicolor
Apogon erythrinus
Apogon novae-guineae
Apogon savayensis
Apogon snyderi
Chaetodon multicinctus
Chaetodon trifasciatus
Centropyge flavissimus
Cephalopholis leopardus
Epinephelus merra
Grammistops ocellatus
Scorpaenodes guamensis
Taenionotus triacanthus
Caracanthus unipinna
Dinematichthys iluocoeteoides
Paracirrhites arcatus
Synodus variegatus
Dorryrhamphus melanopleura
Flammeo sammara
Callechelys marmoratus
Moringua sp.
Enchelycore bayeri
Gymnothorax buroensis
Acentrogobius sp. (cf. decoratus)
Eviota distigma
Eviota sebreei
Gobiodon sp. 4
Paragobiodon echinocephalus
Paragobiodon xanthosoma
Paragobiodon sp. 17
Trimma caesiura
Gobiidae sp. 5
Gobiidae sp. 20
Myripristis argyromus
Trypterygiidae sp. 1
Trypterygiidae sp. 2
— Invasions
— Extinctions
49 Species
183 Individuals
Abudefduf dicki
Dascyllus aruanus
Pomacentrus albofasciatus
Cheilinus chlorourus
Parapercis quinquelineata
Oxymonacanthus longirostris
Coris aygula
14 Invasions
— Extinctions
14 Species
311 Individuals
Labridae sp. 1
Scaridae sp. 1
7 Invasions
5 Extinctions
16 Species
193 Individuals
Labroides dimidiatus
Thalassoma amblycephalum
Labridae sp. 2
Chaetodon citrinellus
Chromis ovalis
8 Invasions
6 Extinctions
18 Species
2949 Individuals
Anampses sp.
Hemigymnus fasciatus
Halichoeres marginatus
Novaculichthys grandoculis
Pteragogus tricolor
Thalassoma amblycephalum
12 Invasions
6 Extinctions
24 Species
403 Individuals
2 Invasions
11 Extinctions
15 Species
370 Individuals
Stethojulis axillaris
Aspidontus taeniatus
Blenniidae sp.2
Lutjanus kasmira
13 Invasions
1 Extinction
27 Species
359 Individuals
Stethojulis strigiventer
Kyphosus sp.
Scorpaenodes kelloggi
Cephalopholis variolosus
Cirrhitichthys nigripectis
Gobiidae sp. 18
Myripristis murdjan
Cephalopholis urodelus
Adioryx spinifer
Callogobius sp. (cf. sclateri)
Holocentrus lacteoguttatus
21 Invasions
1 Extinction
47 Species
309 Individuals

TABLE 19

Invasions and Extinctions on Reef No. 8 (Natural Defaunation Reef). (+) indicates the appearance of a species; (-) indicates its subsequent extinction. An arrow indicates the last date a species was recorded.

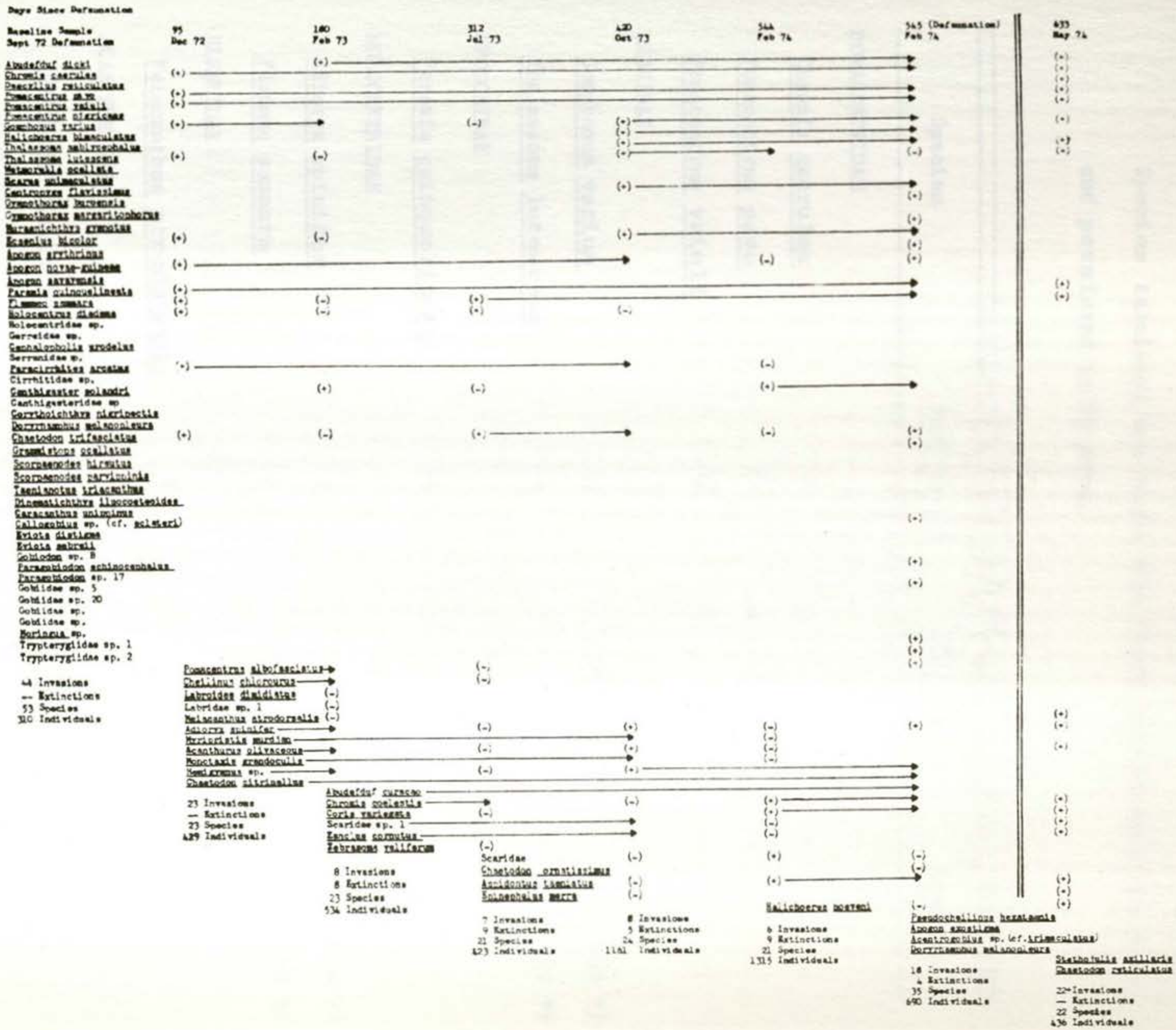

Days Since Defaunation
Baseline Sample
Sept 72 Defaunation
95 Dec 72
180 Feb 73
312 Jul 73
420 Oct 73
544 Feb 74
545 (Defaunation) Feb 74
635 May 74
Abudefduf dicki
Chromis caerulea
Dascyllus reticulatus
Pomacentrus sp.
Pomacentrus vaiuli
Pomacentrus nigricans
Gomphosus varius
Halichoeres biocellatus
Thalassoma amblycephalus
Thalassoma lutescens
Scarus unimaculatus
Centropyge flavissimus
Gymnothorax javanensis
Gymnothorax margaritophorus
Ecsenius bicolor
Apogon erythrinus
Apogon novae-guineae
Apogon savayensis
Paramia quinquelineata
Holocentridae sp.
Gerreidae sp.
Serranidae sp.
Paracirrhites arcatus
Cirrhitidae sp.
Canthigaster solandri
Canthigasteridae sp.
Chaetodon trifasciatus
Scorpaenodes hirsutus
Scorpaenodes parvipinnis
Caracanthus unipinna
Callogobius sp. (cf. sclateri)
Eviota distigma
Gobiodon sp. 8
Paragobiodon echinocephalus
Paragobiodon sp. 17
Gobiidae sp. 5
Gobiidae sp. 20
Gobiidae sp.
Gobiidae sp.
Trypterygiidae sp. 1
Trypterygiidae sp. 2
44 Invasions
— Extinctions
53 Species
310 Individuals
Pomacentrus albofasciatus
Cheilinus chlorourus
Labroides dimidiatus
Labridae sp. 1
Adioryx spinifer
Acanthurus olivaceus
Chaetodon citrinellus
23 Invasions
— Extinctions
23 Species
429 Individuals
Abudefduf curacao
Chromis coelestis
Coris variegata
Scaridae sp. 1
Zanclus cornutus
Zebrasoma veliferum
8 Invasions
8 Extinctions
23 Species
534 Individuals
Scaridae
Chaetodon ornatissimus
Acanthurus triostegus
Epinephelus merra
7 Invasions
9 Extinctions
21 Species
423 Individuals
8 Invasions
5 Extinctions
24 Species
1161 Individuals
Halichoeres hortulanus
6 Invasions
9 Extinctions
21 Species
1315 Individuals
Pseudocheilinus hexataenia
Apogon exostigma
Acentrogobius sp. (cf. trimaculatus)
Dorryrhamphus melanopleura
18 Invasions
4 Extinctions
35 Species
690 Individuals
Chaetodon reticulatus
22 Invasions
— Extinctions
22 Species
436 Individuals

Table 20. The Frequency of Occurrence of Immigrants on Reef No. 3,5,8. Species tabulated are those that first invaded Reef No. 8 and persisted to 95 days.

Species	Reef No. 8	Reef No. 3	Reef No. 5
POMACENTRIDAE			
Chromis caerulea	+	+	+
Pomacentrus pavo	+	+	+
Pomacentrus vaiuli	+	+	+
LABRIDAE			
Gomphosus varius	+	- (180 days +)	- (180 days +)
Thalassoma lutescens	+	+	- (150 days +)
APOGONIDAE			
Paramia quinquelineata	+	+	+
HOLOCENTRIDAE			
Adioryx spinifer	+	-	- (619 days +)
Flammeo sammara	+	- (312 days +)	- (420 days +)
BLENNIDAE			
Meiacanthus atrodorsalis	+	+	-
ACANTHURIDAE			
Acanthurus olivaceous	+	- (180 days +)	-

TABLE 21

Short-term Colonization of Natural Reef No. 9. Numbers in parenthesis indicate the number of days since the last defaunation; * denotes data from defaunation collections, others are from visual censuses.

Species	Days Since First Defaunation (Days Since Last Defaunation)													
	0(0) Sept 72	Baseline *	98(98)* Dec 72	116(8) Dec 72	192(76) Feb 73	193(77)* Feb 73	198(5) Feb 73	200(7) Feb 73	204(11) Feb 73	312(108)* Jul 73	314(2) Jul 73	320(8) Jul 73	412(92) Oct 73	533(121) May 74	534(122)* May 74
Amphiprion percula	3				2					1			1		
Chromis caerulea	19		7	2						28		12			
Dascyllus aruanus	1														
Dascyllus reticulatus	2													3	
Pomacentrus pavo	20		11	4	42	16	16	30	30	31	22	42	50	28	11
Apogon erythrinus	2		2												12
Apogon gracilis	420														
Apogon novaeguineae	47		39		32	55				61	1	28	3	3	13
Ecsenius bicolor	1		1	3						2	2	2	1	1	4
Monotaxis grandoculis	1		1												
Chaetodon trifasciatus	2														
Corythoichthys nigr.rectis	2		2							5					
Gymnothorax melagris	1														
Gymnothorax zonipectis	1									1					
Callogobius sp. (cf. sclateri)	1									1					
Kyiota distigma	4					1				3					-
Kyiota nebrei	22		7			5				6					
Kyiota smaragdus	16					3									
Kyiota sp. 16	15		9			1				24					
Paragobiodon echinocephalus	1	1	1							5					
Paragobiodon lacunicola	1									3					
Trimma caesiura	4														
Pomacentrus albofasciatus			3							2					
Cheilinus chlorourus			3											1	
Paramia quinquelineata			1	12				1	3	2		8	16	1	4
Acanthurus olivaceous			1	1				1							
Stethojulis strigiventer			11												
Scaridae sp. 1			7												
Gymnothorax sp.			1												
Apogon exostigma			7	2											4
Acentrogobius cf. decoratus			1			14				10					
Electroides sp. 18			4			1									
Gymnothorax buroensis			1												
Gnatholepis anjerensis			2												
Trypterygiidae sp.1			1				3			1					
Trypterygiidae sp.2			1												
Pomacentrus vaiuli					2	2	1		3	1			3	2	
Acanthuridae sp. 1					2		1		2						
Apogon savayensis						1									
Zebrasoma veliferum						1									
Gobiidae sp. 20						1				13					
Cheilodipterus sp.						1									
Halichoeres sp.						1									
Chromis coelestis							8	8	8			1	22	6	6
Canthigaster solandri								1					1	1	1
Thalassoma amblycephalus										3				1	
Gomphosus varius										1					
Labridae sp. 1										3					
Dotyrrhamphus melanopleura										5					1
Halichoeres marginatus										1			1		
Cephalopholis urodelus										1					
Ophichthidae sp.										3					
Cheilinus sp. 1										1					
Pterelectris evides										15					1
Bryaninops ridens										1					
Gymnothorax margaritaceous										3					
Cailechelys marmoratus										1					
Kyiota nebulosa										1					
Pterecaesio tricolor													1		
Labridae sp. 2													1		
Coris variegata													1	1	1
Aspidontus taeniatus													1		
Epinephelus merra													1		
Trammistops prellatus													2		1
Holocentrus diadema														1	1
Halichoeres hoeveni														1	1
Cheilodipterus lineatus														1	1

TABLE 22

Short-Term Colonization of Natural Reef No. 13. Numbers in parenthesis indicate the number of days since the last defaunation; * denotes data from defaunation collections, others are from visual censuses.

Species	Days Since First Defaunation (Days Since Last Defaunation)												
	0(0) Sept 72	Baseline	98(98)* Dec 72	101(3) Dec 72	104(12) Dec 72	171(67)* Feb 73	177(6) Mar 73	181(10)** Mar 73	294(123) Jul 73	297(226) Oct 73	531(360)* Feb 74	626(455) May 74	627(456)* May 74
Chromis caerulea	12		45						6				
Pomacentrus albofasciatus	4					6		1	12	27	7	4	1
Pomacentrus sp.o	32		11		1	23	34	17	60	190	220	350	33
Pomacentrus vaiuli	4			1			1		4	5			
Gomphosus varius	1				1				1				
Apogon aurolineatus	1		5			5							12
Apogon fragilis	21		9						400				
Apogon novaeguineae	25		180	2		120	17	11	200	7	200	100	32
Ecsenius bicolor	1								1	2	2		
Ecsenius sp.	1												
Acanthurus olongatus	1												
Oxymonacanthus longirostris	1												
Holocentrus diadema	1										1	1	1
Myripristis argyromus	1		3			1							
Canthigaster solandri	1								1	2	2		2
Corythoichthys nigripectis	1		3										4
Labillus sp.	1												
Eviota zebrali	18		4			5							
Eviota smaragdus	13		5			2							
Eviota sp. cf. prasites	1												
Paragobiodon xanthosoma	1												
Valenciena longipinnis	1					1							
Lamethrus sp.	1												
Gobiidae sp. 1	10		4										
Gobiidae sp. 2	22		2										
Tryptergyllidae sp. 1	4											1	2
Paragobiodon sp. 17	2												
Epinephelus merra	1									2	1	2	4
Chellinus chlorourus			1						2	2	5	1	1
Chaetodon citrinellus			1			2							
Dascyllus melanopleura			6										4
Stethojulis striaventer			2										
Apogon erythrinus			4										
Apogon sp.			8										
Paramonacanthus echinocephalus			1										
Trimma sylviopus			1										1
Callogobius sp. (cf. sclateri)			1			2							1
Trimma caesiura			2										
Blenniidae sp. 2			1										
Hemigymnus melapterus			1										
Metacrolla ocellata			1										
Thalassoma sp.				11			1	50	43	4	32	101	
Paramia quinquelineata						3			5	6	4	1	1
Abudefduf curacao						6				1			
Dascyllus aruanus						1							
Plectroglyphidodon sp.						1							
Stegastes diencaeus						1							
Chromis dimidiata						1							
Pomacentrus pavo						1							
Paracirrhites arcatus						1							
Chellinus sp						3							
Chellinus trilobatus						4							4
Acanthogobius cf. decoratus						1							
Gobiidae sp.						1							
Gobiidae sp. 1						1							
Cephalopholis leopardus						1							
Chaetodon meriaensis						1							
Chromis actilis						1							
Scorpaenodes kallogi						1							
Serythoichthys flavofasciatus							2	1	20	20	16	14	2
Chromis caeruleus							2	4	2	2			
Acanthurus olivaceous							5	4					
Acanthuridae sp. 1							5		1				
Acanthuridae sp. (larvae)									1				
Coris gaimardi									1				
Coris variegatus									1			1	2
Macolabis grandoculis									1				
Halichoeres marginatus									2				
Scaridae sp. 1									2				
Scaridae sp. 2									10	300	10	30	
Malloidichthys auriflamma									1				
Melacanthus strodorsalis									6				
Blenniidae sp. 3									3				
Acanthuridae sp. 5										1			
Thalassoma lutescens										5			
Labrus xanthir										1			
Bodianus axillaris										1			
Pterocaesio sp.											1		
Stethojulis axillaris											50	180	66
Myripristis murdjan											1		
Scarus prasiognatus											1		
Halichoeres hoevenl											1		
Scaridae sp. 3											1		
Lutjanidae sp.													1
Epinephelus sp.													

TABLE 23

Short-Term Colonization of Natural Reef No. 17. Numbers in parenthesis indicate the number of days since the last defaunation; * denotes data from defaunation collections, others are from visual censuses.

Species	Days Since First Defaunation (Days Since Last Defaunation)														
	0(0) Baseline Sept 72	98(98)* Dec72	106(8) Dec 72	186(74) Feb 73	181(75)* Feb 73	184(3) Feb 73	189(8) Feb 73	193(12) Feb 73	300(123)* Jul 73	301(1) Jul 73	304(4) Jul 73	311(11) Jul 73	391(91)* Oct 73	512(121)* Feb 74	605(214) May 74
Abudefduf dicki	1														
Chromis caerulea	2	4												18	
Pomacentrus pavo	1	12		12	1				38		20	8	4	133	
Pomacentrus vaiuli	3			2	2		1	1				2	10	6	-
Wetmorella ocellata	1														
Apogon erythrinus	4	5			1									1	
Apogon gracilis	255														
Apogon properuptus	7														
Apogon novaeguineae	27	14	25	18									13		28
Paramia quinquelineata	10	32	9	2	60							6	70	1	2
Ecsenius bicolor	7								4				3		4
Cortholichthys flavofasciatus	1														
Corythoichthys nigripectis	2														
Dorryhamphus melanopleura	1	1							6						
Canthigaster solandri	1												1	1	
Grammistops ocellatus	2														
Taeniamotus triacanthus	1														
Dinematichthys iluocoeliodes	1														
Myripristis argyromus	1				1										
Acentrogobius cf. decoratus	2				1				4						
Eviota distigma	1								3						
Eviota zebrell	2	1			1										
Eviota smaragdus	5	1													
Gobiodon sp. 15	1														
Paragobiodon lacunicola	1														
Trimma evitops	2														
Gobiidae sp. 5	11	1			2				18						
Gobiidae sp. 22	2														
Tryoterygiidae sp. 1	5	2			1				10				1		
Tryptterygiidae sp. 2	6	1													
Labridae sp. 1		1	1									1			
Halichoeres margaritaceus		1													
Epinephelus merra		1	1	2					2				1	1	2
Holocentrus microstomus		1													
Apogon sp.		1													
Pomacentrus albofasciatus			2												1
Amphiprion varius			5					1						1	1
Chaetodon citrinellus			1										1	1	1
Labridae sp.			1												
Chromis ternatensis				5	1										
Coris variegata				1	1								1		
Halichoeres bimaculatus				7											
Scaridae sp. 1				6					1				1	1	
Bramidae sp.				1											
Cheilinus chlorourus					1								1		
Ctenochaetus binotatus					2				4						
Stethojulis strigiventer					1								1		
Holocentrus diadema					1								1		1
Gobiidae sp. 18					1										
Chromis coelestis									5						
Thalassoma amblycephalus									1						
Gobiidae sp. 20									7						
Gobiidae sp. 21									1						
Canthigaster sp. (cf. epilampris)									1						
Scorpaenodes guamensis									1						
Dascyllus aruanus											2	1		19	5
Pomacentrus nigricans													1		
Labrichthys unicolor													1		
Cheilinus oxycephalus													1		
Melacanthus atrodorsalis													1		
Canthigaster janthopterus													1		
Halichoeres hoevenii													1		
Ctenochaetus strigosus													2		
Dascyllus reticulatus														2	7
Stethojulis axillaris														1	
Scarus unimaculatus														2	2
Labroides dimidiatus															1
Aspidontus taeniatus															1
Plagiotremus rhinorhynchos															1
Myripristis murdjan															5
Thalassoma lutescens															1
Centropyge flavissimus															1
Lutjanus kasmira															4
Lutjanidae sp.															1
Labridae sp. 8															1
Abudefduf sp.															1

Table 24. Persistence of First Immigrants to Reefs No. 9,13, 17, Which Were Defaunated Several Times. Numbers show percent of total censuses in which each species was recorded at 12 and 67-123 days after the first defaunation.

Species	Days Post Reef Defaunation	
	12 Days (n=8)	67-125 Days (n=10)
Pomacentrus pavo	75%	100%
Pomacentrus vaiuli	63	60
Paramia quinquelineata	63	70
Apogon novaeguineae	50	100
Chromis coelestis	38	20
Gomphosus varius	38	20
Labridae sp. 1	25	0
Pomacentrus albofasciatus	25	40
Acanthuridae sp. 1	25	10
Acanthurus olivaceous	25	10
Ecsenius bicolor	25	50
Chromis caerulea	25	70
Dascyllus aruanus	13	10
Chaetodon citrinellus	13	10
Epinephelus merra	13	20
Ptereleotris tricolor	13	0
Apogon exostigma	13	30

Table 25. Equilibrium number of species on natural and artificial reefs. Data are from censuses that were conducted at approximately 100-day intervals. CV is coefficient of variation. The five heads added to reef No. 22 contained resident fish - the other heads added were empty.

Reef Category	$\bar{X}$	CV	Sample Size
Artificial No. 18,21,22	9.8	30%	11
Artificial No. 2,4,6	9.3	36%	14
Natural No. 3,5,8	20.8	8%	17
Artificial No. 21 with 10 heads added	13.5	16%	2
Artificial No. 22 with 5 heads added	12.5	6%	2
Artificial No. 2 with 10 heads added	13.5	5%	2
Artificial No. 4 with 10 heads added	12.0	8%	3

Table 26. Species composition of natural and artificial reefs. Values represent the frequency of occurrence of species 200 days after initial observation/installation. Only species occurring in ≥50% of the samples are listed individually (35 other species were recorded <50% of the time on natural reefs and 19% on artificial reefs).

Species	Natural Control Reefs (7,10,11,12,30) (n=5)	Artificial Reefs (2,4,6,18,20,22) (n=6)
Pomacentrus vaiuli	100	50
Apogon novaeguineae	100	67
Ecsenius bicolor	100	0
Pomacentrus pavo	80	100
Paramia quinquelineata	80	67
Chromis coelestis	60	0
Chromis agilis	60	0
Labridae sp. 1	60	50
Gomphosus varius	60	17
Pomacentrus nigricans	60	0
Pomacentrus albofasciatus	20	67
Epinephelus merra	0	67
	$\bar{X}$ = 18.8 CV=32%	$\bar{X}$ = 10.7 CV=36%

Table 27. Persistence of first immigrants to artificial reefs No. 16,19,20. Values are percent occurrence at 100 and 200 days. n = number of observations.

Species	Days Since Installation 100 days (n=4)	200 days (n=4)
Pomacentrus pavo	100%	100%
Paramia quinquelineata	75	100
Labridae sp. 1	75	0
Acanthuridae sp. 1	50	50
Pomacentrus vaiuli	50	100
Pomacentrus albofasciatus	50	100
Other species (20)	25	40

Table 28. Faunistic recovery of artificial reefs following defaunation. Values represent the number of species present when the reefs were defaunated at 100 days after installation and again 100 days later.

	Days After Installation					
	Reef No. 16		Reef No. 19		Reef No. 20	
	100	200	100	200	100	200
No. of Spp.	11	6	15	7	20	16
No. of Spp. in Common	3		5		7	
Species in Common	Epinephelus merra Pomacentrus pavo Cheilinus chlorourus		Pomacentrus albofasciatus Pomacentrus pavo Chromis ternatensis Apogon novaeguineae Paramia quinquelineata		Pomacentrus albofasciatus Pomacentrus pavo Apogon exostigma Apogon novaeguineae Paramia quinquelineata Trypterygiidae sp. 1 Acanthurus olivaceous	

Table 29. Short period invasion and persistence on artificial reefs 16,19,20 (based on visual censuses only). Values are % frequency of occurrence. n = number of samples.

Species	Days Since Defaunation 1-2 n=3	3-4 n=6	5-7 n=4	10-14 n=7	83-96 n=6
Pomacentrus pavo	100%	100%	100%	100%	100%
Labridae sp. 1	67	0	25	43	50
Thalassoma lutescens	33	0	0	14	0
Apogon gracilis	33	33	0	0	0
Chromis ternatensis	67	17	0	0	33
Pomacentrus albofasciatus	33	50	25	29	67
Apogon novaeguineae	33	17	0	14	67
Paramia quinquelineata	33	50	50	43	67
Scaridae sp. 1	33	33	50	43	33
Epinephelus merra	0	33	25	29	50
Unidentified larvae	0	17	0	14	17
Chromis coelestis	0	17	0	29	0
Acanthurus olivaceous	0	17	25	14	17
Zebrasoma velliferum	0	17	0	0	17
Labridae sp. #3	0	17	0	14	17
Apogon exostigma	0	17	0	0	17
Acanthuridae sp. 1	0	0	25	43	17
Canthigaster sp.	0	0	25	14	17
Chaetodon citrinellus	0	0	25	14	17
Thalassoma amblycephalus	0	0	25	14	0
Ctenochaetus binotatus	0	0	0	14	17
Coris variegata	0	0	0	14	33
Labridae sp. #2	0	0	0	14	17
Apogon novemfasciatus	0	0	0	14	0
Adioryx spinifer	0	0	0	14	0
Chaetodon epphipium	0	0	0	14	0
Labroides dimidiatus	0	0	0	14	0
Cheilinus chlorourus	0	0	0	0	33
Canthigaster solandri	0	0	0	0	17
Labridae sp. #5	0	0	0	0	17
Cheilinus sp.	0	0	0	0	17
Blennidae sp. #1	0	0	0	0	17
Ptereleotris tricolor	0	0	0	0	17
Abudefduf dicki	0	0	0	0	17
Holocentrus diadema	0	0	0	0	17
Halichoeres hortulanis	0	0	0	0	17
Doryrhamphus melanopleura	0	0	0	0	17
Stethojulis strigiventer	0	0	0	0	17
$\bar{X}$ Number of Species/Census	4.7	3.5	4.3	5.6	9.0
Total Number of Species	9	14	11	23	30

Table 30. Effect of addition of dead coral heads on the species composition of artificial reefs. Species listed are those never seen prior to the addition of heads.

Species	Reef No. 2	4	16	19	20	21	22
Chromis caerulea	+	+	+	+	+	+	+
Dascyllus reticulatus		+			+		+
Dascyllus aruanus				+			+

Table 31. Seasonality of recruitment. Table values represent the frequency of occurrence of juveniles (designated as individuals less than 3 cm total length) on seasonal censuses conducted on nine artificial reefs throughout the years 1972, 1973, and 1974. n = number of observations; replicate censuses were combined.

Species	Winter (n=16)	Fall (n=28)	Spring (n=12)	Summer (n=9)
Chromis caerulea	.06	.29	.42	.00
Pomacentrus albofasciatus	.19	.46	.33	.00
Pomacentrus pavo	.81	.61	.50	.22
Pomacentrus vaiuli	.25	.07	.33	.67
Apogon gracilis	.00	.04	.08	.22
Apogon novaeguineae	.38	.25	.17	.00
Paramia quinquelineata	.19	.43	.08	.11
Aspidontus taeniatus	.00	.00	.00	.33
Labroides dimidiatus	.13	.07	.00	.11
Thalassoma amblycephalus	.06	.00	.08	.00
Labridae sp. 1	.25	.25	.25	.11
Chromis coelestis	.19	.14	.50	.22
Ecsenius bicolor	.13	.11	.33	.33
Coris variegata	.19	.00	.08	.33
Dascyllus reticulatus	.06	.04	.17	.00
Pterelotris tricolor	.06	.00	.00	.00
Sum of Row Ranks	45.0	36.5	43.5	39.0
Expected Value	41.0	41.0	41.0	41.0

Friedman's test W = .036, therefore differences not significantly different at $p \leq .01$.

Table 32. Seasonality of species (composition). Values represent frequency of occurrence of species on multiple defaunations of Artificial Reefs No. 16,19,20. Data are from defaunation collections in which species occurred in two or more samples. n = number of observations, asterisks designate gobies.

Species	Fall (n=4)	Winter (n=4)	Spring (n=1)	Summer (n=3)
Chromis ternatensis	.50	.00	.00	.33
Pomacentrus albofasciatus	.50	.75	.00	.00
Pomacentrus pavo	.75	1.00	1.00	1.00
Pomacentrus vaiuli	.00	.00	1.00	.67
Cheilinus chlorourus	.50	.25	.00	1.00
Stethojulis strigiventer	.25	.50	.00	.00
Cheilinus sp.	.25	.25	.00	.25
Scaridae sp. 1	.25	.00	.00	.67
Apogon erythrinus	.50	.50	1.00	.67
Apogon exostigma	.25	.25	1.00	.67
Apogon novaeguineae	.50	.50	1.00	.67
Paramia quinquelineata	.50	.50	.00	.67
Chaetodon citrinellus	.00	.25	1.00	.00
Adioryx spinifer	.00	.00	1.00	.33
Holocentrus diadema	.00	.25	1.00	.00
Acanthurus olivaceous	.25	.25	.00	.00
Ctenochaetus binotatus	.00	.25	1.00	.33
Acanthuridae sp. #1	.00	.25	.00	.67
Epinephelus merra	.25	.50	.00	.67
Corythoichthys nigripectis	.50	.25	1.00	.67
Doryrhamphus melanopleura	.00	.50	.00	.33
Ecsenius bicolor	.00	.25	1.00	.25
Acentrogobius cf. decoratus*	.00	.50	1.00	.67
Gobiidae sp. #5*	.25	.25	1.00	.33
Gobiidae sp. #18*	.00	.25	.00	.67
Gobiidae sp. #20*	.00	.50	1.00	.50
Gobiidae sp. #22*	.00	.25	.00	.33
Trypterygiidae sp. #1	.50	.25	.00	1.00
Trypterygiidae sp. #2	.00	.25	1.00	.33
Sum of Row Ranks	53.5	66.2	80.0	84.5
Expected Value	71.0	71.0	71.0	71.0

Friedman's test W = 0.139, differences not significant at $p \leq .01$.

Table 33. Seasonality of occurrence of members of the family Gobiidae. Data are from natural, multiple defaunation reefs. Values represent frequency of occurrence of species at defaunation.

Species	Fall (n=3)	Winter (n=4)	Spring (n=2)	Summer (n=2)
Callogobius cf. sclateri	.33	.25	.50	.50
Eviota distigma	.67	.25	.00	1.00
Eviota sebreii	1.00	1.00	.00	.50
Eviota smargadus	1.00	.75	.00	.00
Eviota sp. #16	.33	.25	.00	.50
Paragobiodon echinocephalus	.33	.00	.00	.50
Paragobiodon lacunicola	.67	.00	.00	.50
Trimma caesiura	.33	.50	.00	.00
Eleotroides sp. #12	.00	.25	.00	.00
Gobiidae sp. #20	.00	.25	.00	1.00
Acentrogobius cf. decoratus	.67	.75	1.00	1.00
Pterelotris evides	.00	.00	.50	.50
Gobiidae sp. #15	.67	.00	.00	.00
Trimma eviotops	.33	.50	.00	.00
Gobiidae sp. #22	.67	.25	.00	.00
Gobiidae sp. #18	.00	.25	.00	.00
Gobiidae sp. #5	.33	.25	.00	.50
Gobiidae sp. #21	.00	.00	.00	.50
Cabillus sp. B	.33	.25	.00	.00
Eviota cf. prasites	.33	.00	.00	.00
Paragobiodon xanthosoama	.33	.00	.00	.00
Valenciennea longippinis	.33	.00	.00	.00
Xenisthmus sp. #8	.33	.25	.00	.00
Paragobiodon sp. #17	.00	.00	.50	.00
Gobiidae sp. #2	.00	.25	.00	.00
Gobiidae sp. #19	.00	.25	.00	.00
Sum of Row Ranks	73.5	68.0	50.0	65.5
Expected Values	64.3	64.3	64.3	64.3

Friedman's test W = 0.09, differences not significant at $p \geq .1$.
($x^2 = 7.02$, 3° freedom)

TABLE 34

Invasions and Extinctions on Artificial Reef No. 22. (+) indicates the appearance of a species; (-) indicates its subsequent extinction. An arrow portrays the last date the species was recorded.

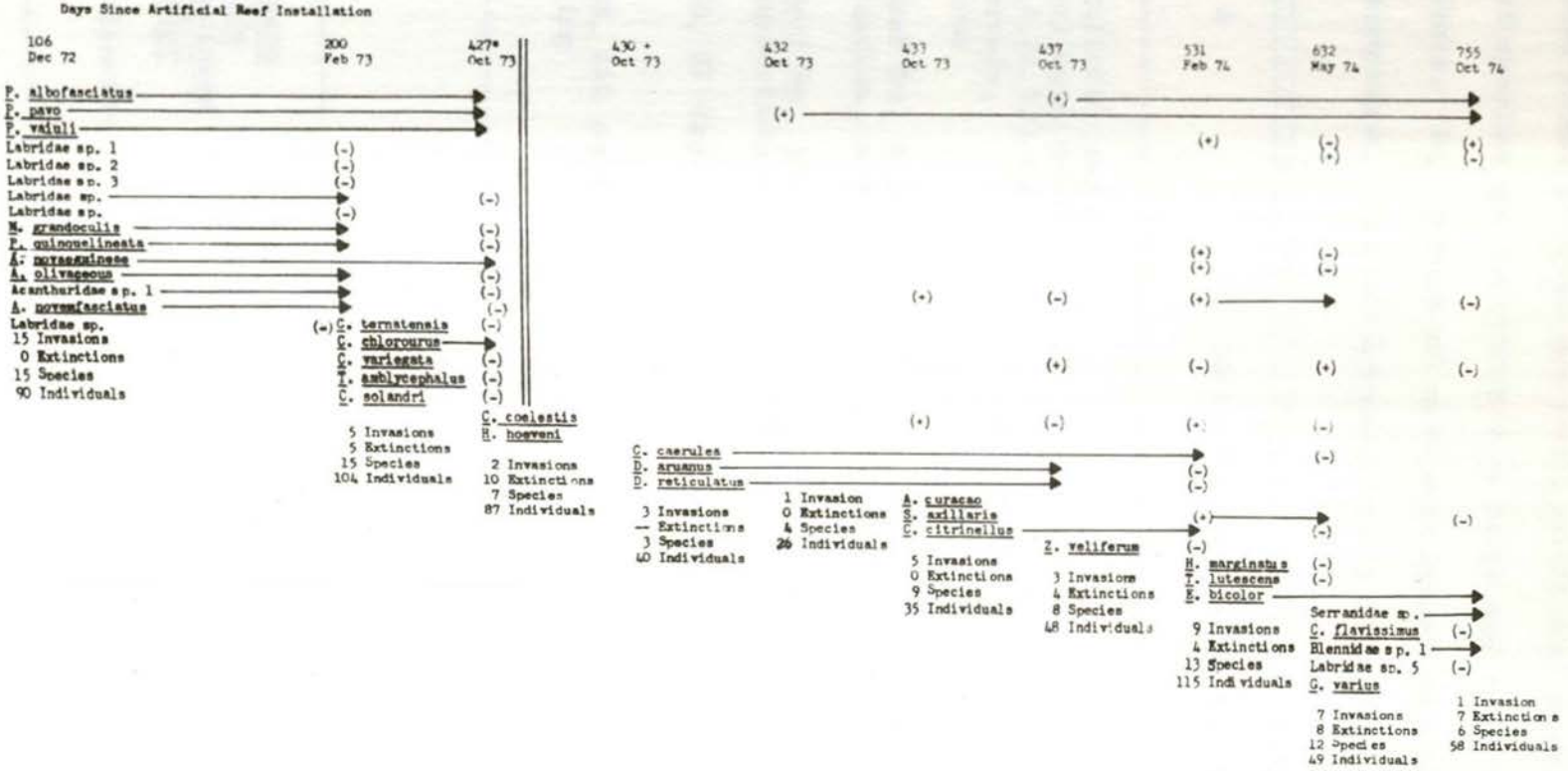

Days Since Artificial Reef Installation
106
Dec 72
200
Feb 73
427*
Oct 73
430 +
Oct 73
432
Oct 73
433
Oct 73
437
Oct 73
531
Feb 74
632
May 74
755
Oct 74
P. albofasciatus
P. pavo
P. vaiuli
Labridae sp. 1
Labridae sp. 2
Labridae sp. 3
Labridae sp.
Labridae sp.
M. grandoculis
P. quinquelineata
A. nigrocinctus
A. olivaceous
Acanthuridae sp. 1
A. novemfasciatus
Labridae sp.
15 Invasions
0 Extinctions
15 Species
90 Individuals
C. ternatensis
C. chlorourus
C. variegata
T. amblycephalus
C. solandri
5 Invasions
5 Extinctions
15 Species
104 Individuals
C. coelestis
H. hoeveni
2 Invasions
10 Extinctions
7 Species
87 Individuals
C. caerulea
D. aruanus
D. reticulatus
3 Invasions
— Extinctions
3 Species
40 Individuals
1 Invasion
0 Extinctions
4 Species
26 Individuals
A. curacao
S. axillaris
C. citrinellus
5 Invasions
0 Extinctions
9 Species
35 Individuals
Z. veliferum
3 Invasions
4 Extinctions
8 Species
48 Individuals
H. marginatus
T. lutescens
E. bicolor
9 Invasions
4 Extinctions
13 Species
115 Individuals
Serranidae sp.
C. flavissimus
Blennidae sp. 1
Labridae sp. 5
G. varius
7 Invasions
8 Extinctions
12 Species
49 Individuals
1 Invasion
7 Extinctions
6 Species
58 Individuals

Table 35. Fish fauna of large and small artificial reefs. A. Number of species and individuals on large and small artificial reefs. B. Effects of reef enlargement upon fish assemblage structure. Values represent number of individuals.

A	Mean No. Species CV	Mean No. Individuals
Standard artificial reefs prior to coral head addition (No. 2,4,21,22) at 100-day intervals, 16 observations	9.3 (39%)	81.3 (34%)
Artificial Reef No. 6 preceding combination, n = 5	6.8 (28%)	167.2 (81%)
Artificial Reef No. 18 preceding combination, n = 5	11.2 (17%)	48.0 (57%)
Reef No. 6-18, 87 days after combining	15	60
Reef No. 6-18, 242 days after combining	10	8245

B	Pre-Combination Reef No. 6	Pre-Combination Reef No. 18	Post Combination 6-18 87 days	Post Combination 6-18 242 days
Pomacentrus pavo	74	12	40	145
Apogon gracilis	0	0	0	8000
Apogon novaeguineae	86	0	0	63
Ecsenius bicolor	1	0	6	8
Total Fish Species Present	272	32	60	8245

Table 36. Populations of selected species on large and small natural control reefs (adults and juveniles combined) in July 1973.

Species	Reef No. Large Reef 31	Small Reefs 7	10	11	12	30	Mean No. Individuals on Small Reefs
Abudefduf curacao	5	--	--	--	--	--	0.0
Chromis caerulea	88	--	--	--	230	--	46.0
Pomacentrus pavo	26	96	313	26	111	--	91.8
Pomacentrus vaiuli	31	16	27	4	6	22	15.2
Apogon novaeguineae	23	10	11	10	1	54	17.2
Flammeo sammara	20	1	--	--	1	--	0.4
Cephalopholis urodelus	5	--	1	--	--	--	0.2
Dascyllus reticulatus	6	--	--	1	--	10	2.2
Number Individuals	463	125	426	59	388	102	220.0

Table 37. Effects of coral head addition on populations inhabiting artificial reefs. Values are number of individuals preceding head addition in Oct. 1973 and approximately 100 days later in February 1974.

	No. Heads	Number of Individuals Preceding Addition	Number of Individuals Following Addition
Reef No. 2	10	108	190
Reef No. 4	10	51	147
Reef No. 16	5	40	100
Reef No. 19	5	75	275
Reef No. 20	5	44	135
Reef No. 21	10	52	178
Reef No. 22	5	40	115

$\bar{x}$ = 97.0 (CV=77%) reefs with 10 heads

$\bar{x}$ = 90.0 (CV=32%) reefs with 5 heads

TABLE 38

Short-Term Invasion and Extinction on Experimental and Control Reefs. The data are from ten days of observations in which the first appearance and subsequent extinction of damsel fish juveniles were montored. C.c. represents Chromis caerulea; P.p., Pomacentrus pavo; D.r., Dascyllus reticulatus; D.a., Dascyllus aruanus; D.t., Dascyllus trimaculatus. Two labrid juveniles, Thalassoma lutescens (T.l.) and Thalassoma amblycephalus (T.a.) are also included.

Experimental Regime	Day No. 1 13 Oct (1300)	Day No. 2 14 Oct(1700)	Day No. 3 15(1700)	Day No.4 16(1700)	Day No. 5 17(1500)	Day No. 6 18(0730)	Day No. 7 19(1700)	Day No.8 20(1700)	Day No. 9 21(1700)	Day No. 10 22(0630)	Day No. 10 22(1900) hrs
Artificial Reef No. 20 (Experimental). Reef defaunated 12 Oct and two heads with C.c. added	68/3-5 cm C.c. added	+ 0 - 10 C.c	+0 -0	+ 3 C.c. - 0	+ 1 C.c. - 0	+0 -0	+ 4 C.c. (unsuccessful Caranx melampygus attack)	—	+ 20 C.c. + 2 P.p. - 0	+ 130 C.c. - 0	+0 -0
Artificial Reef No. 21 (Experimental) Reef defaunated 12 Oct and two heads without C.c. were added.	+0	+0	+0	+0	+0	+0	+ 6 C.c. + 1 D.r. - 0		+ 8 C.c. - 0	+4 C.c. +2 D.a. +1 P.p. -0	+ 2 P.p. + 2 T.a. - 8 C.c.
Artificial Reef No. 4 (Experimental). Reef at equilibrium when two heads with C.c.were added.	60/3-6 cm C.c. added	+0 -0	+0 -0	+0 -0	+ 4 C.c.	+0 - 3 C.c.	+ 31 C.c. - 0	—	+ 120 C.c. P.p.observed chasing C.c.	+150 C.c. +1 D.r. + 3 C.m. + 1 P.a. - 0	+ 1 D.r. + 3 D.a. + 1 D.t. - 150 C.c.
Artificial Reef No. 2 (Experimental). Reef at equilibrium when two heads lacking fish were added.	+0	+0	+0	+ 2 P.p.	+0 -0	+0 -0	+0 -0	—	+ 3 C.c. + 1 P.p. + 1 T.a. - 0	+ 3 C.c. + 3 D.r. + 1 P.p. + 1 P.a. - 0	+ 2 C.c. + 1 T.a. - 3 C.c. - 2 D.r.
Artificial Reef No. 19 (Control). Reef at equilibrium with C.c. present on pre-existing heads.	Baseline 9 C.c. 2 D.a.	+0	+0	+0	+ 1 C.c.	+ 1 C.c. - 0	+ 16 C.c. - 0	—	+0 - 0	+ 5 C.c. + 1 P.p.	+ 1.P.p. -0
Artificial Reef No. 22 (Control). Reef at equilibrium. No pre-existing heads or C.c. present.	no manipulations	+0	+0	+0	+0	+0	+0	—	+0	+0	-0
Natural Reef No. 5 (Control). Reef at equilibrium with C.c. naturally present.	Baseline 6 C.c. adults 3 D.r. adults	+0	+0	+0	+0	+0	+0	—	+ 1 D.r.	+ 22 C.c. - 0	+ 1 D.r.
Natural Reef No. 11 (Control). Reef at equilibrium without C.c. due to lack of proper substrate.	Baseline large pop. of P.p.	+0	+0	+0	+0	+0	+0	—	+ 0	+ 18 C.c.	+0 - 18 C.c.

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Appendix 1. Census Data From Natural Defaunation Reef No. 3. Values are number of individuals. Reef No. 3 was defaunated 2 Sept. 72. * indicates transient species.

Species	Days Since Initial Defaunation						
	Base-line	94	180	312	420	544	618
	Sept. 1972	Dec. 1972	Feb. 1973	Jul. 1973	Oct. 1973	Feb. 1974	May 1974
Abudefduf curacao			1	1	1	1	
Abudefduf dicki							2
Chromis caerulea		135	400	175	356	56	85
Chromis coelestis						3	
Chromis dimidiatus	2	1	1	1	2	1	1
Chromis leucurus			1				
Chromis ternatensis			2	1			7
Dascyllus aruanus	10	3	2	5	6	4	4
Dascyllus reticulatus	3	1	2	5	1	6	4
Pomacentrus albofasciatus		1		3			
Pomacentrus nigricans		1	1	2		1	1
Pomacentrus pavo	6	205	200	252	73	29	52
Pomacentrus vaiuli	6	3	3	8	5	12	8
Cheilinus chlorourus		1					
Cheilinus sp.			1				
Coris variegata					1	1	
Gomphosus varius			1				
Halichoeres hoeveni				1			
Halichoeres marginatus		2	1				1
Halichoeres trimaculatus*	5	1	8	8	3	7	6
Hemigymnus melapterus				5		1	
Thalassoma amblycephalus		1	1			1	10
Thalassoma lutescens		17			1		
Labridae sp. 1		2				1	
Labridae sp. 2		1			1		
Labridae sp. 6							
Labridae sp. 7		1					
Scaridae sp. 1			3				
Scaridae sp. 2			1				
Aspidontus taeniatus				1	1	2	1
Ecsenius bicolor			2	4	1	4	2
Meiacanthus atrodorsalis	2				1		1
Blennidae sp.		1					1
Apogon erythrinus	5						
Apogon exostigma	6						

Appendix 1, Cont'd.

Apogon novaeguineae	35	138	40	100	26	24	105
Paramia quinquelineata	1	17	5	2			
Acanthurus olivaceous			3				
Ctenochaetus striatus*	3	4	7	8	10	2	4
Naso lituratus*			1				
Zebrasoma velliferum		1	1				
Lutjanus kasmira							2
Gerres oblongus		1	1		1		
Anthiidae sp.							2
Chaetodon auriga*		1		2			2
Chaetodon epippium*				1			
Chaetodon citrinellus		2		2	2	2	1
Megaloprotodon trifascialis			1	2			
Centropyge flavissimus	2		1				
Cephalopholis urodelus	1						
Grammistops ocellatus	2	2					
Paracirrhites arcuatas	6						
Epinephelus merra			2	2	3	2	2
Serranidae sp.	1						
Scorpaenidae sp.	1						
Corythoichthys nigripectis	1					1	1
Doryrhamphus melanopleura	2						
Flammeo sammara				1			2
Myripristis argyromus	7						
Gymnothorax buroensis	1						
Muraenichthys gymnotus	1						
Eviota smaragdus	2						
Paragobiodon echinocephalus	3						
Paragobiodon sp. 17	3			7			
Ptereleotris tricolor							
Trimma caesiura	4						
Gobiidae sp. 5	6						
Trypterygiid sp. 1	1						
Number Resident Species	27	22	25	21	17	19	22
Number Individuals	120	537	677	578	482	152	295

Appendix 2. Census Data From Natural Defaunation Reef No. 5. Values are number of individuals. Reef No. 5 was defaunated 2 Sept. 72 and 11 May 74; five empty coral heads on pedistals were installed 29 Oct. 73. * indicates transient species.

	Days Since Initial Defaunation							
Species	Baseline Sept. 1972	95 Dec. 1972	180 Mar. 1973	312 Jul. 1973	420 Oct. 1973	544 Feb. 1974	618 May 1974	619 May 1974
Abudefduf dicki		2	2	1	2	2	2	
Chromis caerulea	8	150	12	300	6	0	2	2
Chromis coelestis				6			1	1
Chromis agilis	1							
Dascyllus aruanus		2			1			
Dascyllus reticulatus	6	1	1	1	2		4	4
Pomacentrus albofasciatus		2			6	1	5	4
Pomacentrus bipunctata	1							
Pomacentrus nigricans	3		1	1	1		1	1
Pomacentrus pavo	11	65	80	530	284	300	256	125
Pomacentrus vaiuli	11	6	3	9	7	11	11	9
Anampses sp.					1			
Cheilinus chlorourus		1	2		2		2	2
Coris aygula		1						
Coris variegata	1			5				
Gomphosus varius	2			1			2	1
Halichoeres marginatus					1		1	1
Halichoeres trimaculatus*	9	7	10	40	15	6	16	12
Hemigymnus fasciatus (melapterus)					1		1	1
Labroides dimidiatus				1				
Pseudocheilinus hexataenia	1		1				2	1
Stethojulis axillaris								1
Stethojulis strigiventer					4	3	2	2
Thalassoma amblycephalus					1			
Thalassoma lutescens	1		1					
Thalassoma umbrostigma				1				
Wetmorella ocellata	1					1		
Labridae sp. 1			1					
Labridae sp. 2				1				

Appendix 2, Cont'd.

Scarus unimaculatus	1			2	2	1	1	3
Scaridae sp. 1			4					
Aspidontus taeniatus							2	1
Cirripectus variolosus								3
Ecsenius bicolor	1			1		2	11	11
Blennidae sp. 2							1	
Apogon erythrinus	3							6
Apogon novaeguineae	12	53	62	47	27	1	6	12
Apogon savayensis	1							
Apogon exostigma	7	2					1	2
Paramia quinquelineata		22	14	26	18	1	9	9
Ctenochaetus striatus*		5	4	11	9	2	20	18
Lutjanus kasmira							5	4
Monotaxis grandoculis					1	2	1	1
Chaetodon auriga*		2						
Chaetodon citrinellus				1	2	4	1	1
Chaetodon cf. multiscinctus	1							
Chaetodon trifasciatis	1							
Centropyge flavissimus	1		1	1	2	2	2	2
Cephalopholis leopardus	2							
Cephalopholis urodelus								1
Epinephelus merra	2	2	3	1	1	3	5	4
Grammistops ocellatus	5		1					
Rypticus sp.								1
Scorpaenodes guamensis	6							
Scorpaenodes kellogi								3
Taenianotus triacanthus	1							
Caracanthus unippinus	1							
Dineamatichthys iluocoeteoides	1							
Paracirrhites arcuatus	1							
Synodus variegatus	2							1
Corythoicthys nigripectis								1
Doryrhamphus melanopleura	1							
Oxymonacanthus longirostris		1						1
Adioryx spinifer					1			5
Flammeo sammara	1							1
Holocentrus lacteoguttatus								26
Myripristis argyromus	11							14
Myripristis murdjan								2
Callechelys marmoratus	1							
Moringua sp.	1							
Enchelycore bayeri	1							2
Gymnothorax buroensis	1							
Acentrogobius cf. decoratus	1							15
Callogobius cf. sclateri								1
Eviota distigma	3							

Appendix 2, Cont'd.

Eviota sebreii	2							
Gobiodon sp. 4	4							2
Paragobiodon echino-cephalus	4							6
Paragobiodon xanthosoma	1							
Paragobiodon sp. 17	1							
Ptereleotris tricolor					1	44	22	8
Trimma caesiura	8							
Gobiidae sp. 5	16							4
Gobiidae sp. 18								1
Gobiidae sp. 20	4							
Trypterygiidae sp. 1	4							
Trypterygiidae sp. 2	4							
Unidentified larvae*								
Total No. Resident Species	49	14	16	18	24	14	27	46
Total Number Individuals	183	311	193	2949	403	378	359	309

Appendix 3. Census Data From Natural Defaunation Reef No. 8. Values are number of individuals. Reef No. 8 was defaunated 2 Sept. 72 and 12 Feb. 74. * indicates transient species.

	Days Since Initial Defaunation							
Species	Base-line Sept. 1972	95 Dec. 1972	180 Mar. 1973	312 Jul. 1973	420 Oct. 1973	544 Feb. 1974	545 Feb. 1974	633 May 1974
Abudefduf curacao			1	3	4	3	3	
Abudefduf dicki	2		2	1	1	1	1	1
Chromis caerulea	54	253	425	80	1000	570	350	300
Chromis coelestis			3	1		9	9	8
Dascyllus reticulatus	3							1
Pomacentrus albofasciatus		1	7				2	
Pomacentrus nigricans	2							
Pomacentrus pavo	71	122	62	300	100	700	230	78
Pomacentrus vaiuli	5	2	4	10	20	9	9	12
Cheilinus chlorourus		1	1					
Coris variegata			1			3	3	2
Gomphosus varius	1	3	1		1	1	1	2
Halichoeres bimaculatus	1							
Halichoeres hoeveni						1		2
Halichoeres trimaculatus*	15	4	1	20	35		1	
Hemigymnus sp.		1	1		1	1	1	
Labroides dimidiatus		1						
Pseudocheilinus hexataenia							1	
Stethojulis axillaris								1
Thalassoma amblycephalus	1				3	1	1	6
Thalassoma lutescens	2	1			6	1		1
Wetmorella ocellata	1							
Labridae sp. 1		7						
Scarus unimaculatus	1							
Scaridae sp. 1			3	1	1			1
Scaridae sp.				1		1		
Chaetodon auriga*		3			2			1
Chaetodon citrinellus		3	2	2	1	1	1	
Chaetodon ornatissimus				1	1	1		
Chaetodon reticulatus								1
Chaetodon trifascialis	1	2		1	1		1	
Centropyge flavissimus	1			1	1	1		
Zanclus cornutus			1	1	1			1
Gymnothorax buroensis	2						1	
Gymnothorax margaritophorus	1							

Appendix 3, Cont'd.

Muraenichthys gymnotus	1						3	
Moringua sp.	2							
Aspidontus taeniatus				1		1	1	1
Ecsenius bicolor	9	1			1	1	6	
Meiacanthus atrodorsalis		1						11
Apogon erythrinus	1						1	
Apogon exostigma							8	
Apogon novaeguineae	12	3	7	6	3		20	
Apogon savayensis	2							
Apogon cf. trimaculatus							2	
Paramia quinquelineata	6	14	6	9	6	7	12	1
Adioryx spinifer		1	1		1		1	2
Flammeo sammara	4	1		1	1	2	2	1
Holocentrus diadema	2	1		1				
Myripristis murdjan		1	1	1	1			
Holocentridae sp.	1							
Acanthurus olivaceous		6	1		1			2
Ctenochaetus striatus*	4	7	7	6	9		1	3
Zebrasoma velliferum			2					
Monotaxis grandoculis		1	1	1	3			
Gerreidae sp.	2							
Cephalopholis leopardus	3							
Epinephelus merra				2				1
Serranidae sp.	1							
Grammistops ocellatus	3						2	
Paracirrhites arcuatus	2	2	1	1	1			
Cirrhitidae sp.	1							
Canthigaster solandri	1		1			1	1	
Canthigasteridae sp.	1							
Corythoichtys nigripectis	4						1	
Doryrhamphus melanopleura								
Scorpaenodes hirsutus	1							
Scorpaenodes parvippinis	1							
Taenianotus triacanthus	1							
Dinematichthys iluocoeteoides	2							
Caracanthus unipinnus	1							
Callogobius cf. sclateri	1						3	
Eviota distigma	29							
Eviota sebreii	1							
Gobiodon sp. B	3						1	
Paragobiodon echinocephalus	5							
Paragobiodon sp. #17	3						9	
Gobiidae sp. 5	18						2	
Gobiidae sp. 20	11							
Gobiidae sp.	3							
Gobiidae sp.	1						2	
Trypterygiidae sp. 1	3						2	
Trypterygiidae sp. 2	2							

Appendix 3, Cont'd.

Total No. Resident Species	52	23	23	21	24	21	35	22
Total Number Individuals	310	429	534	423	1161	1315	690	436

APPENDIX 4

Species Composition of Artificial Reef No. 16. * indicates defaunations, + indicates the addition of five empty coral heads at 541 days.

Days Since First Defaunation (Days Since Last Defaunation)

Species	108(108)* Sept 72	202(94)* Dec 72	288(92)* Feb 73	291(3) Feb 73	295(7) Feb 73	300(12) Feb 73	439(139)* Jul 73	440(1) Jul 73	445(5) Jul 73	451(12) Jul 73	541(89) + Jul 73	553(12) Oct 73	631(90) Feb 74	721(80) May 74
Pomacentrus pavo	7	2	20	8	26	36	17	10	20	32	24	14	30	19
Pomacentrus vaigli	1						10							
Apogon novaeguineae	7						16							
Enneapterygius marra	1	1	2	1	1					1		1	2	2
Corythoichthys nigrirostris	1						1							
Tripterygiidae sp. 1	1													
Antennatus bigibbus	1													
Acanthurus elongatus	3													
Cheilinus chlorourus	1	1									1			1
Adioryx spinifer	1						1					1		
Gobiidae sp. 18	1													
Pomacentrus albofasciatus		2									1			
Zebrasoma veliferum		1									1			
Canthigaster sp.		2			1	2								
Abudefduf dicki			1											
Chaetodon citrinellus			1		1	1	1	1	1				2	1
Holocentrus diadema			1				1							
Halichoeres hortulanis			1											
Dorryhamphus melanopleura			1								2			
Stethojulis strigiventer			1											
Apogon erythrinus			1				1				1			
Tripterygiidae sp. 2			5				2				2			
Gobiidae sp. 20			2				1				2			
Acanthurus olivaceous					3	3								
Scaridae sp. 1					1									1
Labridae sp. 1						1		1	1			1	1	
Labridae sp. 2						3								
Apogon novemfasciatus						1								
Cheilodipterus macrodon							20							
Stenochaetus binotatus							2				3			
Dascyllus aruanus							1							
Eviota distigma							3	1					1	2
Thalassoma lutescens							1	1				1	1	
Apogon exostigma							1							
Gobiidae sp.							1							
Acentrogobius cf. decoratus							6				3			
Gobiidae sp. 5							2				1			
Eviota distigma							2							
Apogon gracilis								6						1
Thalassoma amblycephalus									1	1				1
Scorpaenodes kelloqi											1			
Chaetodon ephippium												2	2	
Prionas caerulea													60	82
Cheilinus sp.													1	
Coris bicus varius														1
Acanthuridae sp. 1														1
Stethojulis axillaris														2
Blenniidae sp. 1														1
Serranidae sp.														1

APPENDIX 5

Species Composition of Artificial Reef No. 19. * denotes defaunation, + indicates the addition of five coral heads at 420 days.

Days Since Artificial Reef Placement (Days Since Last Defaunation)

Species	101(101)* Dec 72	190(85) Feb 73	191(86)* Feb 73	192(1) Feb 73	195(3) Feb 73	202(7) Feb 73	207(12) Feb 73	322(115)* Jul 73	324(2) Jul 73	328(4) Jul 73	338(14) Jul 73	420(96) * Oct 73	512(188) Feb 74	611(287) May 74
Chromis ternatensis	6	1												
Pomacentrus albofasciatus	3	5	4	1	1	1	1	3				4	2	1
Pomacentrus pavo	5	14	14	3	1	1	8	29	5	33	35	39	47	74
Cheilinus chlorourus	1							1				1	1	1
Cheilinus sp.	1		1											
Coris variegata	1											2		
Stethojulis strigiventer	7													
Apogon novaeguineae	69		32	22				6				18	1	4
Parasia quinquelineata	8	12	11			48		6		1	8	5	1	2
Carangidae sp.	1													
Scorpaenidae sp.	1													
Corythoichthys flavofasciatus	1													
Gobiidae sp. 5	1							4						
Trypterygiidae sp. 1	2		5					16						
Bolinichthys photothorax	1													
Labroides dimidiatus		1												
Acanthuridae sp. 1		3	1			1	3							
Xenius bicolor			1											
Ctenochaetus binotatus			2					7						
Corythoichthys nigripectis			2					6						
Apogon erythrinus			3					4						1
Acentrogobius cf. decoratus			7					10						
Gobiidae sp. 18			1											
Unidentified larvae						1000				1000				
Pomacentrus vaiuli								6						1
Canthigaster solandri								2				1		1
Dorrhamphus melanopleura								10						
Apogon exostigma								1						
Scaridae sp. 1								1			1	6		1
Gobiidae sp. 6								2						
Gobiidae sp. 11								1						
Gobiidae sp. 20								2						
Callogobius cf. sclateri								1						
Trimma caesiura								1						
Zonogobius semidoliatus								1						
Labridae sp. 1									1				1	
Acanthurus olivaceous									1					
Chromis coelestis										2	2			
Epinephelus merra												1		
Labridae sp. 5												1		
Chromis caerulea													209	30
Dascyllus aruanus													4	4
Chaetodon citrinellus													2	
Aspidontus taeniatus													1	
Halichoeres marginatus													1	
Halichoeres hoeveni													2	
Thalassoma amblycephalus														1
Stethojulis axillaris														1
Thalassoma lutescens														1

APPENDIX 6

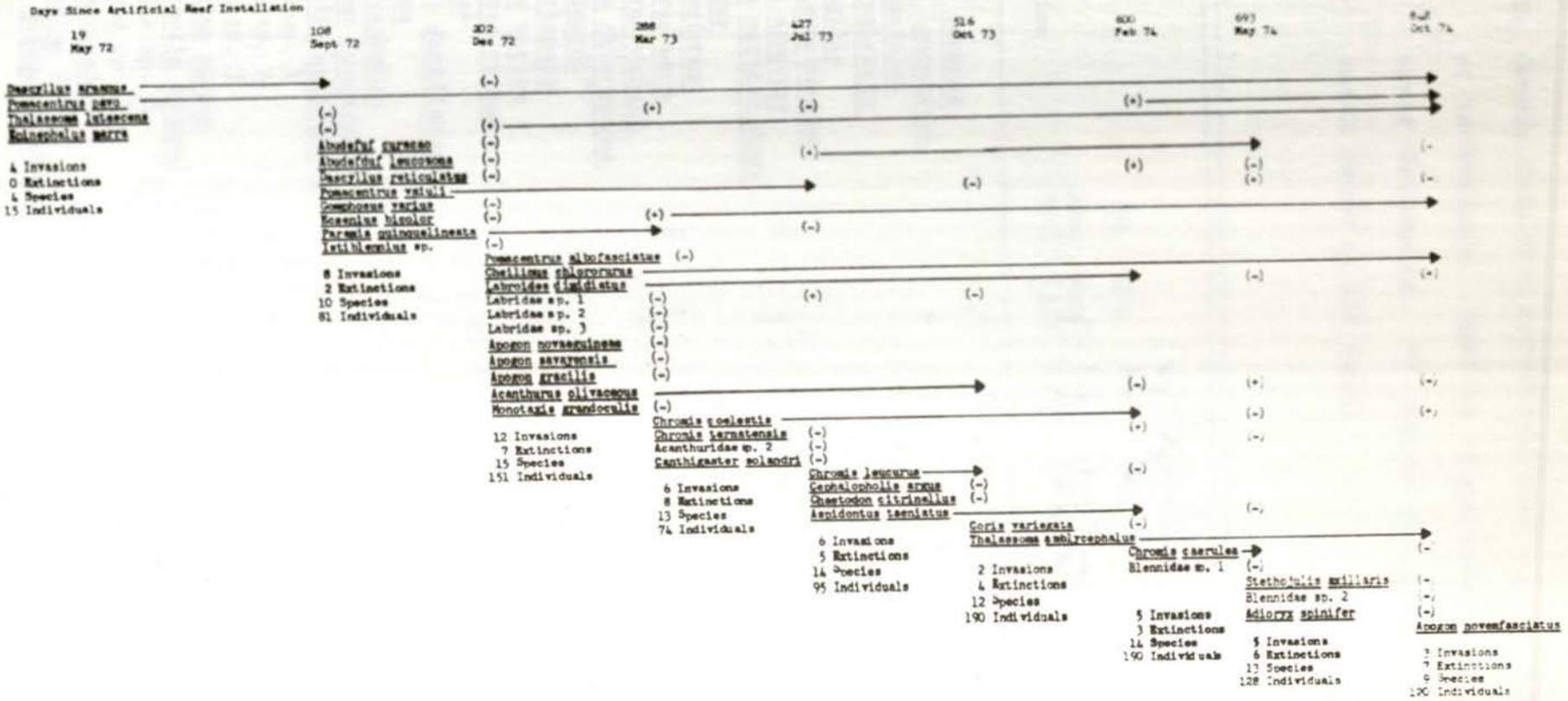
Species Composition of Artificial Reef No. 10. * denotes defaunation, + indicates the addition of five coral heads.

Days Since Artificial Reef Placement (Days Since Last Defaunation)

Species	99(99)* Dec 72	174(75)* Feb 73	177(3) Feb 73	181(7) Feb 73	186(12) Feb 73	296(122)* Jul 73	298(2) Jul 73	300(4) Jul 73	306(10) Jul 73	379(83) * Oct 73	392(96) Oct 73	491(195) Feb 73	590(294) May 74
Chromis ternatensis	10						1	6					
Pomacentrus albofasciatus	3	1				1	3	4	3		4	3	
Pomacentrus pavo	35	16	2	4	11	12	3		60	22	33	41	35
Labridae sp. 1	1						1			1		3	2
Labridae sp. 2	2				1								2
Labridae sp. 3	1				1			1			1		
Apogon erythrinus	2					5							
Apogon exostigma	2	1				1		3					
Apogon novaeguineae	67	23					1		8	8	11	5	22
Paramia quinquelineata	24			1	2	2	3	3	10	10	10	7	1
Cheilinus sp.	1					8							
Acanthurus olivaceous	1	1	1										
Corythoichthys nigripectis	4												
Blenniidae sp. 1	3												
Scaridae sp. 1	1		1	1		1	1	2	2		1		
Gobiidae sp.	1												
Gobiidae sp.	1												
Trypterygiidae sp. 1	2					2							
Unidentified larvae	3000												
Pterelcotris tricolor	18										1	1	1
Cheilinus chlorourus		1				1							
Dorryhamphus melanopleura		4											
Stethojulis strigiventer		4											
Halichoeres marginatus		1						1			1	1	2
Epinephelus merra		2				1							
Petrocirtes miniatus		3											
Acentrogobius cf. decoratus		3				6							
Gobiidae sp. 20		2				2							
Gobiidae sp. 22		1				15							
Zebrasoma veliferum			1						1				
Acanthuridae sp. 1				1	2	2							
Chromis agilis						1							2
Xenius bicolor						1							
Eviota sp. 16						21							
Eviota distigma						2							
Gobiidae sp. 18						1							
Gobiodon sp. B						1							
Trypterygiidae sp. 2						11							
Cabillus sp. A						1							
Labridae sp.						11							
Coris variegata									1	3	4		1
Labridae sp.									1				
Dascyllus reticulatus											1		1
Pomacentrus vaiuli											1	1	2
Chromis caerulea												60	70
Chromis coelestis												5	2
Coris gaimardi												2	
Goemphosus varius												1	3
Canthigaster sp.												1	
Halichoeres hoeveni												1	
Bodianus axillaris													1
Stethojulis axillaris													

APPENDIX 7A

Species Composition of Artificial Reef No. 2.


Days Since Artificial Reef Installation
19 May 72
108 Sept 72
202 Dec 72
288 Mar 73
427 Jul 73
516 Oct 73
600 Feb 74
693 May 74
Oct 74
Dasyllus aruanus
Pomacentrus pavo
Thalassoma lutescens
Halichoeres margaritaceus
4 Invasions
0 Extinctions
4 Species
15 Individuals
Abudefduf curacao
Abudefduf leucozonus
Dascyllus reticulatus
Pomacentrus vaiuli
Gomphosus varius
Scarus hipolar
Parma polylepis
Petroscirtes sp.
8 Invasions
2 Extinctions
10 Species
81 Individuals
Pomacentrus albofasciatus
Cheilinus chlorourus
Labroides dimidiatus
Labridae sp. 1
Labridae sp. 2
Labridae sp. 3
Apogon novaeguineae
Apogon savayensis
Apogon gracilis
Acanthurus olivaceus
Monotaxis grandoculis
12 Invasions
7 Extinctions
15 Species
151 Individuals
Chromis caerulea
Chromis lepidura
Acanthuridae sp. 2
Canthigaster solandri
6 Invasions
8 Extinctions
13 Species
74 Individuals
Chromis lepidura
Cephalopholis argus
Chaetodon citrinellus
Aspidontus taeniatus
6 Invasions
5 Extinctions
14 Species
95 Individuals
Coris variegata
Thalassoma amblycephalum
2 Invasions
4 Extinctions
12 Species
190 Individuals
Chromis caerulea
Blennidae sp. 1
5 Invasions
3 Extinctions
14 Species
190 Individuals
Stethojulis axillaris
Blennidae sp. 2
Adioryx spinifer
5 Invasions
6 Extinctions
13 Species
128 Individuals
Apogon novemfasciatus
3 Invasions
7 Extinctions
9 Species
190 Individuals

Appendix 7B. Census Data From Artificial Reef No. 2. Values are number of individuals. Reef No. 2 was installed 17 May 72 and was never defaunated. ** denotes the addition of ten empty coral heads at 518 days.

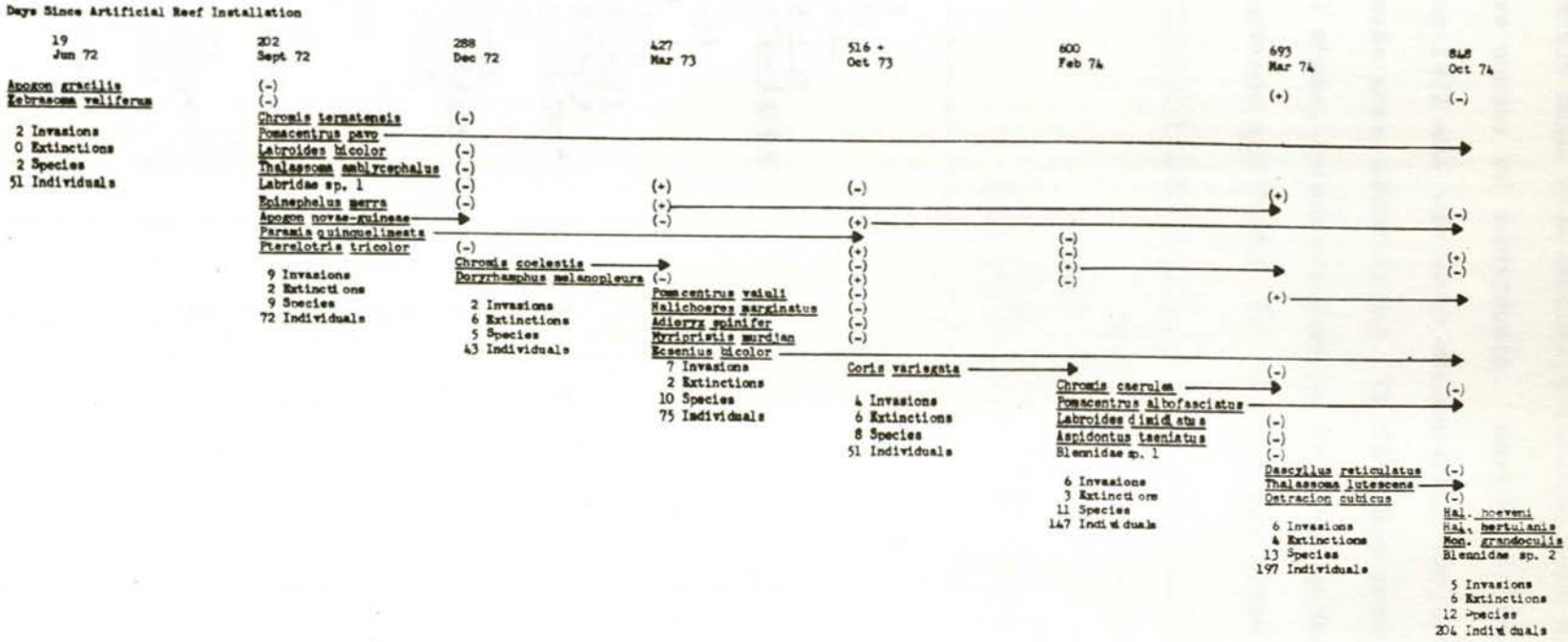
	No. Days Since Installation								
Species	19 June 1972	108 Sept. 1972	202 Dec. 1972	288 Mar. 1973	427 Jul. 1973	516** Oct. 1973	600 Feb. 1974	693 May 1974	848 Oct. 1974
Abudefduf curacao		1							
Abudefduf leucozona		1			1	1	1	1	
Chromis caerulea							124	65	
Chromis coelestis				14	1	8	7		1
Chromis agilis					2	2			
Chromis ternatensis				2			2		
Dascyllus aruanus	2	1							
Dascyllus reticulatus		2					1		
Pomacentrus albofasciatus			1						
Pomacentrus pavo	6	50	64	31	54	53	31	35	100
Pomacentrus vaiuli		3	1	3	5			1	
Cheilinus chlorourus			1	1	2	3	2	1	1
Coris gaimardi*			1						
Coris variegata						2			
Gomphosus varius		1							
Halichoeres trimaculatus*		4	3			1	1		
Labroides dimidiatus			2	1	2	2	2		3
Thalassoma amblycephalus						11	4	5	6
Thalassoma lutescens	5			8			2	5	2
Stethojulis axillaris								1	
Labridae sp. 1			50		3				
Labridae sp. 2			6						
Labridae sp. 3			1						
Epinephelus merra	1		1	2	5	5	3	2	3
Cephalopholis argus					1				
Blenniidae sp. 1							2		
Blenniidae sp. 2								1	
Ecsenius bicolor		6		1	2	2	5	3	3
Istibiennius sp.		1							
Paramia quinquelineata	15	2	4						

Appendix 7B, Cont'd.

Apogon gracilis			1						
Apogon novaeguineae			17						
Apogon novemfasciatus									1
Apogon savayensis			1						
Adioryx spinifer								1	
Acanthurus olivaceous			1	2	10	12		3	
Ctenochaetus striatus*	1	2	1	2	2	4	3	4	
Acanthuridae sp. 2				1					
Gerres oblongus			1						
Chaetodon auriga*			2	2				2	
Chaetodon citrinellus					1				
Chaetodon epphipium*				2					
Chaetodon lunula*		2							
Aspidontus taeniourus					4	3	1		
Canthigaster solandri				2					
Number Resident Species	4	10	15	13	14	12	14	13	9
Total Number Individuals	15	81	151	74	95	108	190	128	120

APPENDIX 8A

Species Composition of Artificial Reef No. 4. (+) indicates the addition of five coral heads at 530 days.


Days Since Artificial Reef Installation
19 Jun 72
202 Sept 72
288 Dec 72
427 Mar 73
516 + Oct 73
600 Feb 74
693 Mar 74
848 Oct 74
Apogon gracilis
Zebrasoma veliferum
2 Invasions
0 Extinctions
2 Species
51 Individuals
Chromis ternatensis
Pomacentrus pavo
Labroides bicolor
Thalassoma amblycephalus
Labridae sp. 1
Epinephelus merra
Apogon novae-guineae
Paramia quinquelineata
Pterelotris tricolor
9 Invasions
2 Extinctions
9 Species
72 Individuals
Chromis coelestis
Dorzyrhamphus melanopleura
2 Invasions
6 Extinctions
5 Species
43 Individuals
Pomacentrus vaiuli
Halichoeres marginatus
Adioryx spinifer
Myripristis murdjan
Ecsenius bicolor
7 Invasions
2 Extinctions
10 Species
75 Individuals
Coris variegata
4 Invasions
6 Extinctions
8 Species
51 Individuals
Chromis caerulea
Pomacentrus albofasciatus
Labroides dimidiatus
Aspidontus taeniatus
Blenniidae sp. 1
6 Invasions
3 Extinctions
11 Species
147 Individuals
Dascyllus reticulatus
Thalassoma lutescens
Ostracion cubicus
6 Invasions
4 Extinctions
13 Species
197 Individuals
Hal. hoeveni
Hal. hortulanis
Mon. grandoculis
Blenniidae sp. 2
5 Invasions
6 Extinctions
12 Species
204 Individuals

Appendix 8B. Census Data from Control Artificial Reef No. 4. Values are number of individuals. Reef No. 4 was installed 17 May 1972 and was never defaunated. Ten uninhabited coral heads were added 23 Oct. 73 (530 days post installation); of these, seven remained in Feb. 74, in May 74, and two survived until Oct. 74. * indicates transient species.

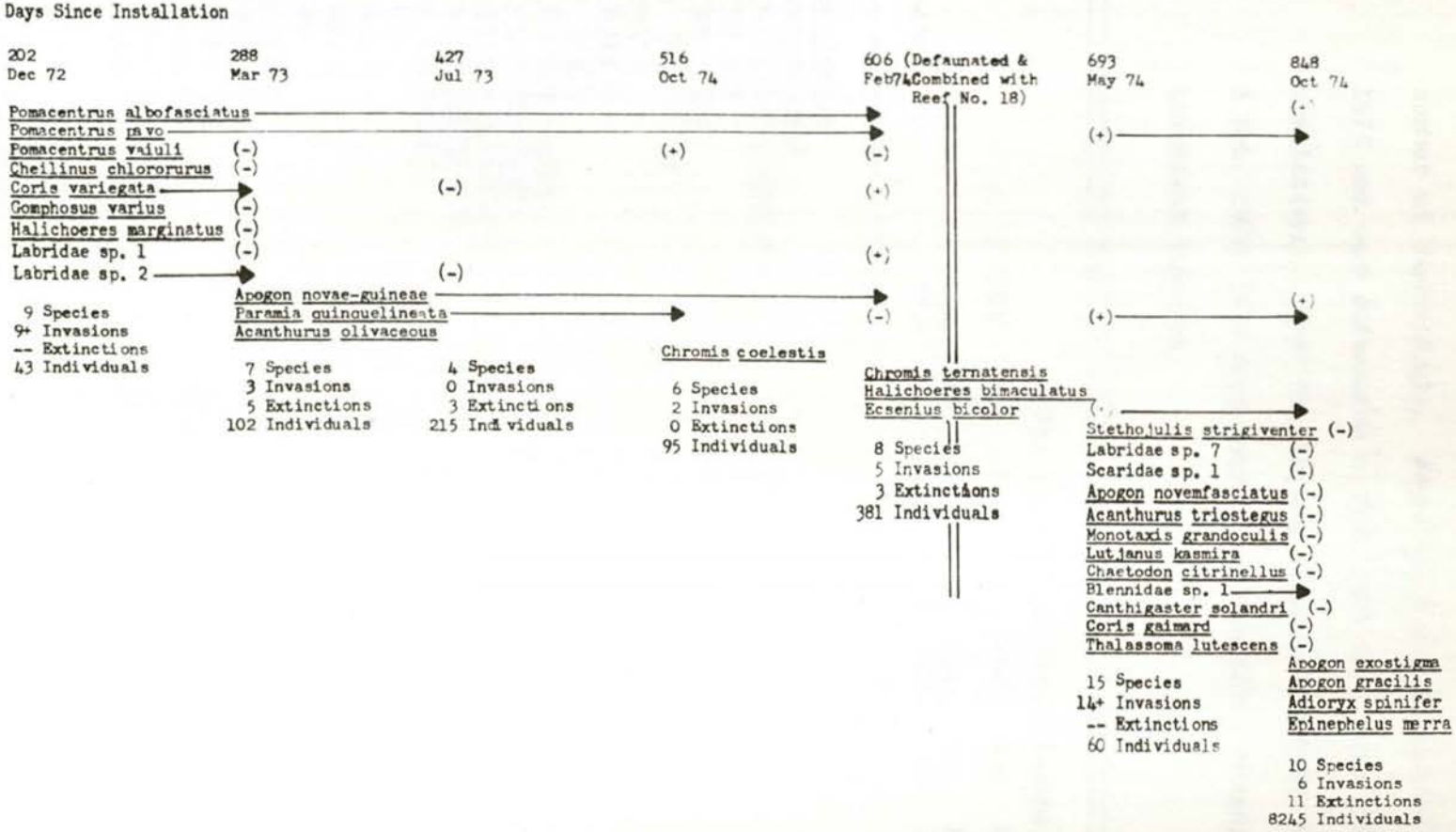
	No. Days Since Installation							
	19	202	288	427	516	600	693	848
Species	June 1972	Sept. 1972	Dec. 1972	Mar. 1973	Oct. 1973	Feb. 1974	May 1974	Oct. 1974
Chromis caerulea						72	21	
Chromis coelestis			6	6		6	2	
Chromis ternatensis		1						
Dascyllus reticulatus							5	
Pomacentrus albofasciatus						1	2	2
Pomacentrus pavo		34	21	56	27	39	53	168
Pomacentrus vaiuli				1			3	1
Coris variegata					1	1		
Halichoeres hoeveni								1
Halichoeres hortulanis								1
Halichoeres marginatus				1				
Halichoeres trimaculatus*		7	14	4	4	11	1	3
Labroides bicolor		1						
Labroides dimidiatus						1		
Thalassoma amblycephalus		1						
Thalassoma lutescens							2	3
Labridae sp. 1		1		3			1	1
Epinephelus merra		2		2	1	2	1	
Apogon gracilis	50							
Apogon novaeguineae		20	4		12	16	100	20
Paramia quinquelineata		10	10	1	3			
Adioryx spinifer				1				
Myripristis murdjan				1				
Ctenochaetus striatus*		4	2	3			3	
Zebrasoma velliferum	1						1	
Gerres oblongus								1
Aspidontus taeniourus						1		
Ecsenius bicolor				3	2	6	5	3
Blennidae sp. 1						1		
Blennidae sp. 2								2

Appendix 8B, Cont'd.

Ptereleotris tricolor		2			4			1
Doryrhamphus melanopleura			2		1			
Chaetodon auriga*						1		
Ostracion cubicus							1	
Number Resident Species	2	9	5	11	8	11	13	12
Number Individuals	51	72	43	75	51	147	197	204

APPENDIX 9A

Species Composition of Artificial Reef No. 6. An arrow portrays the last date the species was recorded.


Days Since Installation
202
Dec 72
288
Mar 73
427
Jul 73
516
Oct 74
606 (Defaunated & Combined with Reef No. 18)
Feb74
693
May 74
848
Oct 74
Pomacentrus albofasciatus
Pomacentrus pavo
Pomacentrus vaiuli (-) (+) (-) (+)
Cheilinus chlororurus (-)
Coris variegata (-)
Gomphosus varius (-)
Halichoeres marginatus (-)
Labridae sp. 1 (-)
Labridae sp. 2 (-)
Apogon novae-guineae
Paramia quinquelineata (-) (+)
Acanthurus olivaceous
9 Species
9+ Invasions
-- Extinctions
43 Individuals
7 Species
3 Invasions
5 Extinctions
102 Individuals
4 Species
0 Invasions
3 Extinctions
215 Individuals
Chromis coelestis
6 Species
2 Invasions
0 Extinctions
95 Individuals
Chromis ternatensis
Halichoeres bimaculatus
Ecsenius bicolor
8 Species
5 Invasions
3 Extinctions
381 Individuals
Stethojulis strigiventer (-)
Labridae sp. 7 (-)
Scaridae sp. 1 (-)
Apogon novemfasciatus (-)
Acanthurus triostegus (-)
Monotaxis grandoculis (-)
Lutjanus kasmira (-)
Chaetodon citrinellus (-)
Blennidae sp. 1
Canthigaster solandri (-)
Coris gaimard (-)
Thalassoma lutescens (-)
15 Species
14+ Invasions
-- Extinctions
60 Individuals
Apogon exostigma
Apogon gracilis
Adioryx spinifer
Epinephelus merra
10 Species
6 Invasions
11 Extinctions
8245 Individuals

Appendix 9B. Census Data From Artificial Reef No. 6. Values are number of individuals. Reef No. 6 was installed 22 Aug. 1974 and was defaunated 4 Feb. 1974 (519 days after installation). Reef No. 18 was added to Reef No. 6 on 5 Feb. 1974 (610 days post installation). * indicates transient species.

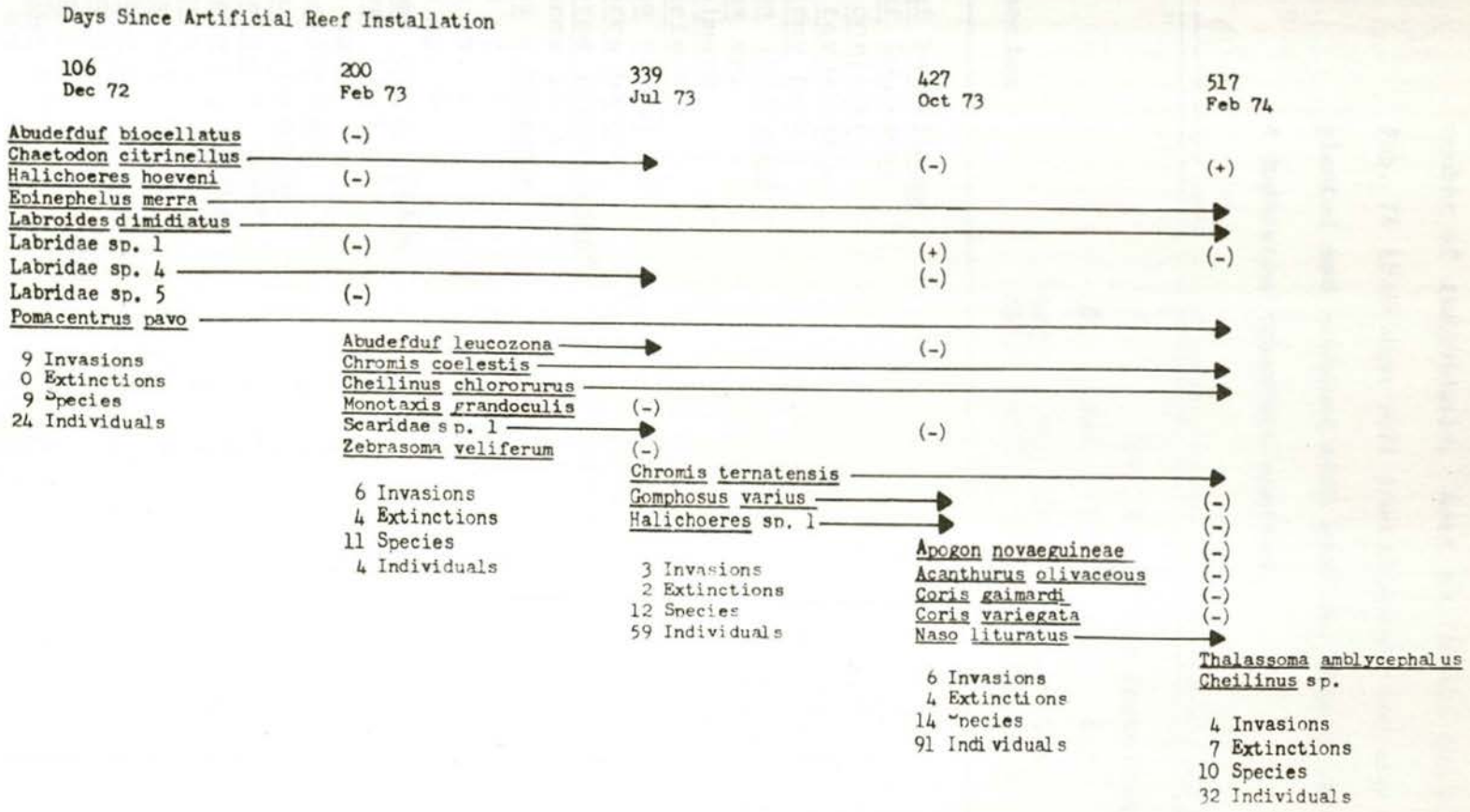
	No. Days Since Installation							
	202	288	427	516	606	609	693	848
Species	Sept. 1972	Dec. 1972	Mar. 1973	Oct. 1973	Feb. 1974	Feb. 1974	Mar. 1974	Oct. 1974
Chromis coelestis				1				
Chromis ternatensis					1			
Pomacentrus albofasciatus	1	1	1	4				1
Pomacentrus pavo	29	43	150	49	64	74	40	145
Pomacentrus vaiuli	2			2				
Cheilinus chlorourus	2							
Coris gaimard							1	
Coris variegata	1	2			1	1		
Gomphosus varius	1							
Halichoeres bimaculatus					10			
Halichoeres marginatus	1							
Halichoeres trimaculatus*	5	11	8	7		6	4	2
Stethojulis strigiventer						3		
Thalassoma lutescens							2	
Labridae sp. 1	5				1			
Labridae sp. 2	1	2						
Labridae sp. 7							1	
Scaridae sp. 1							1	
Apogon exostigma								2
Apogon gracilis								8000
Apogon erythrinus						1		
Apogon novaeguineae		32	61	12	302	86		63
Apogon novemfasciatus							1	
Paramia quinquelineata		21	3	27	0	1	1	24
Adioryx spinifer								1
Acanthurus olivaceous		1						
Acanthurus triostegus							1	
Ctenochaetus binotatus						3		
Ctenochaetus striatus*	3		3	1			5	6
Epinephelus merra								1

Appendix 9B, Cont'd.

Gerres oblongus							1	
Lutjanus kasmira							2	
Chaetodon auriga*		2		7	2			2
Chaetodon citrinellus						1	1	
Chaetodon lunula	1							
Ecsenius bicolor					2	1	6	8
Blennidae sp. 1							1	1
Corythoichthys nigripectis						7		
Doryrhamphys melanopleura						9		
Canthigaster solandri							1	
Trypterygiidae sp. 1						12		
Trypterygiidae sp. 2						12		
Acentrogobius cf. decoratus						13		
Eviota distigma						1		
Eviota inflatus						2		
Eviota smaragdus						35		
Eviota sp. (#16)						7		
Gobiidae sp. 21						2		
Gobiidae sp. 22						2		
Number Resident Species	9	7	4	6	8	20	15	10
Total Number Individuals	43	102	215	95	381	272	60	8245

APPENDIX 10A

Species Composition of Artificial Reef No. 18. An arrow portrays the last date the species was recorded.


Days Since Artificial Reef Installation
106
Dec 72
200
Feb 73
339
Jul 73
427
Oct 73
517
Feb 74
Abudefduf biocellatus
Chaetodon citrinellus
Halichoeres hoeveni
Epinephelus merra
Labroides dimidiatus
Labridae sp. 1
Labridae sp. 4
Labridae sp. 5
Pomacentrus pavo
(-)
(-)
(-)
(+)
(+)
(-)
(-)
(-)
9 Invasions
0 Extinctions
9 Species
24 Individuals
Abudefduf leucozona
Chromis coelestis
Cheilinus chlororurus
Monotaxis grandoculis
Scaridae sp. 1
Zebrasoma veliferum
(-)
(-)
(-)
(-)
(-)
(-)
6 Invasions
4 Extinctions
11 Species
4 Individuals
Chromis ternatensis
Gomphosus varius
Halichoeres sp. 1
(-)
(-)
(-)
3 Invasions
2 Extinctions
12 Species
59 Individuals
Apogon novaeguineae
Acanthurus olivaceous
Coris gaimardi
Coris variegata
Naso lituratus
(-)
(-)
(-)
(-)
(-)
6 Invasions
4 Extinctions
14 Species
91 Individuals
Thalassoma amblycephalus
Cheilinus sp.
4 Invasions
7 Extinctions
10 Species
32 Individuals

Appendix 10B. Census Data From Artificial Reef No. 18. Values are number of individuals. Reef No. 18 was defaunated 4 Feb. 74 (519 days post installation) and was transplanted and combined with Reef No. 6 on 5 Feb. 74.

* indicates transient species.

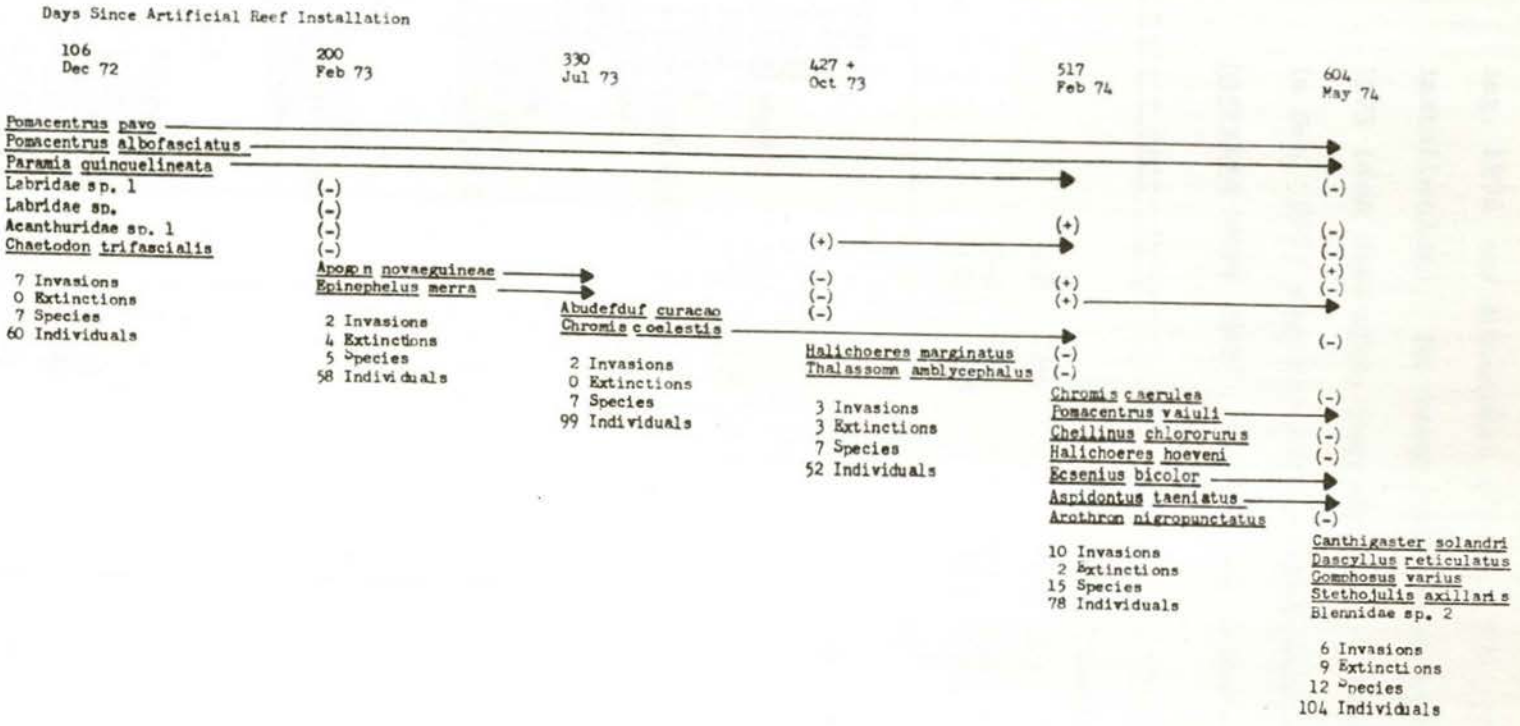
	No. Days Since Installation						
	12	106	200	339	427	517	519
Species	Sept. 1972	Dec. 1972	Feb. 1973	Jul. 1973	Oct. 1973	Feb. 1974	Feb. 1974
Abudefduf biocellatus		1					
Abudefduf leucozona			2	2		3	3
Chromis coelestis			6	3	6	6	6
Chromis ternatensis				2	1	1	1
Pomacentrus pavo		14	14	36	23	12	12
Cheilinus chlorourus			2	2	1	2	2
Cheilinus sp.							1
Coris gaimard					1		
Coris variegata					1		
Gomphosus varius				1			
Halichoeres hoeveni		1					
Halichoeres trimaculatus*		4	20			1	4
Halichoeres sp. 1				1	1		
Labroides dimidiatus		2	2	2	2	2	2
Labridae sp. 1		2			1		
Labridae sp. 4		1	1	1			
Labridae sp. 5		1					
Thalassoma amblycephalus						1	1
Thalassoma lutescens							1
Scaridae sp. 1			3	5			
Apogon novaeguineae					40		
Acanthurus olivaceous					10		
Ctenochaetus striatus*		3	6	8	6	4	2
Ctenochaetus binotatus							1
Naso lituratus					1	1	
Zebrasoma velliferum			1				
Gerres oblongus			1				
Chaetodon citrinellus		1	1	1		2	2
Corythoichthys nigripectis							1
Epinephelus merra		1	1	3	2	2	2
Moringua sp.							2
Acentrogobius cf. decoratus							1

Appendix 10B, Cont'd.

Callogobius cf. *sclateri*							1
Eviota distigma							2
Gobiidae sp. 5							1
Gobiidae sp. 20							3
Trypterygiid sp. 1							3
Trypterygiid sp. 2							3
Number Resident Species	0	9	11	12	14	10	21
Total Number Individuals	0	24	34	59	91	32	51

APPENDIX 11A

Species Composition of Artificial Reef No. 21. (+) indicates the addition of ten coral heads at 440 days.


Days Since Artificial Reef Installation
106
Dec 72
200
Feb 73
330
Jul 73
427 +
Oct 73
517
Feb 74
604
May 74
Pomacentrus pavo
Pomacentrus albofasciatus
Paramia quinquelineata
Labridae sp. 1
Labridae sp.
Acanthuridae sp. 1
Chaetodon trifascialis
7 Invasions
0 Extinctions
7 Species
60 Individuals
(-)
(-)
(-)
(-)
Apogon novaeguineae
Epinephelus merra
2 Invasions
4 Extinctions
5 Species
58 Individuals
Abudefduf curacao
Chromis coelestis
2 Invasions
0 Extinctions
7 Species
99 Individuals
(+)
(-)
(-)
(-)
Halichoeres marginatus
Thalassoma amblycephalus
3 Invasions
3 Extinctions
7 Species
52 Individuals
(+)
(+)
(-)
(-)
Chromis caerulea
Pomacentrus vaiuli
Chellinus chlororurus
Halichoeres hoeveni
Ecsenius bicolor
Aspidontus taeniatus
Arothron nigropunctatus
10 Invasions
2 Extinctions
15 Species
78 Individuals
(-)
(-)
(-)
(-)
(-)
(+)
(-)
(-)
(-)
Canthigaster solandri
Dascyllus reticulatus
Gomphosus varius
Stethojulis axillaris
Blennidae sp. 2
6 Invasions
9 Extinctions
12 Species
104 Individuals

Appendix 11B. Census Data From Artificial Reef No. 21. Values are number of individuals. Reef No. 21 was installed 22 Aug. 1974 and defaunated 12 Oct. 1974 (756 days post installation). Ten coral heads were added in Oct. 1973 (440 days after installation). These were removed in Oct. 1974 when two living heads lacking Chromis caerulea were added. * indicates transient species.

	No. Days Since Installation							
	106	200	339	427*	517	604	755	756
Species	Dec. 1972	Feb. 1973	Jul. 1973	Oct. 1973	Feb. 1974	May 1974	Oct. 1974	
Abudefduf curacao			1					
Chromis caerulea					10			
Chromis coelestis			2	4	1			
Dascyllus reticulatus						1		
Pomacentrus pavo	20	35	90	42	43	93	174	175
Pomacentrus vaiuli					8	1	2	1
Pomacentrus albofasciatus	3	2	3	1	1	1	1	1
Cheilinus chlorourus					3			
Coris variegata								1
Gomphosus varius						1		
Halichoeres hoeveni					1			
Halichoeres marginatus				1				
Halichoeres trimaculatus*	15	21	35	6	2	11	2	4
Labridae sp. 1	1						1	
Labridae sp.	1				1			
Labridae sp.								1
Stethojulis axillaris						1	1	
Thalassoma amblycephalus				2			1	1
Thalassoma lutescens						1	1	
Scaridae sp. 1							1	1
Ecsenius bicolor					1	1	3	4
Blennidae sp. 2								3
Aspidontus taeniourus					1	1		
Ptereleotris tricolor								3
Paramia quinquelineata	33	2	1	1	1			
Apogon novaeguineae		18	1		4		1	1
Ctenochaetus binotatus*								2
Ctenochaetus striatus*	5	4	1	1	3			
Acanthuridae sp. 1	1			1	1			

Appendix 11B, Cont'd.

Chaetodon auriga*					4			
Chaetodon citrinellus								1
Megaloprotodon trifascialis	1					1		
Centropyge flavissimus								
Arothron nigropunctatus					1			
Myripristis murdjan								1
Corythoichthys nigripectis								1
Doryrhamphus melanopleura								2
Epinephelus merra		1	1		1	1	1	1
Scorpaenodes kellogi								1
Canthigaster solandri						1	1	1
Rhinecanthus aculeatus							1	
Number Resident Species	7	5	7	7	15	12	11	18
Total Number Individuals	60	58	99	52	78	104	190	195

Appendix 12. Census Data From Artificial Reef No. 22. Values are number of individuals. Reef No. 22 was installed 23 Aug. 1972 and defaunated 19 Oct. 1973 (427 days post installation). Five coral heads with resident fishes were added 22 Oct. 1973 (at 470 days). * indicates transient species.

	No. Days Since Installation										
	106	200		(427)	430**	432	433	437	531	632	755
Species	Dec. 1972	Feb. 1973	Jul. 1973	Oct. 1973	Oct. 1973	Oct. 1973	Oct. 1973	Oct. 1973	Feb. 1974	May 1974	Oct. 1974
Abudefduf curacao							1				
Chromis caerulea					35	19	27	31	41		
Chromis coelestis				1			1		1		
Chromis ternatensis		1									
Dascyllus aruanus					1	1	1	1			
Dascyllus reticulatus					4	2	2	2			
Pomacentrus albofasciatus	4	8		1				2	2	4	1
Pomacentrus pavo	27	63		46		4	9	9	56	32	52
Pomacentrus vaiuli	1	4		1					1		1
Cheilinus chlorourus		1		1							
Coris variegata		1						1		2	
Gomphosus varius										1	
Halichoeres hoeveni				1							
Halichoeres marginatus									2		
Halichoeres trimaculatus*	10	7		5		2	2	5	5	1	
Stethojulis axillaris							1		1	1	
Thalassoma amblycephalus		1									
Thalassoma lutescens									2		

Appendix 12, Cont'd.

Labridae sp. 1	20								2	
Labridae sp. 2	1									
Labridae sp. 3	1									
Labridae sp. 4	1	3								
Labridae sp.	1									
Labridae sp.	1									
Labridae sp. 5									1	
Ecsenius bicolor								4	2	2
Blennidae sp. 1									1	1
Gerres oblongus	1	1								
Chaetodon auriga*	1				2	2				
Chaetodon citrinellus						1	1	1		
Centropyge flavissimus									1	
Paramia quinquelineata	23	6						1		
Apogon novaeguineae	5	10	29					1		
Apogon novemfasciatus	1	1								
Acanthurus olivaceous	2	2								
Ctenochaetus striatus*	4	2	2					1	3	
Acanthuridae sp. 1	1	1				1		2	1	
Zebrasoma veliferum							1			
Canthigaster solandri		1								
Serranidae sp.									1	1
Acentrogobius cf. decoratus			5							
Cabillus sp. B			1							
Zonogobius semidoliatus			1							
Number Resident Species	15	15	10	3	4	9	8	13	12	6
Total Number Individuals	90	104	87	40	26	35	48	115	49	58