REEF FISH POPULATION INVESTIGATIONS THROUGH THE USE OF PERMANENT TRANSECTS

Oct. 1981 to Sept. 1982

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JOB PROGRESS REPORT
RESEARCH PROJECT SEGMENT

STATE: Territory of Guam

PROJECT NO.: FW-2R-18
SUB-PROJECT NO.: F
STUDY NO.: F-1
JOB NO.: 5

JOB TITLE: Reef Fish Population Investigations through the use of Permanent Transects

PERIOD COVERED: October 1, 1981 to September 31, 1982

SUMMARY

Coral-reef fishes were monitored monthly at four upper reef-slope depths (5, 9, 18 and 30 m) at two locations on Guam between September 1979 and November 1980. Overall fish density increased markedly at all depths during the spring and summer months, corresponding to the onset of the rainy season and the diminishing of the tradewinds. Maximum abundances were recorded between May and July. A less pronounced increase in fish abundance occurred in the fall. Most of the observed seasonal variation in abundance resulted from juvenile recruitment and the movements of subadults and adults of a relatively small group of abundant species at each depth. Planktivores, piscivores and benthic-invertebrate feeders, primarily in deeper water, were largely responsible for the spring/summer peak, while the fall increase was significantly influenced by herbivores at shallower depths. Fluctuations of fish abundance may be related to variations in the availability of food resources. Climatological and oceanographical phenomena may have favorably influenced food resource availability as well as reproductive success during certain months. Estimates of site- and depth-related annual variation in abundance and species composition of 35 ubiquitous fish species indicated relative constancy over extensive areas of reef. Fish species richness was found to be greatest at 18 m. An explanation for this trend in species richness based on the "intermediate disturbance hypothesis" is offered.

BACKGROUND

During the past ten years increased emphasis has been given to studying the patterns of seasonal and annual variation of marine reef-fish assemblages. Such research may contribute to our understanding of basic principles underlying the functioning of coral-reef ecosystems, as well as provide potential practical insight into certain processes of fishery dynamics such as reproduction and recruitment.

During 1978 and 1979, the Division of Aquatic and Wildlife Resources (DAWR) used a steel barge artificial reef to increase the available fish habitat near the 18-m depth contour on the upper reef slope. During that project, fish counts made over a period of 20 months on the barge and along line transects permanently placed over surrounding areas of natural reef were used to monitor changes in the fish community. A result of the study was the documentation of a marked seasonal fluctuation in total fish abundance over the natural reef areas (Kock 1982). Seasonal increases among certain species were attributed partly to the immigration of adults and older juveniles, and partly to juvenile recruitment. Although no spawning peaks were observed, maximum settlement of juveniles occurred between March and June, and the highest overall fish abundance was recorded in May. Lowest overall abundance occurred during the winter months and reached similar levels in both years. Annual variability in species composition of the fish community was not examined.

Since it would be quite useful for fisheries managers and other ecologists to know how seasonal and annual fluctuations in fish abundance are manifested at different depths on the upper reef slope, the present investigation was undertaken. Work accomplished in this study has been reported annually since FY 79. Since that time the project has undergone minor revisions in its scope although its major objective has remained the same. This account is the final progress report for Job 5 and, therefore, supersedes all previous interim reports. It also represents an edited version of an M.S. thesis submitted to the Marine Laboratory, University of Guam.

OBJECTIVE

The objective of this study is to document the patterns of seasonal and annual variability within the conspicuous upper reef-slope fish community as they are manifested along a depth-related environmental gradient over a 15-month time period.

PROCEDURES

Study Sites

Fishes were monitored on the upper reef slope at Asan Pt. and Ipao Pt. on the leeward (western) side of Guam (Figure 1). Randall and Holloman (1974) stated that this zone in the Asan area is very similar to that found near Ipao Pt. At both sites the coral community showed evidence of past disturbance from *Acanthaster* predation.

Fishing effort observed in the vicinity of the transects during the study was minimal. In addition, monthly DAWR interviews of offshore anglers and divers returning to the Agana Boat Basin after fishing near either study site were relatively few both before and during the study period. Thus, the fishing pressures that occurred at both sites during the study are estimated to be relatively light and comparable in degree.

Transect Stations

During the spring of 1979, duplicate 50-m transects were placed along approximate depth contours of 5, 9, 18 and 30 m at each study site. A transect consisted of six unconnected rebar stakes embedded into reef rock at 10-m intervals. All stakes were flagged with a piece of yellow plastic marking tape to make them easier to locate on subsequent field days.

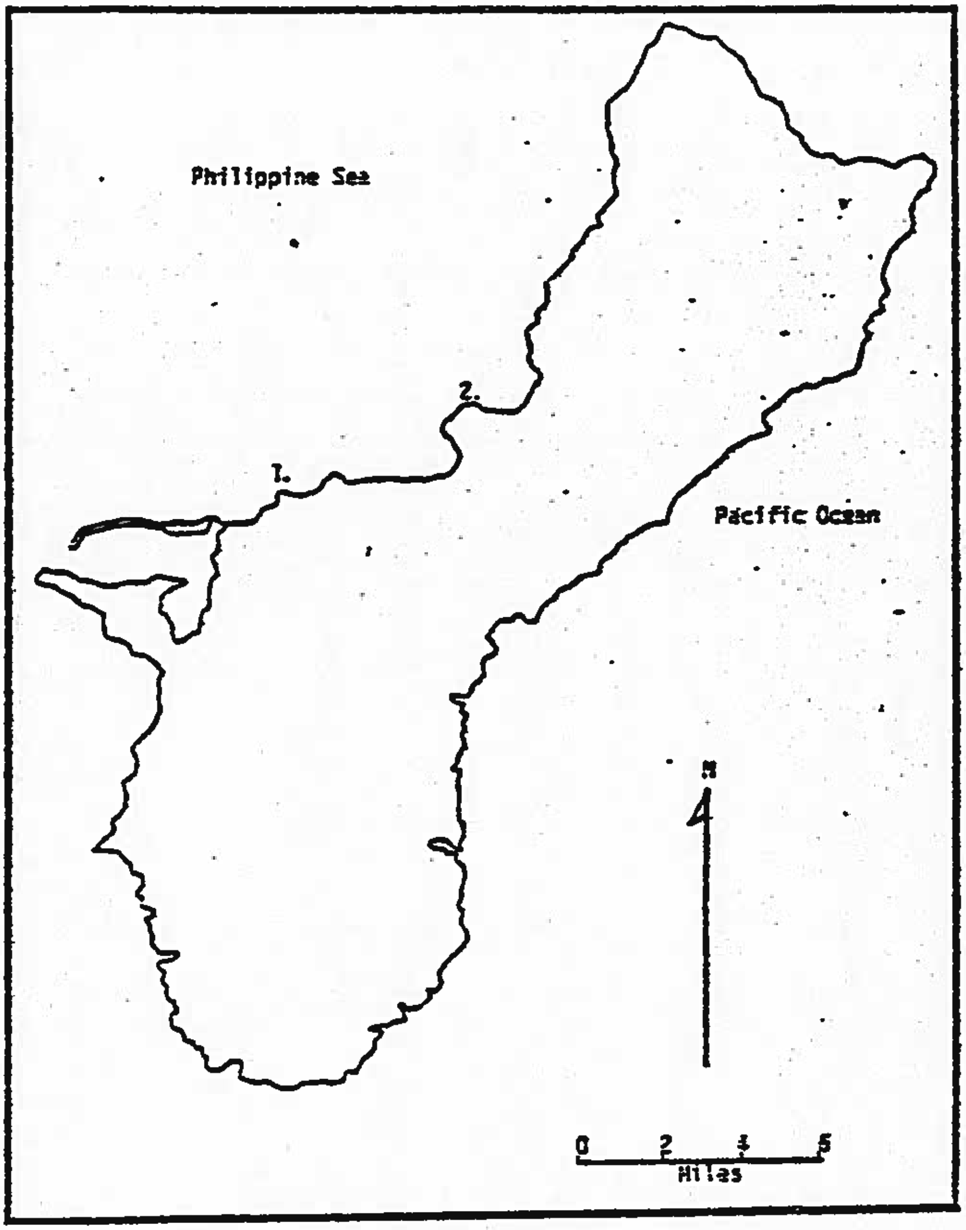

Figure 1. Map of Guam showing the locations of the Asan Pt. and Ipao Pt. study sites. 1. = Asan Pt.; 2. = Ipao Pt.

Data for the study were recorded on a submersible microcassette tape deck. Both the plexiglass housing for the tape deck and the special scuba regulator mouthpiece containing the remote microphone were manufactured under the name "Wet-Tape" by Sound-Wave Systems, Inc.

Formal monthly fish counts were begun in September 1979. Data collection was limited to the time between 1000 and 1400 hrs. Counts of individuals were made for all fish species observed as much as two meters above the substrate within a two-meter wide path between stakes. Dives were limited to a maximum of two depths per day, normally paired as 30 and 5 m, and 18 and 9 m. On a single field day, both 50-m transects at each of the two depths were censused twice (down and back) yielding monthly counts of fish over 400 m^2 of reef at each depth. Four to six field days per month were required to census the transects. Data collection was terminated with the November 1980 censuses.

Data Analyses

The Wet-Tape recording system failed temporarily in January 1980, resulting in the deletion of that month from the analysis. The system failed permanently after August 1980 so the remaining counts were compiled by hand. Because of the relatively short no-decompression time limit (25 minutes) for dives to 30 meters, and since it took longer to write down observations than it did to speak them, there was sufficient safe bottom time to record data on only one pass along these transects during the last three months of the study. These counts were, therefore, adjusted to reflect the number of individuals per 400 m^2 before being analyzed. To make the overall analysis more manageable, a conservatively selected subset of ubiquitous fish species was formed. Species composing this group were selected if they were counted on at least seven of the eight transect stations. The 35 species that qualified were used to compare seasonal climatological patterns with observed seasonal fluctuations in fish abundance.

Representative seasonal peak abundances for each of the most ubiquitous species were identified by their maximum mean monthly counts. Depths of greatest representation were chosen for each of these species based on the highest mean number per depth when the counts for all months were combined. In addition, each of the 35 most ubiquitous species was assigned to a general trophic category based on Hiatt and Strasburg (1960), Jones (1968), Randall and Klausewitz (1973), Hobson (1974), Allen (1975), and Ogden and Lobel (1978). Thus, trends in peak abundances across depths and over months could be related to general food habits.

Observed changes in overall fish abundance were compared with seasonal patterns of average monthly rainfall (Fig. 2) based on 24 years of Guam precipitation data from the National Oceanic and Atmospheric Administration (NOAA) (1979, 1980) and with seasonal shifts in average monthly wind patterns (Fig. 3) based on 21 years of unpublished data provided by the U. S. Naval Oceanography Command Detachment (NOCD), U. S. Naval Air Station, Guam. To examine further the influences carnivores and herbivores may have had on the overall counts during different periods of the year, these trophic groups were expanded to consist of 28 species each. These species included the carnivores and herbivores within the most ubiquitous group, as

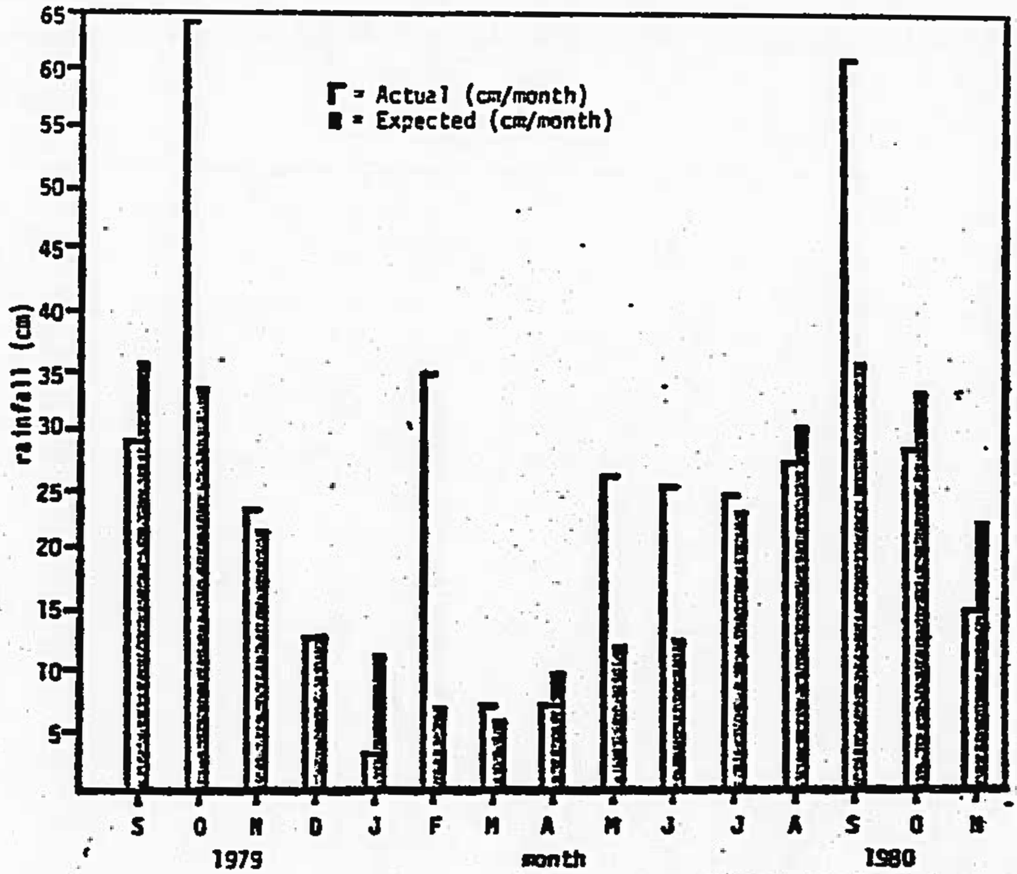

Figure 2. Monthly rainfall on the island of Guam.

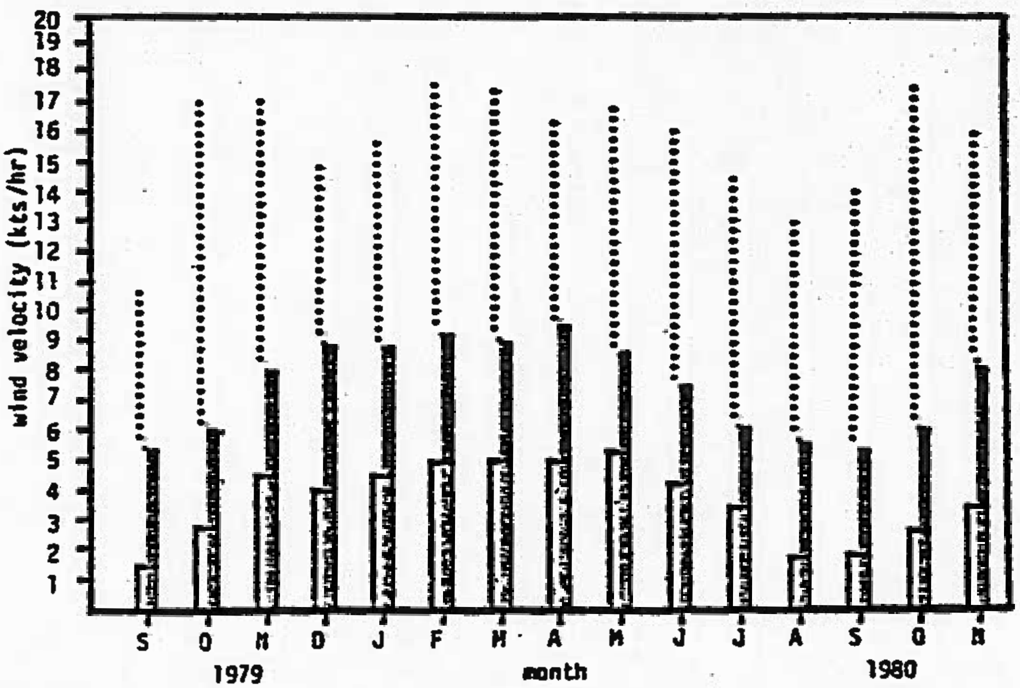

Figure 3. Monthly windspeed on the island of Guam. ⋮ = actual $\bar{x}$ maximum sustained high-hour wind velocity; ▛ = actual $\bar{x}$ wind velocity ▮ = expected $\bar{x}$ wind velocity.

ubiquitous group, as well as additional species which occurred frequently and were of notable abundance.

Estimates of the annual variability in fish species abundance between consecutive years were calculated for the most ubiquitous species group according to the method of Wolda (1978). The formula is as follows:

$$\log R = \log N_i - \log N_{i-1}$$

where N_i equals the number of individuals of a species counted during a particular month in 1980,

N_{i-1} equals the number of individuals of the same species counted in the same month in 1979,

and, R, the net reproductive rate (Andrewartha and Birch 1954) or the gradation coefficient (Benedek 1970), equals a ratio expressing the change in abundance from one year to the next.

Log R's were computed individually for the most ubiquitous species and averaged to provide an estimate of the average net change in species abundance ($\bar{R}$) for the group as a whole. The magnitude of this change was estimated by the variance of the log R's and is expressed as annual variability (AV) (Wolda 1978) in numbers of fish per species between consecutive years. If nearly as many species increased as decreased in abundance between years, $\bar{R}$ would have a value near zero; and, if the magnitude of these increases or decreases was small, AV would also be relatively low.

Values of AV were calculated for each study site based on the most ubiquitous species counts which were lumped across depths. AV's were computed separately for the site-specific September, October and November data and were averaged to give a mean value per site (1600 m^2 of reef). Annual variability (AV) at each depth was calculated using the same 35 species by lumping the data from both sites and computing separate values for September, October and November. The resulting values of AV were averaged across months to obtain mean values per depth (800 m^2 of reef).

Annual variation in species composition within the most ubiquitous species group was estimated for each transect depth and study site by two commonly used similarity indices. These include the following:

1) $$J = \frac{a}{a + b + c}$$

where a equals the number of species recorded during a particular month in both 1979 and 1980,

b equals the number of species recorded during that month in 1980, but not during that month in 1979,

and c equals the number of species recorded during that month in 1979, but not during that month in 1980 (Sokal and Sneath 1963); and

$$2)\quad R = \frac{C}{T_1} + \frac{C}{T_2} \times 0.5$$

where C equals the number of species recorded during a particular month in both 1979 and 1980,

T_1 equals the number of species recorded during that month in 1979,

and T_2 equals the number of species recorded during the that month in 1980 (Smith 1973).

RESULTS

Seasonal Variation

All fish species counted during the study are listed by site and depth in Tables 1 and 2. An increase in overall fish abundance occurred at all depths during the spring and summer months, with maximum monthly counts recorded in May, June and July (Fig. 4). Although there were some variations in these seasonal trends at each depth at the two survey areas, in general the patterns at Asan and Ipao were similar (Fig. 5). Most of the observed seasonal increase in fish abundance is primarily attributable to a relatively small group of species which are well represented at each station (Table 3). In every case, however, other important but less abundant species also contributed to the overall fluctuations. Species that were among the most influential at each depth during the entire investigation are shown Figs. 6a-n.

An examination of the 35 most ubiquitous species (Table 4) revealed a bimodal pattern of seasonal peak abundance (Fig. 7). More of these ubiquitous species peaked in May and November than in any of the other months. Also, the majority of the May peaks (57%) occurred at 18 and 30 m, while 71% of the November peaks were recorded at 5 and 9 m. Nineteen of the ubiquitous species were assigned to a general carnivore group which included planktivores, piscivores and benthic invertebrate-feeders; nine were listed as herbivores; and seven were categorized as omnivores (Table 5). Within the carnivore group, 13 species were observed to peak in abundance at either 18 or 30 m (Table 6). Not surprisingly, most of the herbivores peaked at 5 and 9 m, while the recorded peak abundances among the omnivores were almost equally distributed. The monthly fluctuations in numbers of peaking species per trophic category strongly suggests a temporal partition in peak abundance between carnivore and herbivore groups (Fig. 8). When the carnivore and herivore groups were expanded to include 28 species apiece, the resulting overall pattern in temporal partitioning remained just as strong (Fig. 9).

Although the relationships were less clear at 5 m, fluctuations in overall fish abundance (Fig. 4) seemed to be positively correlated with rainfall (Fig. 2) and negatively correlated with windspeed (Fig. 3). The expanded carnivore and herbivore data were tested to see if rainfall might be a factor influencing the timing of the observed peak abundances. While the

Table 1. Fish species seen on Asan Pt. transects from September 1979 through November 1980. * = seen only on Asan Pt. transects.

FAMILY/SPECIES	DEPTH (m) 5	9	18	30
ACANTHURIDAE (Surgeonfishes)				
Acanthurus glaucoparieus Cuvier	X	X	X	X
A. lineatus (Linnaeus)	X			
A. mata Cuvier	X	X	X	
A. nigrofuscus (Forsskal)	X	X	X	X
A. olivaceus Bloch & Schneider		X	X	X
A. pyroferus Kittlitz			X	X
A. triostegus (Linnaeus)	X	X		
Ctenochaetus striatus (Quoy & Gaimard)	X	X	X	
Naso brevirostris (Valenciennes)			X	X
N. hexacanthus (Bleeker)				X
N. lituratus (Bloch & Schneider)	X	X	X	X
**Paracanthurus hepatus* (Linnaeus)		X	X	
Zebrasoma flavescens (Bennett)		X	X	X
Z. veliferum (Bloch)			X	
APOGONIDAE (Cardinalfishes)				
**Apogon novemfasciatus* Cuvier			X	
Cheilodipterus quinquelineatus (Cuvier)				X
AULOSTOMIDAE (Trumpetfishes)				
Aulostomus chinensis (Linnaeus)	X			X
BALISTIDAE (Triggerfishes)				
Balistapus undulatus (Park)		X	X	X
Balistoides conspicillum (Bloch & Schneider)	X		X	X
**B. viridescens* (Bloch & Schneider)			X	X
Melichthys vidua (Solander)	X	X	X	X
**Odonus niger* (Ruppell)			X	
Pseudobalistes flavomarginatus (Ruppell)			X	
**Rhinecanthus echarpe* (Lacepede)	X			
Sufflamen bursa (Bloch & Schneider)	X	X	X	X
S. chrysopterus (Bloch & Schneider)	X	X	X	
BLENNIIDAE (Blennies)				
Aspidontis taeniatus (Quoy & Gaimard)		X		
Ecsenius bicolor (Day)	X	X	X	
Meiacanthus atrodorsalis (Gunther)	X		X	X
Plagiotremus tapeinosoma (Bleeker)	X	X	X	

FAMILY/SPECIES	DEPTH (m) 5	9	18	30
CARACANTHIDAE (Velvetfishes)				
**Caracanthus maculatus* (Gray)		X		
CARANGIDAE (Jacks, Pompanos)				
**Caranx melampygus* Cuvier		X		
CHAETODONTIDAE (Butterflyfishes)				
Chaetodon auriga Forsskal	X			
C. citrinellus Cuvier	X	X	X	
C. ephippium Cuvier		X		
C. lunula (Lacepede)	X			X
C. mertensii Cuvier			X	X
C. ornatissimus Cuvier	X			
C. punctatofasciatus Cuvier	X	X	X	X
C. reticulatus Cuvier	X	X	X	
C. trifasciatus Park		X		X
C. ulietensis Cuvier			X	X
C. unimaculatus Bloch		X		
Forcipiger flavissimus Jordan & McGregor	X	X		X
F. longirostris (Broussonet)				X
Hemitaurichthys polylepis (Bleeker)				X
Heniochus chrysostomus Cuvier		X	X	
**H. singularis* Smith & Radcliffe			X	
Megaprotodon trifascialis (Quoy & Gaimard)				X
CIRRHITIDAE (Hawkfishes)				
Cirrhitichthys falco Randall		X	X	X
Neocirrhites armatus Castelnau		X		
Paracirrhites arcatus (Cuvier)	X	X	X	
P. forsteri (Bloch & Schneider)	X	X	X	
GOBIIDAE (Gobies)				
Nemateleotris magnifica Fowler		X	X	X
Pogonoculius zebra Fowler	X	X		
Ptereleotris evides (Jordan & Hubbs)	X		X	
Valenciennea strigatus (Brousonnet)	X	X	X	X
HOLOCENTRIDAE (Squirrelfishes)				
Adioryx caudimaculatus (Ruppell)				X
Flammeo sammara (Forsskal)				X

FAMILY/SPECIES	DEPTH (m) 5	9	18	30
LABRIDAE (Wrasses)				
Anampses caeruleopunctatus Ruppell	X			
A. meleagrides Valenciennes			X	X
A. twisti (Bleeker)		X		
Bodianus axillaris (Bennett)				X
Cheilinus chlorourus (Bloch)			X	X
C. fasciatus (Bloch)	X		X	X
C. unifasciatus Gunther	X	X	X	X
C. trilobatus Lacepede	X	X	X	X
C. undulatus Ruppell		X		
Cirrhilabrus sp.	X	X	X	X
Coris gaimard (Quoy & Gaimard)		X	X	X
Epibulus insidiator (Pallas)	X	X	X	X
Gomphosus varius Lacepede	X	X		X
Halichoeres biccellatus Schultz			X	X
H. hortulanus (Lacepede)	X	X		X
H. margaritaceus (Valenciennes)	X	X		
H. marginatus Ruppell	X	X	X	
H. sp.			X	
Hemigymnus melapterus (Bloch)	X	X		X
Hologymnosus doliatus (Lacepede)	X	X	X	X
Labroides bicolor Fowler & Bean	X	X		X
L. dimidiatus (Valenciennes)	X	X	X	X
Labropsis micronesica Randall		X		
L. xanthonotus Randall			X	X
Macropharyngodon meleagris (Valenciennes)		X	X	X
**Novaculichthys taeniourus* (Lacepede)		X	X	
Pseudocheilinus evanidus Jordan & Evermann		X	X	X
P. hexataenia (Bleeker)		X	X	
Stethojulis bandanensis (Bleeker)	X	X	X	X
Thalassoma amblycephalum (Bleeker)	X	X		
T. lutescens (Lay & Bennett)	X	X	X	X
T. quinquevittatum (Lay & Bennett)	X	X		
**Labrid* sp. 1	X			
**Labrid* sp. 2			X	
LETHRINIDAE (Emperors)				
**Monotaxis grandoculis* (Forsskal)				X
LUTJANIDAE (Snappers)				
**Lutjanus bohar* (Forsskal				X
**L. rivulatus* (Cuvier & Valenciennes)				X

FAMILY/SPECIES	DEPTH (m) 5	9	18	30
MALACANTHIDAE (False Whitings)				
*Malacanthus brevirostris Guichenot			X	
MONACANTHIDAE (Filefishes)				
*Cantherhines dumerili (Hollard)			X	
C. pardalis (Ruppell)	X	X	X	
Paraluteres prionurus Bleeker			X	
P. melanocephalus (Bleeker)		X	X	
MUGILOIDIDAE (Sand Perches)				
Parapercis clathrata Ogilby	X	X	X	X
MULLIDAE (Goatfishes)				
Mulloidichthys flavolineatus (Lacepede)	X			
Parupeneus bifasciatus (Lacepede)	X		X	X
P. chryserydros (Lacepede)	X	X	X	X
P. pleurostigma (Bennett)	X		X	X
P. trifasciatus (Lacepede)	X	X	X	X
MURAENIDAE (Moray Eels)				
*Lycodontis richardsoni (Bleeker)		X		
OSTRACIONTIDAE (Boxfishes, Cowfises)				
Ostracion meleagris Shaw		X		X
POMACANTHIDAE (Angelfishes)				
Apolemichthys trimaculatus (Cuvier)	X	X	X	
*Centropyge bicolor Bloch	X			
C. flavissimus (Cuvier)	X	X	X	
C. heraldi Woods & Schultz			X	X
C. shepardi Randall & Yasuda			X	X
Pygoplites diacanthus (Boddaert)			X	X
POMACENTRIDAE (Damselfishes)				
Amphiprion clarkii (Bennett)		X	X	
Chromis acares Randall & Swerdloff		X		
C. amboinensis (Bleeker)			X	
C. margaritifer Fowler	X	X		
Chrysiptera leucopomus (Lesson)	X	X		

FAMILY/SPECIES	DEPTH (m) 5	9	18	30
C. traceyi (Woods & Schultz)	X			
Dascyllus reticulatus (Richardson)	X	X	X	
D. trimaculatus (Ruppell)	X		X	
Plectroglyphidodon dickii (Lienard)	X	X		
**P. imparipennis* (Valliant & Sauvage)	X			
P. johnstonianus Fowler & Ball	X	X	X	
P. lacrymatus (Quoy & Gaimard)		X	X	X
Pomacentrus vaiuli Jordon & Seale	X	X	X	X
Pomachromis guamensis Allen & Larson	X	X	X	X
Stegastes fasciolatus (Ogilby)	X	X		
SCARIDAE (Parrotfishes)				
**Bolbometopon muricatus* (Valenciennes)	X			
Cetoscarus bicolor (Ruppell)		X	X	
Scarus brevifilis (Gunther)	X	X		
S. ghobban Forsskal				X
S. gibbus Ruppell		X	X	
**S. oviceps* Valenciennes		X	X	
S. psittacus Forsskal	X	X	X	X
S. rubroviolaceus (Bleeker)	X	X	X	
S. schlegeli (Bleeker)	X	X	X	X
S. sordidus Forsskal	X	X	X	X
SCORPAENIDAE (Scorpionfishes)				
**Synanceia verrucosa* Bloch & Schneider			X	
SERRANIDAE (Groupers)				
**Cephalopholis argus* (Bloch & Schneider)				X
C. urodelus (Bloch & Schneider)	X	X	X	X
Epinephelus fasciatus (Forsskal)		X	X	X
**Plectropomus melanoleucus* (Lacepede)				X
Variola louti (Forsskal)				X
SIGANIDAE (Rabbitfishes)				
Siganus argenteus (Quoy & Gaimard)			X	X
SYNODONTIDAE (Lizardfishes)				
Synodus variegatus (Lacepede)		X	X	X

FAMILY/SPECIES		DEPTH (m) 5	9	18	30
TETRAODONTIDAE (Smooth Puffers)					
Arothron nigropunctatus (Bloch & Schneider)			X		
Canthigaster bennetti (Bleeker)		X			X
C. coronata (Valliant & Sauvage)				X	
C. janthinoptera (Bleeker)			X		
C. solandri (Richardson)		X	X	X	X
C. valentini (Bleeker)				X	
ZANCLIDAE (Moorish Idols)					
Zanclus cornutus (Linnaeus)		X	X	X	X
Total No. Families	29	17	21	21	23
Total No. Species	155	78	92	96	80

Table 2. Fish species seen on Ipao Pt. transects from September 1979 through November 1980. * = seen only on Ipao Pt. transects.

FAMILY/SPECIES	DEPTH (m) 5	9	18	30
ACANTHURIDAE (Surgeonfishes)				
Acanthurus glaucoparieus Cuvier	X	X	X	X
A. lineatus (Linnaeus)	X	X		
A. mata Cuvier		X		
A. nigrofuscus (Forsskal)	X	X	X	X
A. olivaceus Bloch & Schneider			X	
A. pyroferus Kittlitz	X	X	X	X
A. triostegus (Linnaeus)	X			
Ctenochaetus binotatus Randall			X	
C. striatus (Quoy & Gaimard)	X	X	X	X
Naso annulatus (Quoy & Gaimard)		X		
N. brevirostris (Valenciennes)	X	X	X	X
N. hexacanthus (Bleeker)				X
N. lituratus (Bloch & Schneider)	X	X	X	X
*N. unicornis (Forsskal)	X	X	X	X
*N. vlamingi (Valenciennes)				X
Zebrasoma flavescens (Bennett)			X	X
Z. veliferum (Bloch)			X	X
APOGONIDAE (Cardinalfishes)				
*Apogon sp.				X
Cheilodipterus quinquelineatus (Cuvier)		X		
*C. macrodon (Lacepede)			X	X
AULOSTOMIDAE (Trumpetfishes)				
Aulostomus chinensis (Linnaeus)	X	X	X	X
BALISTIDAE (Triggerfishes)				
Balistapus undulatus (Park)	X	X	X	X
Balistoides conspicillum (Bloch & Schneider)			X	
Melichthys vidua (Solander)	X	X	X	X
Pseudobalistes flavomarginatus (Ruppell)	X			
*Rhinecanthus aculeatus (Linnaeus)				X
Sufflamen bursa (Bloch & Schneider)	X	X	X	X
S. chrysopterus (Bloch & Schneider)	X	X	X	X
BLENNIIDAE (Blennies)				
Aspidontis taeniatus (Quoy & Gaimard)		X		
Ecsenius bicolor (Day)		X	X	
*Exallias brevis (Kner)	X	X		
Meiacanthus atrodorsalis (Gunther)	X	X	X	X

FAMILY/SPECIES	DEPTH (m) 5	9	18	30
Plagiotremus tapeinosoma (Bleeker)	X	X		
Blenniid sp.	X			
ESIONIDAE (Fusiliers)				
Pterocaesio chrysozonus (Cuvier)			X	X
AETODONTIDAE (Butterflyfishes)				
Chaetodon auriga Forsskal	X	X	X	X
C. bennetti Cuvier				X
C. citrinellus Cuvier	X	X	X	X
C. ephippium Cuvier	X	X	X	X
C. lunula (Lacepede)	X			X
C. kleini Bloch			X	
C. lineolatus Cuvier		X	X	
C. lunula Lacepede	X	X	X	
C. mertensii Cuvier			X	X
C. ornatissimus Cuvier	X	X	X	
C. punctatofasciatus Cuvier		X	X	X
C. quadrimaculatus Gray	X	X		
C. reticulatus Cuvier	X	X	X	X
C. trifasciatus Park	X	X	X	X
C. ulietensis Cuvier		X	X	X
C. unimaculatus Bloch	X	X		X
*C. vagabundus Linnaeus				X
Forcipiger flavissimus Jordan & McGregor	X	X	X	X
F. longirostris (Broussonet)				X
Hemitaurichthys polylepis (Bleeker)			X	
Heniochus chrysostomus Cuvier		X	X	X
Megaprotodon trifascialis (Quoy & Gaimard)	X	X	X	X
IRRHITIDAE (Hawkfishes)				
Cirrhitichthys falco Randall		X	X	
Neocirrhites armatus Castelnau	X	X	X	
Paracirrhites arcatus (Cuvier)	X	X	X	
P. forsteri (Bloch & Schneider)	X	X	X	
ISTULARIIDAE (Coronetfishes)				
*Fistularia commersonii Ruppell		X		
OBIIDAE (Gobies)				
Nemateleotris magnifica Fowler		X	X	X
Pogonoculius zebra Fowler	X	X		
Ptereleotris evides (Jordan & Hubbs)	X	X	X	
Valenciennea strigatus (Broussonet)	X	X		

FAMILY/SPECIES	DEPTH (m) 5	9	18	30
HOLOCENTRIDAE (Squirrelfishes)				
Adioryx caudimaculatus (Ruppell)		X	X	X
*A. spinifer (Forsskal)			X	
Flammeo sammara (Forsskal)			X	
*Myrpristis sp.	X		X	X
KYPHOSIDAE (Rudderfishes)				
*Kyphosus cinerascens (Forsskal)			X	
LABRIDAE (Wrasses)				
Anampses caeruleopunctatus Ruppell	X	X	X	X
A. meleagrides Valenciennes	X			
A. twisti (Bleeker)	X	X	X	X
Bodianus axillaris (Bennett)	X	X	X	X
Cheilinus chlorourus (Bloch)	X	X	X	X
C. fasciatus (Bloch)	X			X
C. unifasciatus Gunther	X	X	X	X
C. trilobatus Lacepede	X	X	X	X
C. undulatus Ruppell				X
*Cheilio inermis (Forsskal)	X			
Cirrhilabrus sp.	X	X	X	X
Coris gaimard (Quoy & Gaimard)		X	X	X
Epibulus insidiator (Pallas)	X	X	X	X
Gomphosus varius Lacepede	X	X	X	
Halichoeres biocellatus Schultz	X		X	X
H. hortulanus (Lacepede)	X	X	X	X
H. margaritaceus (Valenciennes)	X	X		
H. marginatus Ruppell	X	X	X	X
H. sp.		X	X	
Hemigymnus melapterus (Bloch)	X		X	
Hologymnosus doliatus (Lacepede)			X	
Labroides bicolor Fowler & Bean	X	X	X	
L. dimidiatus (Valenciennes)	X	X	X	X
Labropsis micronesica Randall			X	
L. xanthonotus Randall	X		X	
Macropharyngodon meleagris (Valenciennes)	X	X	X	
Pseudocheilinus evanidus Jordan & Evermann			X	X
P. hexataenia (Bleeker)			X	X
Stethojulis bandarensis (Bleeker)	X	X	X	X
Thalassoma amblycephalum (Bleeker)	X	X		
*T. fuscum (Lacepede)		X		
T. lutescens (Lay & Bennett)	X	X	X	
T. quinquevittatum (Lay & Bennett)	X	X	X	
*Labrid sp. 3		X		

FAMILY/SPECIES	DEPTH (m) 5	9	18	30
*Labrid sp. 4				X
*Labrid sp. 5		X		
LETHRINIDAE (Emperors)				
*Gnathodentex aureolineatus (Lacepede)	X		X	
*Lethrinus semicinctus Valenciennes			X	
LUTJANIDAE (Snappers)				
*Lutjanus fulvus (Bloch & Schneider)		X		
*L. sp.				X
*Macolor niger (Forsskal)		X		
MONACANTHIDAE (Filefishes)				
*Amanses scopas (Cuvier)	X	X		
Cantherhines pardalis (Ruppell)	X	X		
*Oxymonacanthus longirostris (Bloch & Schneider)		X	X	X X
Paraluteres prionurus Bleeker		X		
P. melanocephalus (Bleeker)	X	X	X	
MUGILOIDIDAE (Sand Perches)				
Parapercis clathrata Ogilby	X	X	X	X
MULLIDAE (Goatfishes)				
Mulloidichthys flavolineatus (Lacepede)	X		X	X
*Parupeneus barberinus (Lacepede)				X
P. bifasciatus (Lacepede)	X	X	X	X
P. chryserydros (Lacepede)	X	X	X	X
P. pleurostigma (Bennett)		X		X
P. trifasciatus (Lacepede)	X	X	X	X
MURAENIDAE (Moray Eels)				
*Gymnothorax sp.				X
OSTRACIONTIDAE (Boxfishes, Cowfishes)				
*Ostracion cubicus Linnaeus	X	X		
O. meleagris Shaw	X	X	X	X
PEMPHERIDAE (Sweepers)				
*Pempheris oualensis Cuvier		X	X	X

FAMILY/SPECIES	DEPTH (m) 5	9	18	30
POMACANTHIDAE (Angelfishes)				
Apolemichthys trimaculatus (Cuvier)		X		
C. flavissimus (Cuvier)	X	X	X	X
C. heraldi Woods & Schultz	X		X	X
C. shepardi Randall & Yasuda			X	X
**Pomacanthus imperator* (Bloch)	X			
Pygoplites diacanthus (Boddaert)	X	X	X	X
POMACENTRIDAE (Damselfishes)				
Amphiprion clarkii (Bennett)	X	X	X	
Chromis acares Randall & Swerdloff	X	X		
**C. agilis* Smith			X	X
C. amboinensis (Bleeker)			X	X
C. margaritifer Fowler	X	X		
Chrysiptera leucopomus (Lesson)	X	X		
C. traceyi (Woods & Schultz)	X	X	X	X
**Dascyllus aruanus* (Linnaeus)	X			
D. reticulatus (Richardson)	X	X	X	X
D. trimaculatus (Ruppell)			X	X
Plectroglyphidodon dickii (Lienard)	X	X		
P. johnstonianus Fowler & Ball	X	X	X	
P. lacrymatus (Quoy & Gaimard)	X		X	
Pomacentrus vaiuli Jordon & Seale	X	X	X	X
Pomachromis guamensis Allen & Larson	X	X		
Stegastes fasciolatus (Ogilby)	X	X		
SCARIDAE (Parrotfishes)				
**Calotomus sandwichensis* (Valenciennes)			X	
Cetoscarus bicolor (Ruppell)	X	X		
**Hipposcarus longiceps* (Valenciennes)			X	
Scarus brevifilis (Gunther)	X	X	X	X
S. ghobban Forsskal	X	X	X	
S. gibbus Ruppell	X		X	
S. psittacus Forsskal	X	X	X	X
S. rubroviolaceus (Bleeker)	X	X	X	
S. schlegeli (Bleeker)	X	X	X	X
S. sordidus Forsskal	X	X	X	X
**S. tricolor* Bleeker			X	X
**Scarid* sp.				X
SERRANIDAE (Groupers)				
Cephalopholis urodelus (Bloch & Schneider)	X	X	X	
Epinephelus fasciatus (Forsskal)		X		X

FAMILY/SPECIES		5	9	18	30
			DEPTH (m)		
*E. merra Bloch				X	X
Variola louti (Forsskal)					X
SIGANIDAE (Rabbitfishes)					
Siganus argenteus (Qucy & Gaimard)				X	X
SYNODONTIDAE (Lizardfishes)					
*Synodus gracilis (Quoy & Gaimard)					X
Synodus variegatus (Lacepede)			X	X	X
TETRAODONTIDAE (Smooth Puffers)					
Arothron nigropunctatus (Bloch & Schneider)				X	X
Canthigaster bennetti (Bleeker)			X	X	
C. coronata (Valliant & Sauvage)					X
C. janthinoptera (Bleeker)		X	X		
C. solandri (Richardson)		X	X	X	X
C. valentini (Bleeker)		X	X	X	
ZANCLIDAE (Moorish Idols)					
Zanclus cornutus (Linnaeus)		X	X	X	X
Total No. Families	23	21	23	26	25
Total No. Species	176	105	114	117	97

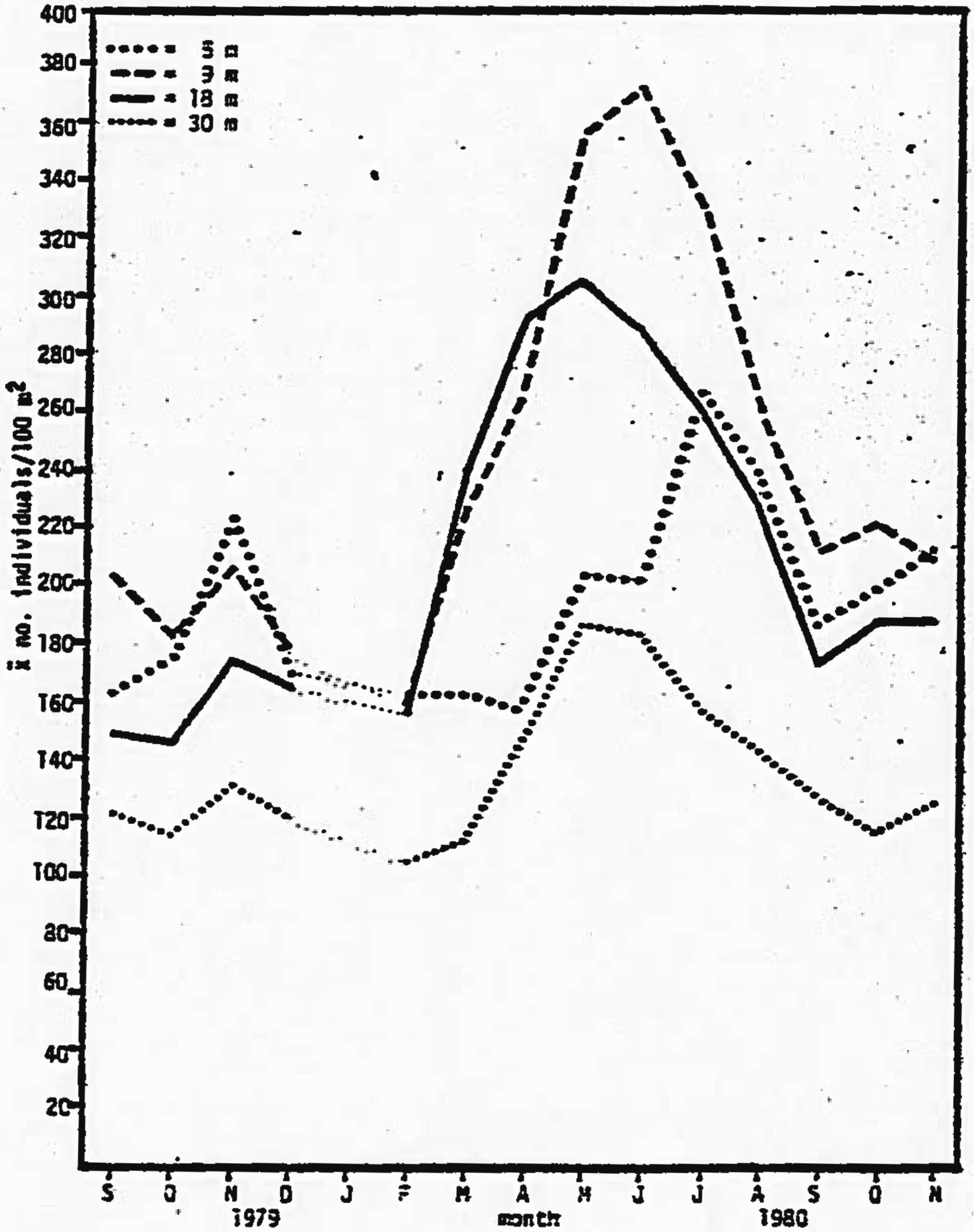

Figure 4. Monthly fluctuations in overall fish abundance (mean number of individuals/100 m^2) recorded from September 1979 through November 1980 by depth.

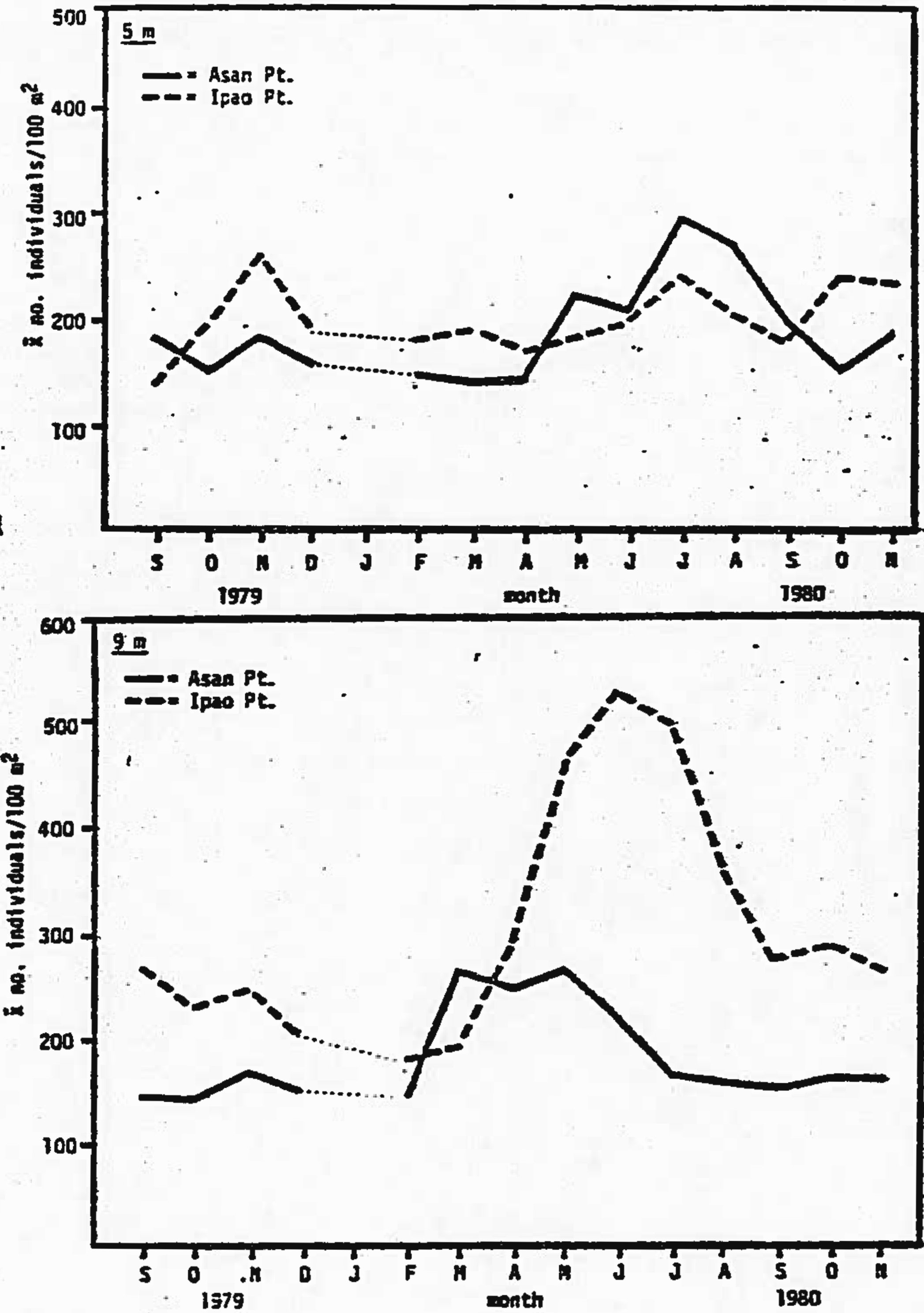

Figure 5. Monthly fluctuations in fish abundance (mean numbers of individuals/100 m^2) recorded at each depth by study site.

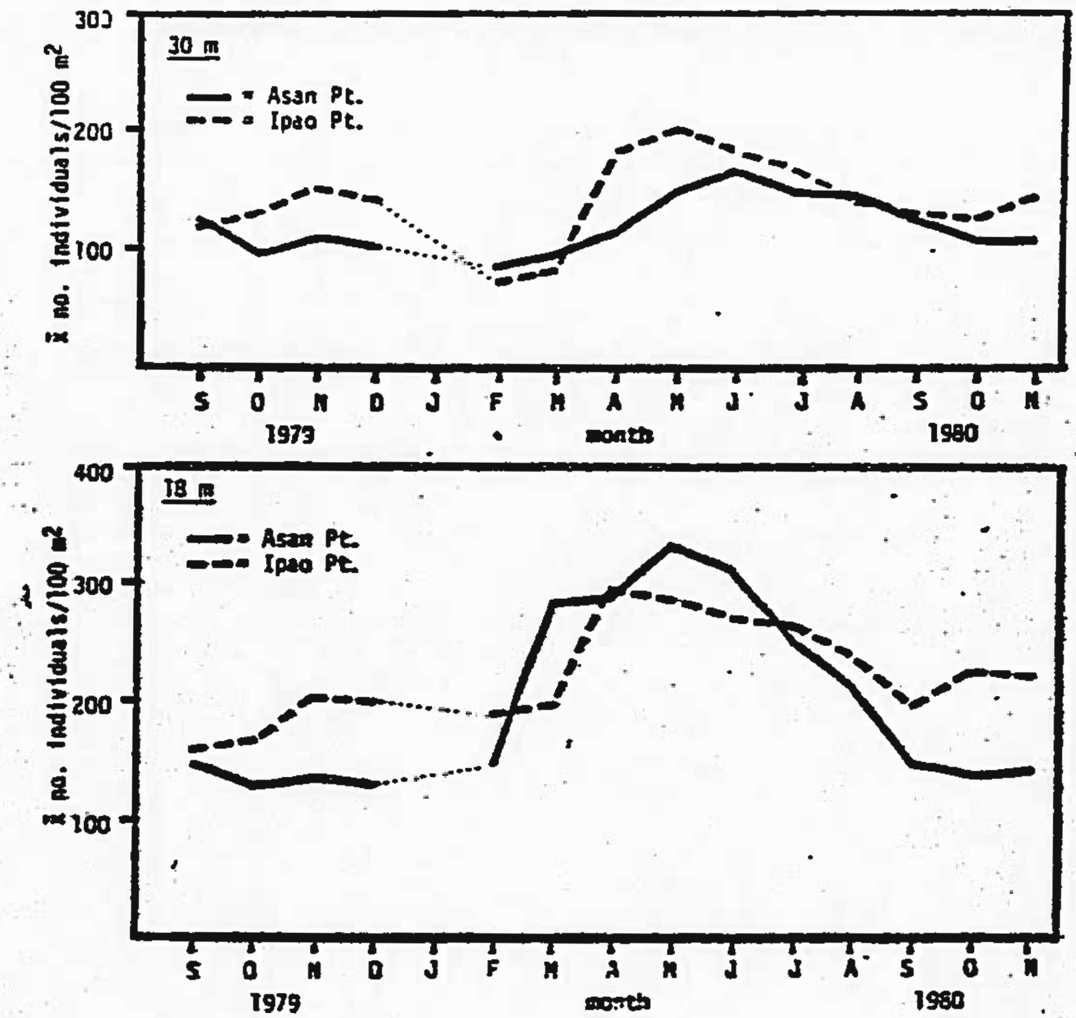

Figure 5. Continued.

Table 3. Most influentially abundant fish species ($\geq$500 individuals) counted at each transect station during the entire study. Numbers equal total number counted at a particular station.

ASAN PT.		IPAO PT.	
5 m:		5 m:	
Chrysiptera leucopomus	2780	Stegastes fasciolatus	3584
Thalassoma quinquevittatum	2095	Plectroglyphidodon dickii	2607
Plagiotremus tapeinosoma	613	T. quinquevittatum	842
Ctenochaetus striatus	549	Acanthurus nigrofuscus	675
9 m:		9 m:	
Pomachromis guamensis	4439	P. guamensis	2133
Dascyllus reticulatus	3044	S. fasciolatus	1480
T. quinquevittatum	1636	T. quinquevittatum	969
Cirrhilabrus sp.	1495	D. reticulatus	794
S. fasciolatus	1261	Pomacentrus vaiuli	685
Plectroglyphidodon johnstonianus	921	P. johnstonianus	568
A. nigrofuscus	535	A. nigrofuscus	524
18 m:		18 m:	
Cirrhilabrus sp.	3123	Chrysiptera traceyi	3014
D. reticulatus	2668	Plectroglyphidodon lacrymatus	2219
P. guamensis	1127	P. vaiuli	2140
P. vaiuli	805	A. nigrofuscus	629
30 m:		30 m:	
P. vaiuli	2598	C. traceyi	4504
C. traceyi	1237	P. vaiuli	734

Total No. Species = 14

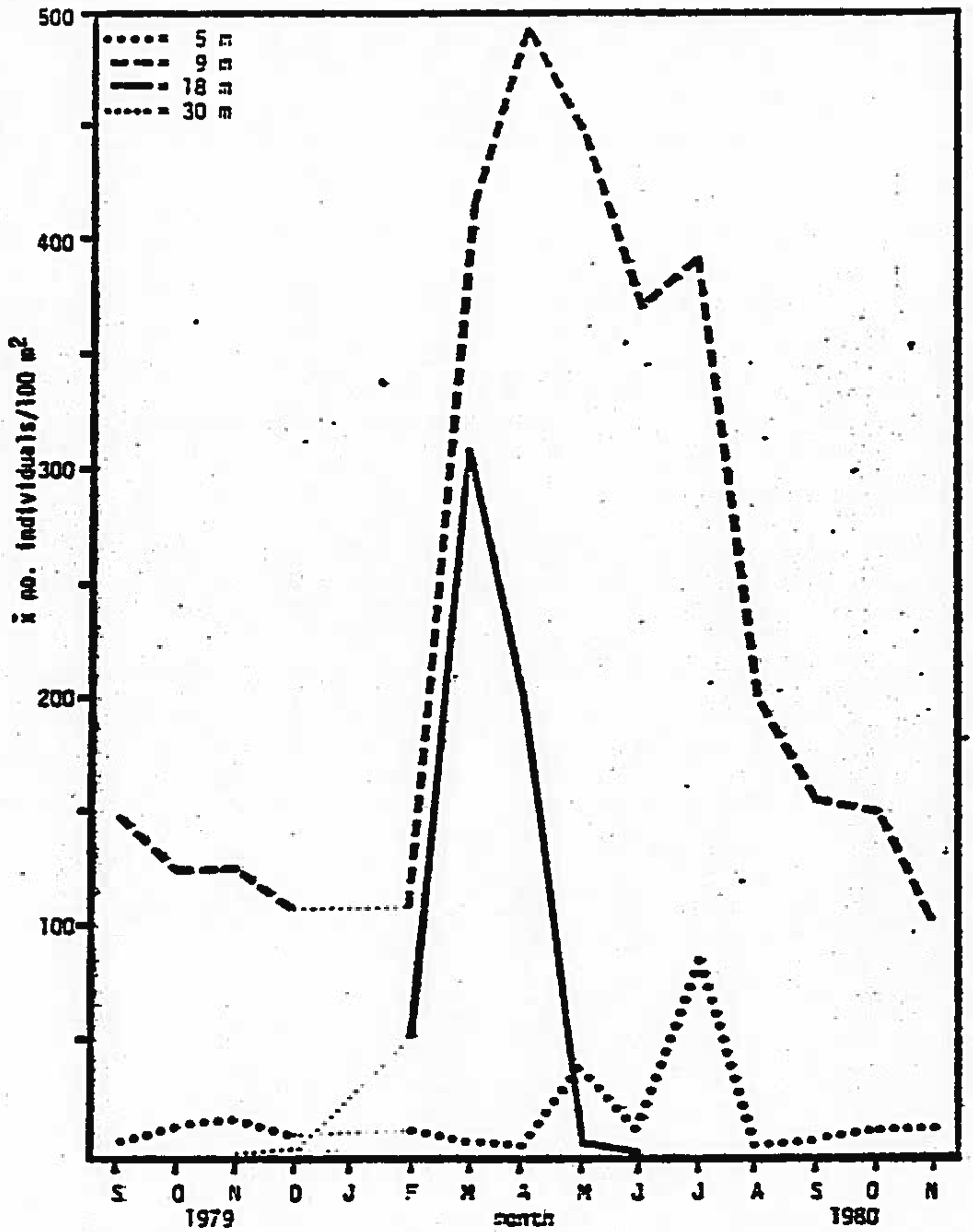

Figure 6. Monthly depth-related fluctuations in abundance (mean number of individuals/100 m^2) among the most influential species recorded during the study. A = Pomachromis guamensis.

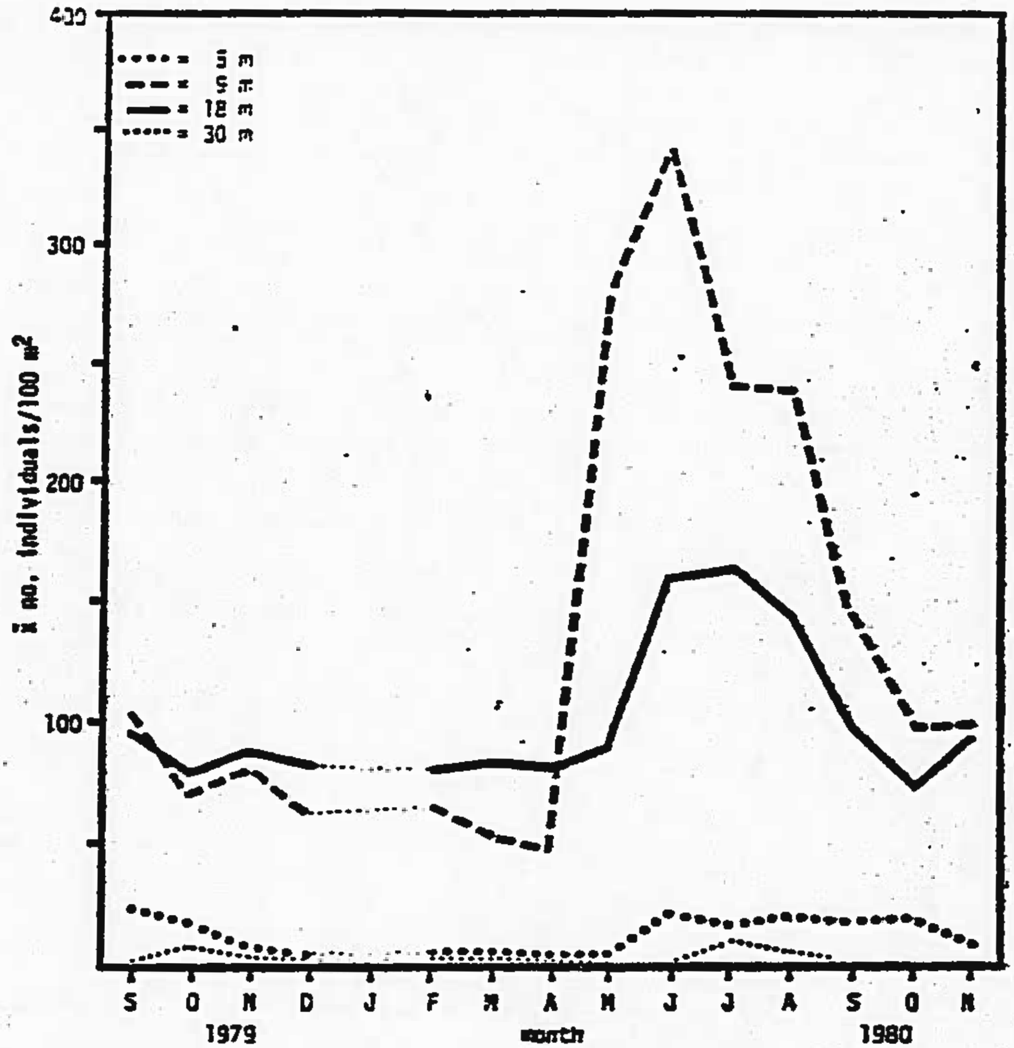

Figure 6. Continued. B = Dascyllus reticulatus

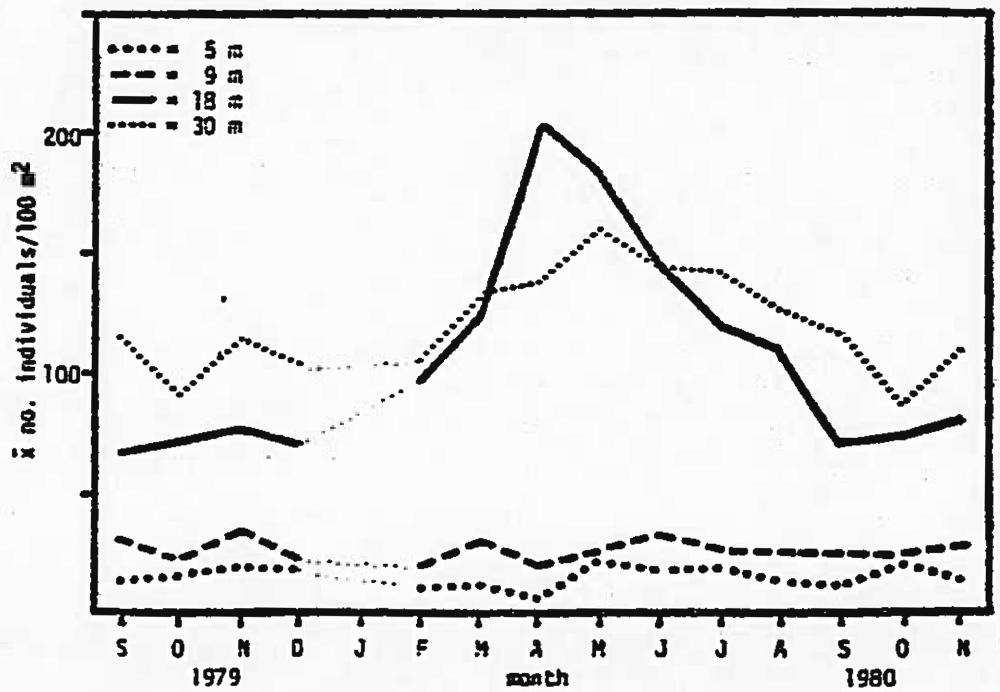

Figure 6. Continued. C = Pomacentrus vaiuli

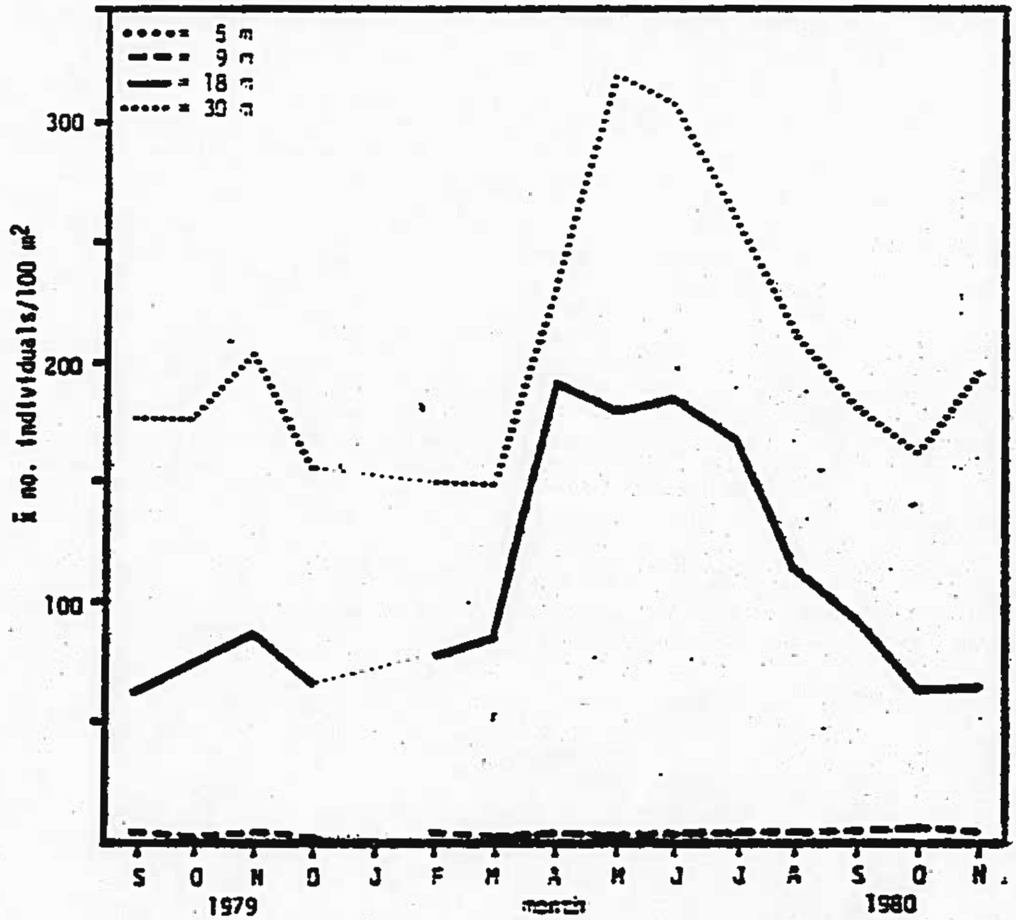

Figure 6. Continued. D = Chrysiptera traceyi

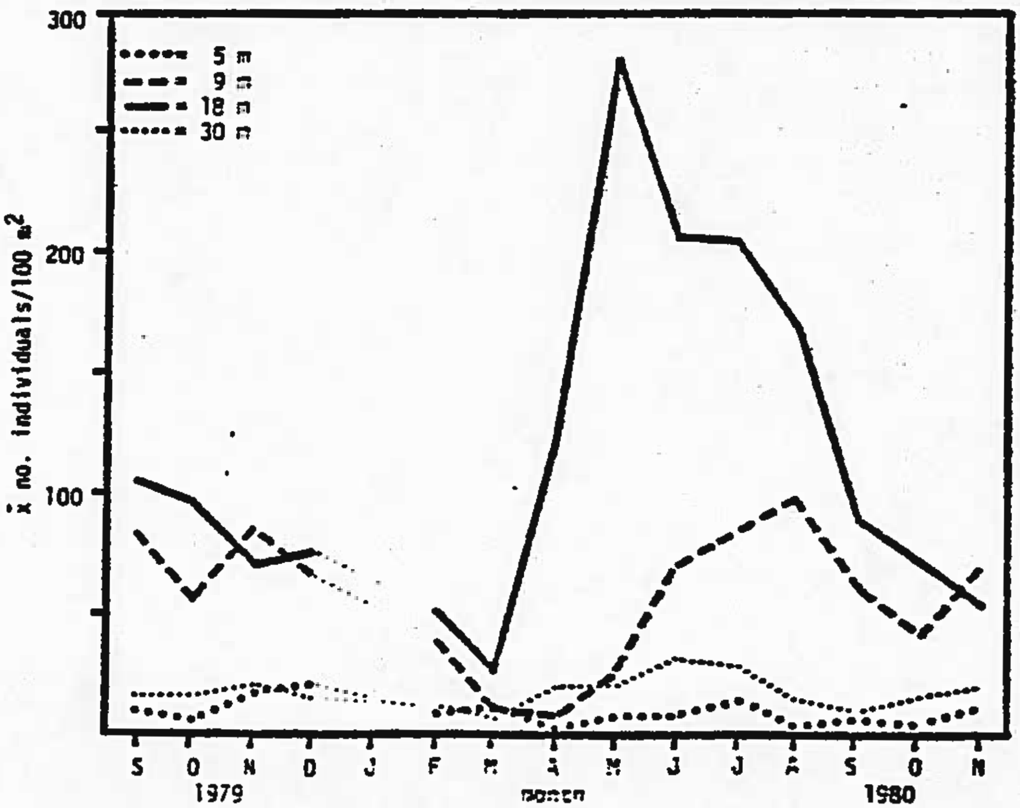

Figure 6. Continued. E = Cirrhilalrus sp.

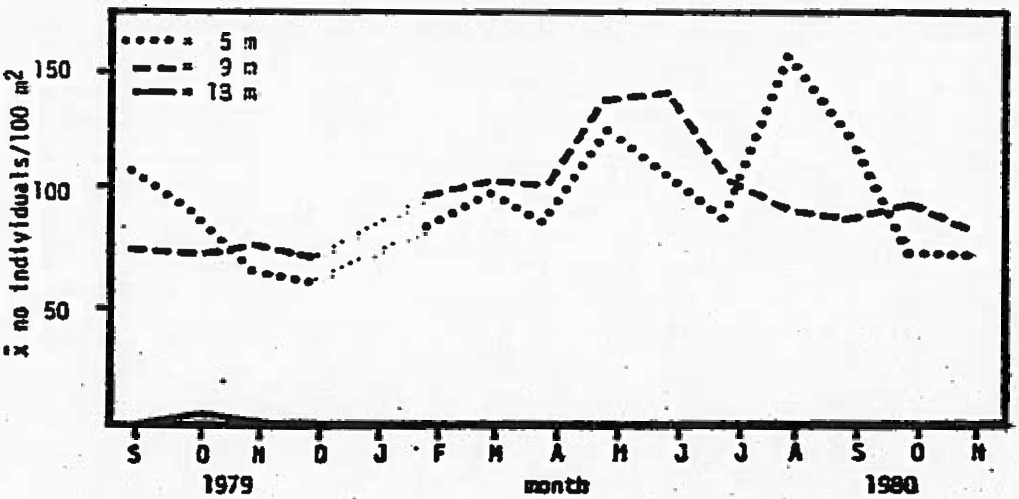

Figure 6. Continued. F = Thalassoma quinquevittatum

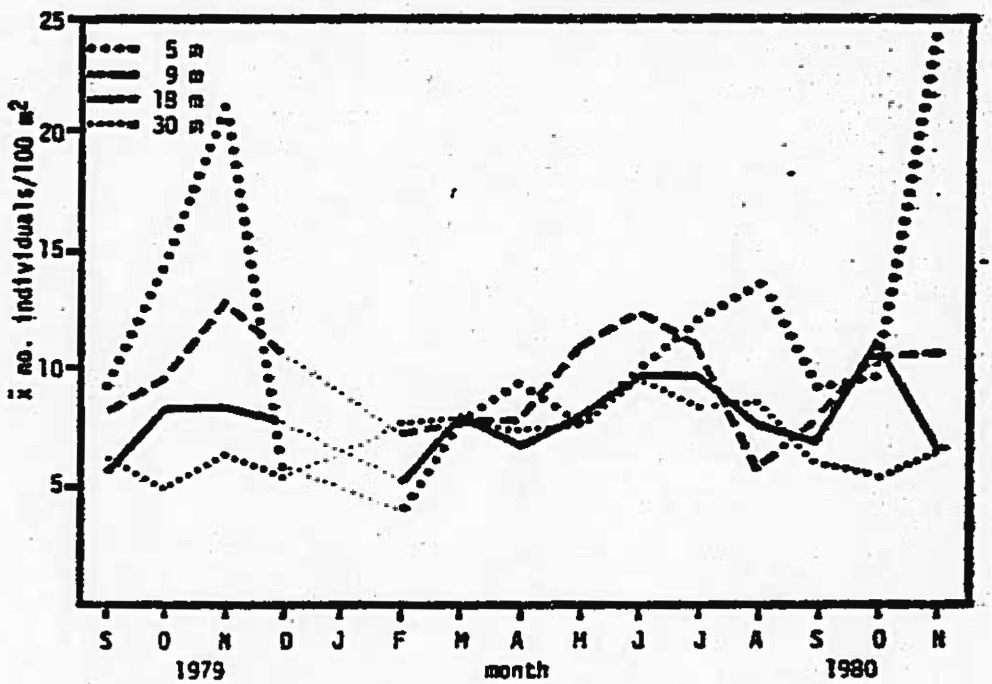

Figure 6. Continued. G = Acanthurus nigrofuscus

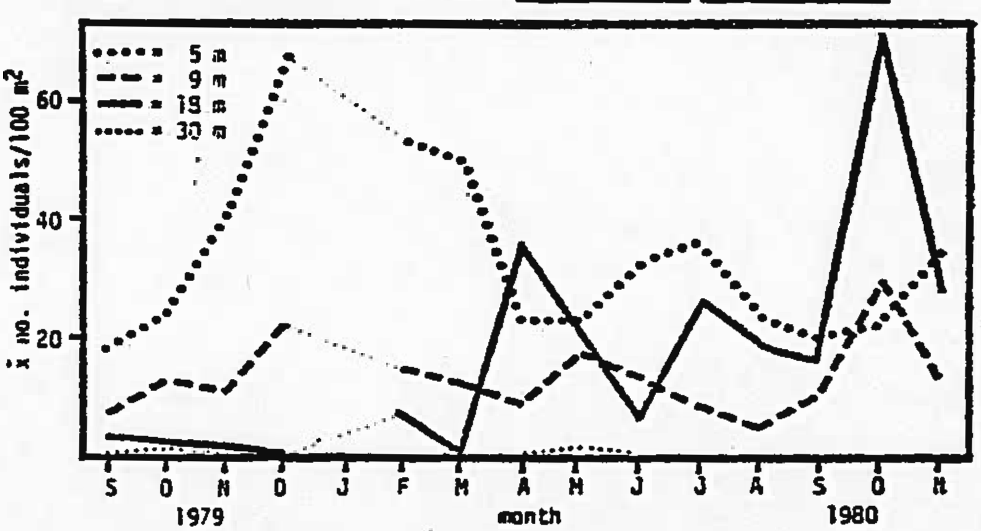

Figure 6. Continued. H = Ctenochaetus striatus

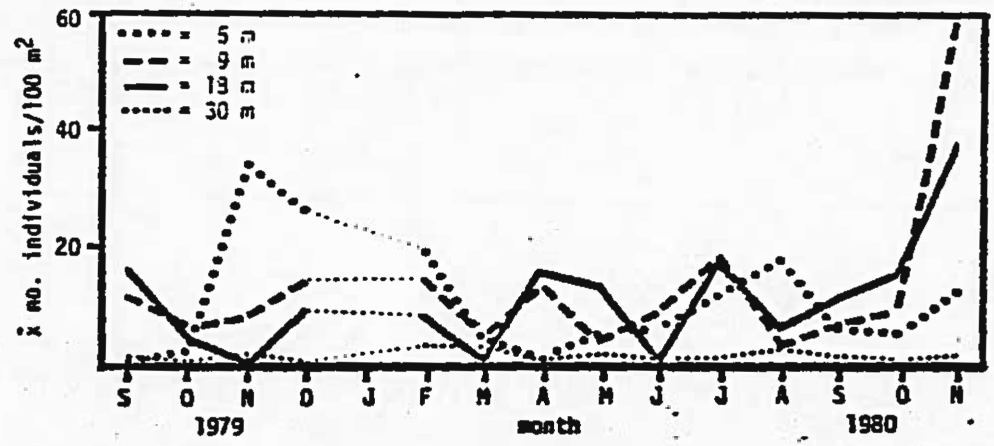

Figure 6. Continued. I = Scarus psittacus

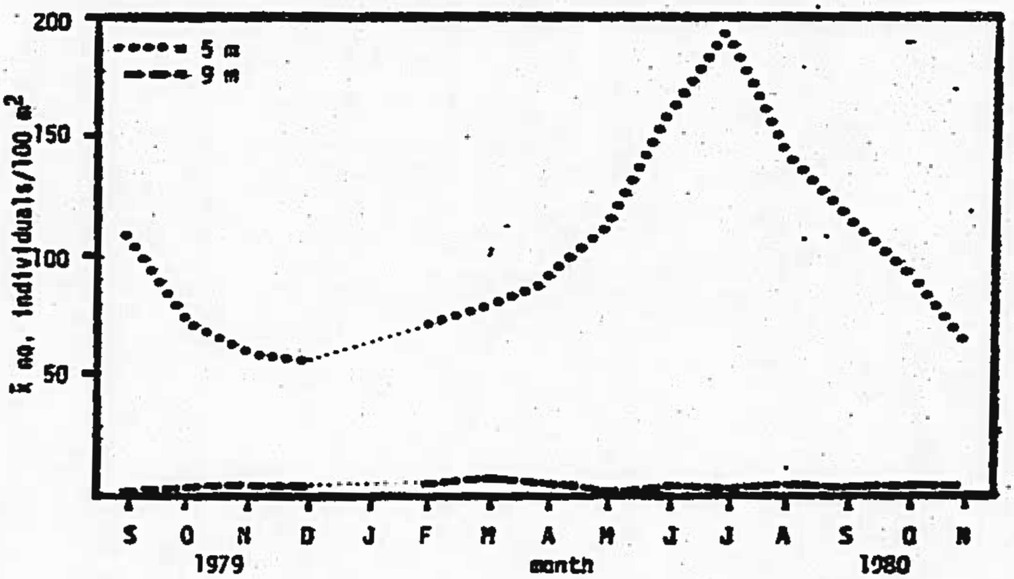

Figure 6. Continued. J = Chrysiptera leucopomus

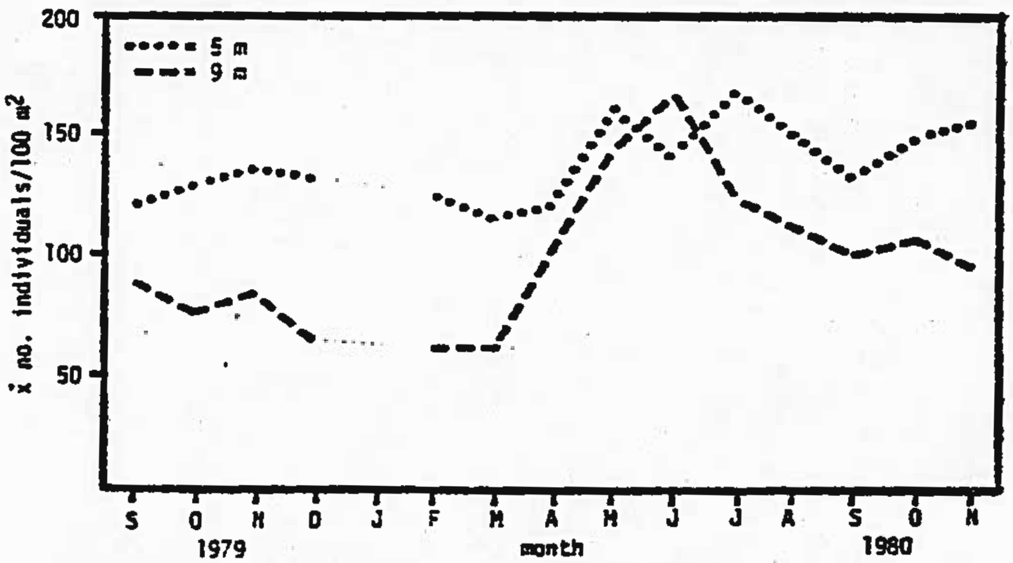

Figure 6. Continued. K = Stegastes fasciolatus

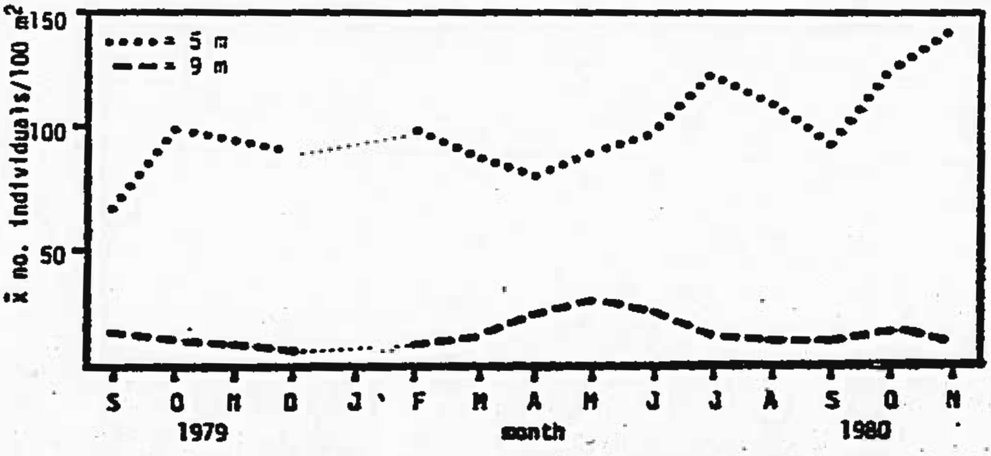

Figure 6. Continued. L = Plectroglyphidodon dickii

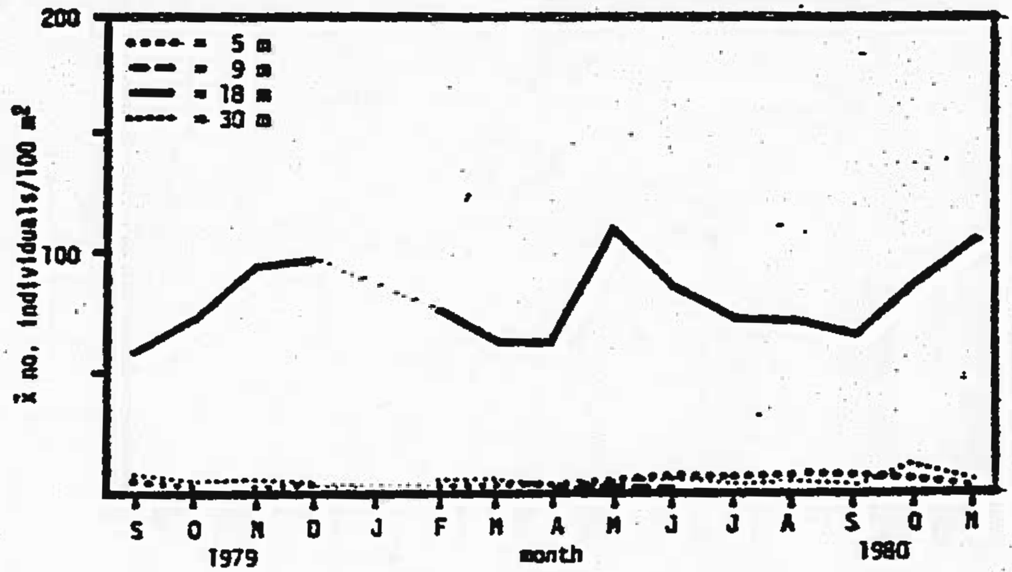

Figure 6. Continued. M = Plectroglyphidodon lacrymatus

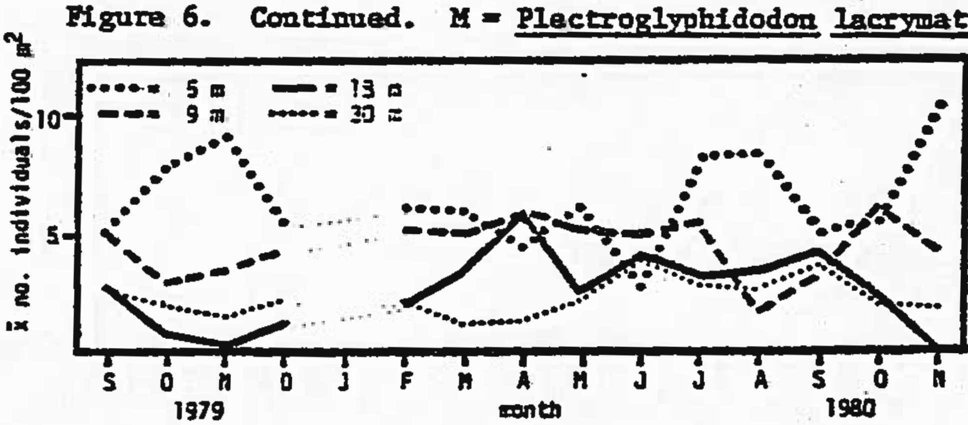

Figure 6. Continued. N = Scarus sordidus

Table 4. Most ubiquitous fish species (counted at 7 or 8 transect stations) seen during the study in order of total abundance.

SPECIES	No. Stations	Total No. Counted
Pomacentrus vaiuli	8	7387
Dascyllus reticulatus	7	7047
Cirrhilabrus sp.	8	5513
Acanthurus nigrofuscus	8	3880
Scarus sordidus	8	1811
Ctenochaetus striatus	7	1744
Scarus psittacus	8	1009
Meicanthus atrodorsalis	7	871
Scarus schlegeli	8	858
Naso lituratus	8	841
Acanthurus glaucoparieus	8	492
Parupeneus trifasciatus	8	434
Chaetodon citrinellus	7	416
Thalassoma lutescens	7	404
Canthigaster solandri	8	391
Zanclus cornutus	8	359
Sufflamen bursa	8	347
Parapercis clathrata	8	337
Stethojulis bandanensis	8	292
Chaetodon punctatofasciatus	7	288
Labroides dimidiatus	8	280
Cheilinus unifasciatus	8	274
Sufflamen chrysopterus	7	214
Cephalopholis urocelus	7	201
Halichoeres hortulanus	7	156
Forcipiger flavissimus	7	124
Melichthys vidua	8	112
Chaetodon reticulatus	8	104
Balistapus undulatus	7	93
Halichoeres marginatus	8	88
Epibulus insidiator	8	74
Centropyge flavissimus	7	71
Cheilinus trilobatus	8	59
Parupeneus bifasciatus	7	56
Parupeneus chryseredros	8	51

Total No. Species = 35

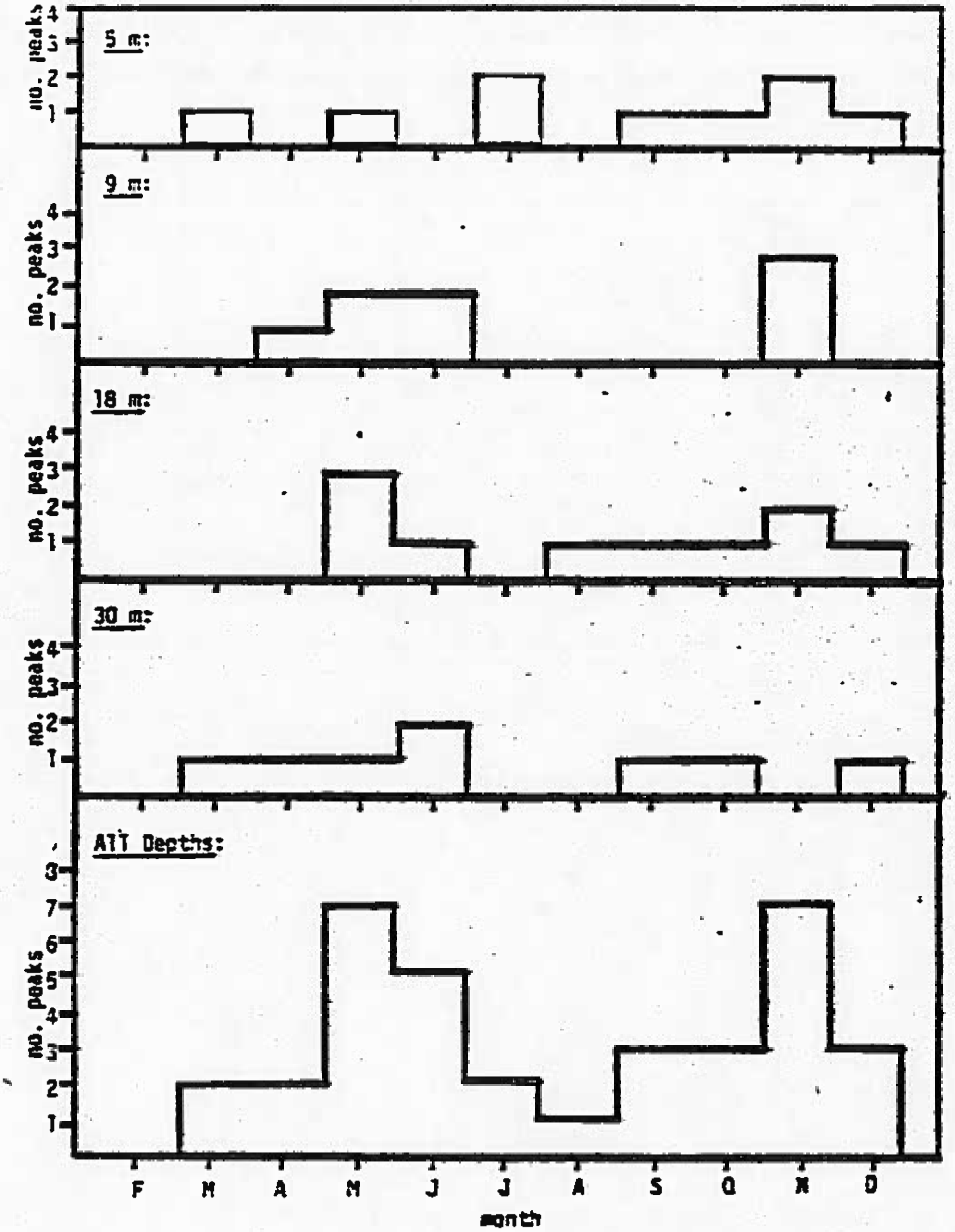

Figure 7. Number of representative peak abundances recorded each month (based on maximum mean monthly counts) within the most ubiquitous species group.

Table 5. General trophic categories to which the members of the most ubiquitous species group were assigned. Species are listed in decreasing order of total abundance relative to each category.

CARNIVORES	HERBIVORES	OMNIVORES
Cirrhilabrus sp.	Acanthurus nigrofuscus	Pomacentrus vaiuli
Meicanthus atrodorsalis	Scarus sordidus	Dascyllus reticulatus
Parupeneus trifasciatus	Ctenochaetus striatus	Chaetodon citrinellus
Thalassoma lutescens	Scarus psittacus	Canthigaster solandri
Zanclus cornutus	Scarus schlegeli	Chaetodon punctatofasciatus
Sufflamen bursa	Naso lituratus	Melichthys vidua
Parapercis clathrata	Acanthurus glaucopareius	Balistapus undulatus
Stethojulis bandanensis	Chaetodon reticulatus	
Labroides dimidiatus	Centropyge flavissimus	
Cheilinus unifasciatus		
Sufflamen chrysopterus		
Cephalopholis urodelus		
Halichoeres hortulanus		
Forcipiger flavissimus		
Halichoeres marginatus		
Epibulus insidiator		
Cheilinus trilobatus		
Parupeneus bifasciatus		
Parupeneus chryseredros		
No. Species/Group = 19	9	7
Total No. Species = 35		

Table 6. Number of species per general trophic category (within the most ubiquitous species group) that peaked in mean abundance at each transect depth.

Trophic Category	Transect Depth 5m	9m	18m	30m	Total No. Species
CARNIVORES	3	3	8	5	19
	32%		68%		
HERBIVORES	6	2	1	0	9
	89%		11%		
OMNIVORES	0	3	1	3	7
	43%		57%		
Total No. Species =	9	8	10	8	35

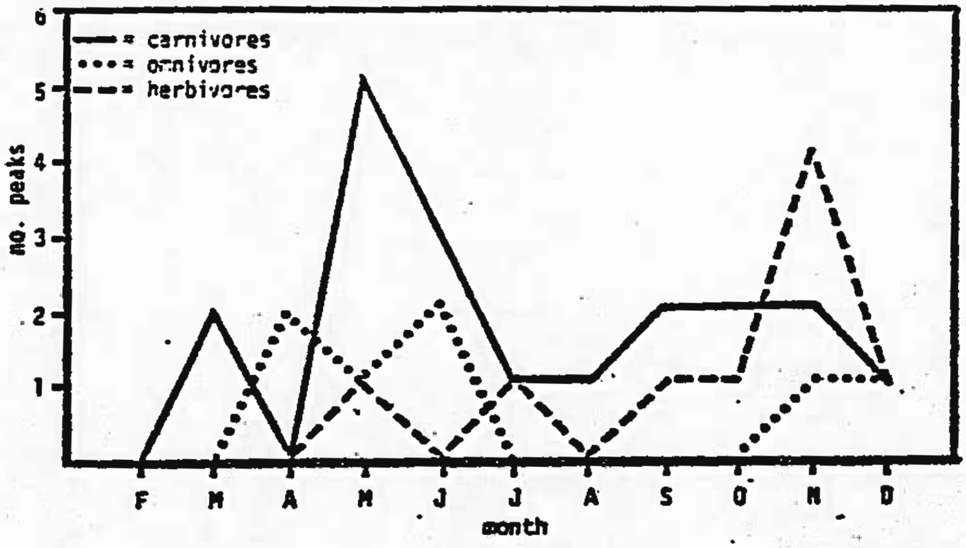

Figure 8. Number of representative peak abundances recorded each month (based on maximum mean monthly counts) among carnivores, herbivores and omnivores within the most ubiquitous species group. Total number of species = 35.

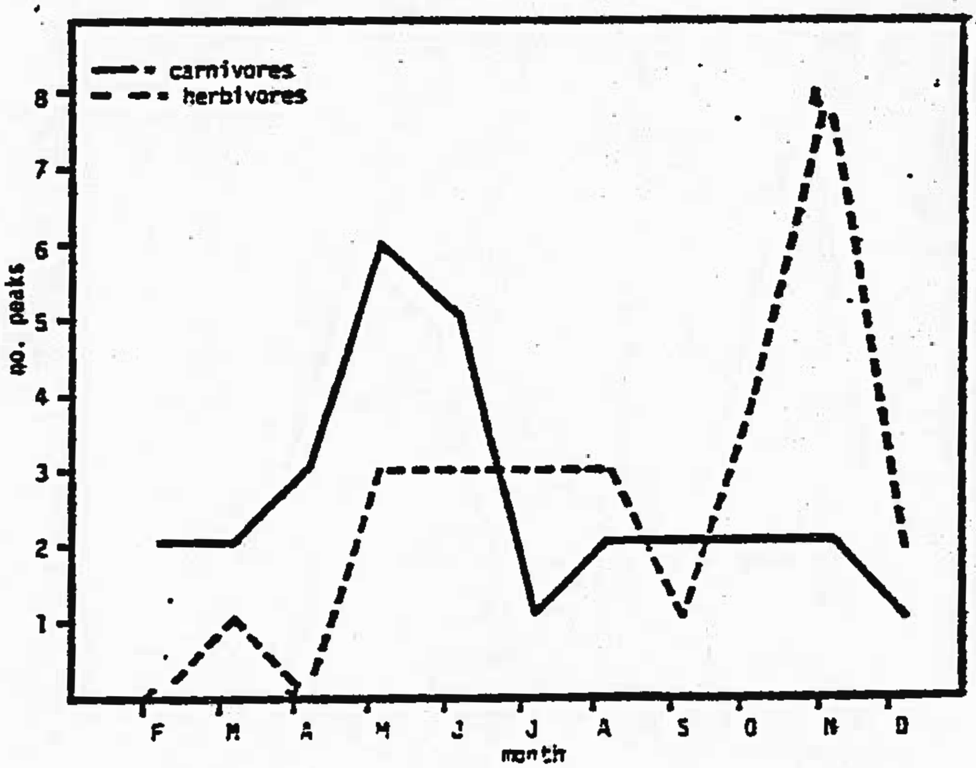

Figure 9. Number of representative peak abundances recorded each month (based on maximum mean monthly counts) among equal numbers of carnivores and herbivores within an expanded ubiquitous species group. Total number of species = 56.

combined fish abundance of both trophic categories was significantly greater (chi-square for a 2 X 2 contingency table, $p < 0.01$) during the wet season (Table 7), it was fishes within the expanded herbivore group that were the major contributors (chi-square for 2 classes, $p < 0.01$) to this increase (Table 8). Chi-square test for more than two classes also supported (herbivores, $p < 0.05$) this result (Table 9). When the carnivore and herbivore data were segregated into quarterly intervals, it was found that these periods were not homogeneous (G-statistic [G_H], $p < 0.025$) in their expected ratios of numbers of species peaks per trophic category; and it was the October-December period that was significantly different (G-statistic [G], $p < 0.05$) (Table 10). Therefore, although the combined fish abundance represented by both trophic categories was greatest during the rainy season, the expanded carnivore group increased early and peaked before the month of maximum rainfall, and the expanded herbivore group did not increase significantly until after the rainiest month had passed. Thus, the seasonal fluctuations among the more ubiquitous and abundant fish species appeared to follow a depth-related pattern that was probably related to food resources.

The first species noted to recruit in appreciable numbers during 1980 was the planktivore Pomachromis guamensis (Fig. 4a), which settled strongly in March at 9 and 18 m. Other relatively abundant plankton-feeders that recruited between March and June included the ominvores Dascyllus reticulatus, Pomacentrus vaiuli, Chrysiptera traceyi and, as juveniles, Cirrhilabrus sp. (Fig. 4b, c, d and e, respectively). Along with other less abundant planktivores, such as Nemateleotris magnifica and Ptereleotris evides, these species probably represented a significant food resource for several piscivores. In fact, maximum mean monthly counts of the groupers, Cephalopholis urodelus and Epinephelus fasciatus, the hawkfishes, Cirrhitichthys falco and Paracirrhites forsteri, the sand perch, Parapercis clathrata, and the wrasses, Cheilinus trilobatus and C. unifasciatus, were all recorded between February and June. Piscivore increases observed during these months were mainly due to the appearances of subadults and adults and additionally included sporadic sightings of larger groupers, snappers and wrasses, such as Variola louti, Lutjanus bohar and Cheilinus undulatus. These latter species are deeper-water predators that may have undergone a seasonal vertical migration in response to increased prey abundance on the upper reef slope (Kock 1982).

Several benthic invertebrate-feeders also exhibited peak abundances during the same period. Increases among these species were primarily due to juvenile recruitment, but older juveniles and adults were also commonly encountered. They included the boxfish, Ostracion meleagris, the triggerfish, Sufflamen bursa and the wrasses, Coris gaimard, Gomphosus varius, Halichoeres hortulanus, H. marginatus, Macropharyngodon meleagris, Stethojulis bandanensis and Thalassoma quinquevittatum (Fig. 4f), amidst others. These species also many have peaked during a time of expanding food resources since the strong planktivore fluctuation suggests the presence of abundant plankton, upon which may benthic invertebrates are known to feed. However, data directly supporting this was not collected during the study.

Of the 14 ubiquitous herbivores that peaked in abundance during the October-December period (Table 10), eight (Acanthurus lineatus, A. nigrofuscus [Fig. 4g], A. triostegus, A. pyroferus, Naso lituratus, N. unicornis, Zebrasoma flavescens and Z. veliferum) were browsing and two

Table 7. Two-by-two test of independence using X^2 (Sokal and Rohlf 1969) to determine if overall fish abundance[1] of equal numbers of carnivores and herbivores was significantly greater during the wet season ($\bar{x}$ rainfall $\geq$ 12.5 cm/month). Data not collected during January.

	DRY SEASON	WET SEASON	
	January-May	June-December	Total
Carnivores	13	15	28
Herbivores	4	24	28
	17	39	56

$$X^2 = \frac{[(13 \times 24) - (15 - 4)]^2\ 56}{(28 \times 28 \times 17 \times 39)}$$

$$= 6.842^{**}$$

** = $p < 0.01$

[1]Based on numbers of maximum monthly mean counts within each trophic group.

Table 8. Two class tests of independence using X^2 (Sokal and Rohlf 1969) to determine if either carnivores or herbivores were significantly more abundant[1] during the wet season ($\bar{x}$ rainfall $\geq$ 12.5 cm/month). Data not collected during January.

CARNIVORES:

	f	$\hat{f}$	$f-\hat{f}$	$(f-\hat{f})^2$	$\frac{(f-\hat{f})^2}{\hat{f}}$
Dry Season (Jan-May)	13	14	-1	1	0.071
Wet Season (Jun-Dec)	15	14	1	1	0.071
Σ	28	28			

$$X^2 = \frac{(13 - 14)^2}{14} + \frac{(15 - 14)^2}{14}$$

$$= 0.142 \text{ ns}$$

HERBIVORES:

	f	$\hat{f}$	$f-\hat{f}$	$(f-\hat{f})^2$	$\frac{(f-\hat{f})^2}{\hat{f}}$
Dry Season (Jan-May)	4	14	-10	100	7.143
Wet Season (Jun-Dec)	24	14	10	100	7.143
Σ	28	28			

$$X^2 = \frac{(4 - 14)^2}{14} + \frac{(24 - 14)^2}{14}$$

$$= 14.286^{**}$$

ns = $p > 0.05$ ** = $p < 0.01$

[1] Based on the numbers of maximum monthly mean counts of 28 carnivores and 28 herbivores.

Table 9. Tests of independence for greater than two classes using X^2 (Sokal and Rohlf 1969) to determine if fish abundance[1] of either carnivores or herbivores was significantly greater during quarterly periods of the year.

CARNIVORES:

	f	$\hat{f}$	$f-\hat{f}$	$(f-\hat{f})^2$	$\frac{(f-\hat{f})^2}{\hat{f}}$
Feb-Mar	4	5.091	-1.091	1.190	0.234
Apr-Jun	14	7.636	6.364	40.500	5.304
Jul-Sep	5	7.636	-2.636	6.948	0.910
Oct-Dec	5	7.636	-2.636	6.948	0.910
Σ	28	27.999			

$$X^2 = \frac{(4 - 5.091)^2}{5.091} + \frac{(14 - 7.636)^2}{7.636} + \frac{(5 - 7.636)^2}{7.636} + \frac{(5 - 7.636)^2}{7.636}$$

$$= 7.358 \text{ ns}$$

HERBIVORES:

	f	$\hat{f}$	$f-\hat{f}$	$(f-\hat{f})^2$	$\frac{(f-\hat{f})^2}{\hat{f}}$
Feb-Mar	1	5.091	-4.091	16.736	3.287
Apr-Jun	6	7.646	-1.636	2.676	0.350
Jul-Sep	7	7.635	-0.636	0.404	0.053
Oct-Dec	14	7.636	6.364	40.500	5.304
Σ	28	27.999			

$$X^2 = \frac{(1 - 5.091)^2}{5.091} + \frac{(6 - 7.636)^2}{7.636} \div \frac{(7 - 7.636)^2}{7.636} + \frac{(14 - 7.636)^2}{7.636}$$

$$= 8.994^{*}$$

ns = $p > 0.05$ * = $p < 0.05$

[1]Based on the numbers of maximum monthly mean counts of 28 carnivores and 28 herbivores.

Table 10. Two-by-two test of independence using the G-statistic (Sokal and Rohlf 1969) to determine if fish abundance[1] of equal numbers of carnivores and herbivores was significantly greater during quarterly periods of the year.

MONTHS	CARNIVORES	HERBIVORES	Σ	G
Feb-Mar	4	1	5	1.927
Apr-Jun	14	6	20	3.291
Jul-Sep	5	7	12	0.335
Oct-Dec	5	14	19	4.439*
Σ	28	28	56	9.992

$$G_H = 2\,[119.905 - 186.603 - 153.725 + 225.419]$$
$$= 9.994^{**}$$
$$G_P = 2\,[186.603 + 19.408 + 19.408 - 225.419]$$
$$= 0$$

$* = p < 0.05$ $** = P < 0.01$

[1]Based on numbers of maximum monthly mean counts within each trophic group.

(Acanthurus mata and Ctenochaetus striatus [Fig. 4h]) were grazing surgeonfishes; two (Scarus brevifilis and S. psittacus [Fig. 4i]) were grazing parrotfishes; and one each (Centropyge flavissimus and Chaetodon reticulatus) were browsing angelfish and butterflyfish, respectively. Of the ten browsers eight are surgeonfishes that were most abundant at 5 m.

Although they were not uncommon, juvenile surgeonfishes seemed generally low in representation on the reef slope. Most of the largest increases in surgeonfish abundance were due to the presence of subadult/adult mixed-species foraging aggregations that appeared to be most numerous and most frequent during the fall. The most conspicuous species included Acanthurus glaucopareis, A. nigrofuscus, A. triostegus, and N. lituratus. In contrast, the majority of the newly recruited juvenile browsers observed during this study were territorial damselfishes that generally peaked in overall abundance during the spring/summer months on the reef front and upper submarine terrace. The most important of these species included Chriysiptera leucompomus (Fig 4j), Stegastes fasciolatus (Fig. 4k), Plectroglyphidodon dickii (Fig. 4l), P. lacrymatus (Fig 4m) and P. johnstonianus. Juvenile parrotfishes were encountered at a rather moderate frequency, often in small groups (10-20 individuals) or as part of larger (100-200 individuals) mixed-species foraging aggregations. However, there were no strong relationships between parrotfish abundance and specific depths or reef zones. S. brevifilis and S. psittacus peaked during the October-December period, while peak abundances were recorded for Cetoscarus bicolor, Scarus rubroviolaceus, S. schlegeli and S. sordidus (Fig. 4n) between May and August. The latter species, however, showed strong increases in the fall, and along with S. psittacus and S. schlegeli often formed substantial portions of foraging aggregations. Since the reef slope algal biomass did not fluctuate noticeably during this study, there seems to be no direct relationship between fluctuations in herbivorous fish abundance and food resources on the upper reef slope. But again, data directly supporting this was not collected during the investigation.

Annual Variation

Annual variation in the counts of the 35 most ubiquitous fish species was estimated with data collected during the months of September, October and November, 1979 and 1980. The counts of these species were lumped across depths and analyzed by site. Values of $\bar{R}$ calculated from the September data show that net decreases in abundance occurred between years in most species at both sites; but based on the October and November data sets these values showed net increases between years at both sites. Values of AV calculated for both sites were generally low, ranging from 0.06 to 0.17, indicating that relatively little overall change in ranked fish abundances had occurred between years. Within the 1600 m^2 area surveyed at each site, the most ubiquitous upper reef slope fishes show fairly stable abundances from year to year ($\bar{x}$ AV Asan and Ipao = 0.11 and 0.09, respectively).

Annual variation was estimated for each depth by lumping depth-specific data across sites. The mean log R's ($\bar{R}$) among months for the 35 ubiquitous species show net decreases to have been prevalant between years in the September data, while net increases are found in the October and November data sets. Comparisons of $\bar{R}$ among depths indicate that the most widespread increases in abundance between years occurred at 18 m. The calculated values of AV range from 0.03 to 0.23, with consistently higher values at 18 m. Table 11 summarizes the values of R and AV calculated for each study site and depth for each pair of months. The results show that on a relatively broader scale of analysis (1600 m^2 of reef), AV's calculated by site are comparatively low and not very different from each other. Values of AV are generally higher when calculated for specific depths and depth-month combinations (800 m^2 of reef). The mean value for all depths ($\bar{x}$ AV = 0.13) is similar to that for both study sites ($\bar{x}$ AV = 0.10), indicating low annual variation in abundance over the extensive reef areas analyzed. In addition, trends in the calculated values of AV across depths seem to be loosely correlated with the depth-related trends in observed species richness (Tables 1 and 2).

Yearly changes in species composition among the 35 most ubiquitous species as estimated by the J and R indices of resemblance show the same trend (Tables 12 and 13). Study sites (all depths combined) show greater species constancy (ie., higher index values) than do individual depth zones indicating that species composition is more stable over broader areas than within narrower zones. The mean values of each index for all depths combined, excluding 30 m, were similar (J = 0.84; R = 0.91) and relatively high, indicating the presence of a fairly constant ubiquitous species composition. Yearly differences in the numbers of species observed at 30 m is misleading since twice the amount of census time was expended at that depth in 1979.

DISCUSSION

The changes in overall fish abundance observed during this study (Fig. 4) conformed to a general pattern consistent with recent work done in Guam (Kock 1982), Micronesia (Johannes 1978), Hawaii (Watson and Leis 1974), the Caribbean (Luckhurst and Luckhurst 1977) and the Great Barrier Reef (Russell et al. 1977; Talbot et al. 1978; Williams and Sale 1981), in which fish abundance fluctuations were found to be highly seasonal and largely related to reproductive activities. Our results also suggest that there is a temporal partitioning in peak abundance across depth, possibly resulting from a more specific temporal partitioning among general trophic groups. Strong planktivore recruitment at 9 and 18 m in March appeared to initiate the observed seasonal increase in overall fish abundance. This was followed closely by increases among other abundant plankton-feeders, primarily at 18 m, through June. Peak abundances among the most ubiquitous carnivores were clustered between April and June, with major piscivore increases being especially prominent at 9 and 18 m. In contrast, peak abundances among the most ubiquitous herbivores were clumped between October and December, at 5 m.

The initial planktivore influx, as well as juvenile recruitment in general, might have been influenced by several factors promoting successful larval survival. Peak juvenile recruitment may be the result of seasonally intensified reproduction that is timed to coincide with factors favorable for larval survival and juvenile settlement. On the other hand, fish reproduction may be relatively constant through the year, and seasonality in recruitment may be the result of intermittently enhanced survival due to these factors. Since spawning was not observed during this study, we have no data supporting the hypothesis that reef fish reproduction is seasonally

Table 11. Annual variation (AV) in ranked fish abundances of the 35 most ubuquitous fish species observed at Asan Pt. and Ipao Pt. Calculations are based on data collected during September, October and November, 1979 and 1980. $\bar{R}$ and AV are explained in text and in Wolda (1978).

Study Site	Transect Depth (m)	September	October	November	$\bar{x}$
$\bar{R}$:					
Asan	All	-0.08	0.06	0.04	0.01
Ipao	All	-0.04	0.08	0.03	0.02
Both	5	0.03	0.01	-0.02	0.01
Both	9	-0.18	0.08	0.10	0.00
Both	18	0.02	0.09	0.09	0.07
Both	30	-0.02	-0.08	0.03	-0.02
AV:					
Asan	All	0.09	0.06	0.17	0.11
Ipao	All	0.10	0.10	0.07	0.09
Both	5	0.14	0.10	0.07	0.10
Both	9	0.14	0.14	0.10	0.13
Both	18	0.15	0.18	0.23	0.19
Both	30	0.04	0.15	0.12	0.10

Table 12. Annual variation in species composition of the 35 most ubiquitous fish species observed at Asan Pt. and Ipao Pt. as estimated by the Jaccard Coefficient (J). Calculations are based on data collected during September, October and November, 1979 and 1980. J is explained in text and in Sokal and Sneath (1963).

Study Site	Transect Depth (m)	September	October	November	$\bar{x}$
Asan	All	0.97	0.91	0.94	0.94
Ipao	All	0.97	0.97	0.91	0.95
Both	5 m	0.81	0.87	0.88	0.85
Both	9 m	0.82	0.85	0.85	0.84
Both	18 m	0.74	0.88	0.88	0.83
Both	30 m	0.82	0.66	0.72	0.73

Table 13. Annual variation in species composition of the 35 most ubiquitous fish species observed at Asan Pt. and Ipao Pt. as estimated by the Resemblance Index (R). Calculations are based on data collected during September, October and November, 1979 and 1980. R is explained in text and in Smith (1973).

Study Site	Transect Depth (m)	September	October	November	$\bar{x}$
Asan	All	0.98	0.96	0.97	0.97
Ipao	All	0.96	0.98	0.98	0.97
Both	5 m	0.90	0.93	0.93	0.92
Both	9 m	0.90	0.92	0.92	0.92
Both	18 m	0.85	0.93	0.94	0.91
Both	30 m	0.91	0.78	0.84	0.84

intensified. Similarly, this study did not examine the possibility of differential larval survival throughout the year or the effects of predation and competition on newly settled recruits. However, because this investigation did yield data indicating that different trophic groups exhibited different patterns of seasonal abundance, it is possible that food availability may be an important "proximate" or "ultimate" cause influencing the observed seasonal peaks in overall fish abundance.

Kock (1982) proposed that seasonally abundant planktonic food may be important in timing the initiation of strong juvenile fish recruitment on Guam's upper reef slope. In doing so, he cited the post-reproductive loosening and fragmentation of Boodlea composita beginning in February (R. T. Tsuda, pers. com.) and the desiccation of Caulerpa racemosa (Peterson 1972) beginning in March, as examples of reef-flat algae that are transported offshore during the midday low-tide season. Accordingly, it was inferred that the suspended particulate material resulting from these and other species of dead algae may somehow indirectly contribute to the nourishment of pelagic fish larvae, and that the added benefit of this condition is ultimately manifested in the form of maximum juvenile settlement between March and June.

Although the diurnal low-spring-tide season at Guam may begin around March, there is evidence that effective reef-flat algal desiccation may not occur until later in the season. Tsuda (1974) has shown that the algae which are most seasonal on Guam are intertidal species, the majority of which are most abundant between January and June. He also emphasized that the desiccation of intertidal algae is regulated by the critical factors of time of day and duration of exposure (Doty 1946; Lawson 1957) which are effectively met on Guam only during the months of May through August. Therefore, if seasonally abundant planktonic food is an important factor influencing successful springtime juvenile recruitment among upper reef-slope fishes, it is likely to result from a source that is of greater influence during the earlier part of the year. The results of the present study suggest a similar but contrasting explanation.

If, in general, the numbers in an animal population are at least partly regulated by food availability (Lack 1954; Pianka 1974), and since fish appear to spawn to gain most from the food available in the production cycle (Cushing 1975; Russell et al. 1977), the rather dramatically successful recruitment of P. guamensis presumably indicated the presence of abundant zooplankton. By the same logic, increases among the benthic invertebrate-feeders may indicate the presence of abundant benthic invertebrate prey, of which many species are also known to feed extensively on plankton. Indeed, Russell et al. (1977) pointed to the significance of a recruitment strategy in which fish abundance increases at a time when maximum food resources ensure conditions most favorable for growth. In addition, they mention evidence leading to the existence of subtle seasonal patterns in tropical primary production (Kinsey and Domm 1974), and the possible link between these patterns and the reproductive cycles in coral-reef fishes. In a northern hemispheric tropical ocean, phytoplankton production, largely controlled by solar radiation and wind, develops slowly through the fall and winter leading to maximum herbivorous zooplankton abundance around February (Cushing 1959, 1975), approximately the time of the initial planktivore influx observed during this study.

The much greater than average rain experienced in February (Fig. 2) may have added additional nutrients through rain-induced terrestrial run-off. The addition of detrital material after April due to the developing seasonal reef-flat algal kill may also be influential. Although peak abundances among the most ubiquitous carnivores did not show a significant relationship with the rainy season (Table 8), it is reasonable to conclude from the observed trends that increased food availability in a variety of forms could have played an important role in their fluctuations. At the very least, the data clearly suggest that many of the planktivores, piscivores and benthic invertebrate-feeders within the fish community are capable of taking advantage of seasonal increases in their food supplies. Besides conferring potential growth benefits to recruiting juveniles, reproduction coincident with maximum levels of fluctuating food resources may allow adults to meet more successfully the increased energy demands spawning places upon them. Therefore, the relationship between food resource availability and fish abundance for spawners as well as recruits may have significance from both "proximate" physiological (Lagler et al. 1962) and "ultimate" evolutionary (Fisher 1930) perspectives.

Data on the herbivores led to the same general conclusion. Since these fishes have generally low assimilation efficiencies (Odum 1970; Chartok 1972), and retain food for only a few hours (Ogden and Lobel 1978), they also have relatively large food biomass requirements (Bardach 1961). In Guam, both adults and juveniles of several surgeonfish and parrotfish species commonly seen on the upper reef slope, are known to frequent the reef flat (Amesbury 1978; Amesbury and Myers 1982; Katnik 1982; Myers 1982), especially during high tides. When the relatively extensive reef-flat area that exists on Guam (Randall and Eldredge 1976) is considered, it is easy to imagine how beneficial the additional algal biomass associated with this zone might be to the shallow-water herbivorous fish community. However, in order to utilize even a limited amount of the energy stored in this biomass, many herbivorous fishes have had to adapt to a distinctive type of production cycle largely controlled by solar radiation, tide and rainfall.

As the diurnal low-spring-tide season develops, both grazers and browsers are excluded from foraging on the reef flat during certain hours of the day (Bakus 1967). Since most herbivorous fishes are nocturnally inactive (Hobson 1965, 1972; Starck and Davis 1966; Rosenblatt and Hobson 1969), this low-tide restriction of diurnal reef-flat foraging might be viewed as a condition less favorable to maximum growth, especially among juvenile browsers. Widespread reduction in food resources due to desiccation (Tsuda 1974) during the fully developed diurnal low-spring-tide season also may be highly stressful to foraging herbivore populations, and in particular to those browsers most intimately associated with the reef flat. The severity of this form of environmental stress is compounded by seasonally high rainfall (Fig. 2) which serves to extend the time period of algal reduction by preventing the reef-flat community from starting to reestablish itself as soon as the critical midday low-tide season ends. Rainfall continuing into the later months of the year could produce reef-flat salinities low enough to delay the reappearance of upper intertidal algae until January (Tsuda 1974). The increase in fish abundance that occurred most notably in shallower water during the fall may have been related to reproduction among grazers in response to lengthening diurnal foraging time on the reef flat, and among browsing surgeonfishes in response to the reestablishment of the reef-flat algal community.

Because of the rather ubiquitous nature of their food source and their wide-ranging foraging habits, parrotfishes may be less dependent than browsing surgeonfishes upon the reef flat, and thus, may also be relatively less affected by the seasonal diurnal restriction of reef-flat foraging. This may be supported by the comparatively lower juvenile representation of the latter species observed during this study, which also suggests that reproduction among browsing surgeonfishes may be more responsive to changes in reef-flat algal biomass. The herbivores that peaked in abundance earlier in the year were mostly territorial damselfishes that commonly inhabit the reef front and submarine terrace. Others included deeper-water angelfishes, parrotfishes and surgeonfishes. The effects of seasonally reduced reef-flat algal biomass might be felt indirectly by these damselfishes and angelfishes in the form of temporarily increased interspecific competition for food (Barlow 1974), particularly since subtidal algae appear to flourish year round (Tsuda 1974).

Certain nonherbivorous fishes may also take advantage of reproducing during the fall for a similar reason, since increasing plankton, algal production and detritus accumulations on the reef flat may support a significant biomass of benthic invertebrates as well. However, reproduction during the fall may be of secondary importance to these species since they are not as directly dependent as herbivores on reef-flat algal biomass. Thus, nonherbivorous species may spread their reproductive activities over a longer period of time which may partially explain why peak abundances within the most ubiquitous carnivore group analyzed in this study did not prove to be significantly correlated with the April to June period (Tables 9 and 10).

Despite numerical variations in seasonal abundance, the fish community in general seems to exhibit a fairly predictable annual cycle returning to similar levels after a 12-month period. The resulting low values of AV (Table 10) characterize the fish community on the upper reef slope as being relatively persistent. The values of AV calculated for upper reef-slope fishes on Guam may be compared with those calculated for organisms in less climatically stable regions (Table 14). The values for Guam are slightly lower but similar to those for marine fishes in southern California (Ebeling et al. 1980), and they are lower than those for marine fishes in northern California (Miller and Geibel 1973; Burge and Schultz 1973) and for estuarine fishes in northern Florida (Livingston 1976).

The high annual constancy in species composition found during this study also indicates the presence of a fairly persistent fish community on the scale analyzed (Tables 15 and 16). These results generally agree with other studies of fish assembleges made on relatively large areas of coral reef (Smith and Tyler 1972, 1975; Smith 1973; Gladfelter et al. 1980; Kock 1982), but are in contrast to the results of studies of very small natural fish assemblages (Sale 1977; Sale and Dybdahl 1975, 1978) and assemblages on comparatively small natural reefs (Nolan 1975; Sale 1980) and artificial reefs (Russell et al. 1974, 1977; Talbot et al. 1978). Differences in either the spatial scale used or the time interval between compared censuses could greatly affect the outcome of such comparisons (Diamond and May 1977; Talbot et al. 1978). In this regard, less variation is predicted for data

Table 14. Comparison of annual variation (AV) in ranked species abundances calculated for some organisms living in different geographical areas and climatic regimes. AV values measure the scope of yearly changes in species abundances, where relatively low values indicate generally little change. (See text and Wolda 1978).

AV	ORGANISM	LOCATION	REFERENCE
0.55*	Estuarine Fishes	North Florida	Livingston 1976
0.34	Arthropods	Dry, unstable climate	Wolda 1978
0.20*	Marine Fishes	Diablo Cove, Calif.	Burge & Schultz 1973
0.17*	Marine Fishes	Monterey Bay, Calif.	Miller & Geibel 1973
0.15	Arthropods	Humid, stable climate	Wolda 1978
0.15	Marine Fishes	Santa Cruz Is., Calif.	Ebeling *et al.* 1980
0.11	Marine Fishes	Naples Reef, Calif.	Ebeling *et al.* 1980
0.11	Marine Fishes	Ipao Pt., Guam	This study
0.09	Marine Fishes	Asan Pt., Guam	This study

* = Values calculated by Ebeling *et al.* (1980)

collected on larger spatial scales and after long inter-census periods. Less variability may also result from comparisons of between-year censuses for a single month than from comparisons of monthly censuses made within a single year.

The trend in observed overall species richness across depth (Tables 1 and 2) raises an interesting point concerning the diversity of coral-reef fishes. The lower species richness found at 30 m in the present study would be expected since greater environmental stability (or conditions of relatively less frequent and less intense natural disturbances) would allow the forces of competition and predation among species to act relatively more continuously over longer periods of time. A result of this would be the elimination of less fit members from the community at a comparatively faster rate. Stability should decrease with decreasing depth as natural disturbances primarily in the form of predation (Talbot _et al_. 1978) are expected to more frequently or more intensely interrupt the competitive process by nonselectively removing a greater proportion of the more fit members from the community, thereby enabling a greater number of species to coexist. This would occur to a depth above which the disturbances may become so frequent or intense that species diversity becomes limited by severe environmental conditions. In this form of the "intermediate disturbance hypothesis" (Connell 1978), it may be that the frequency and intensity of natural disturbances at the surface due to storms, large waves, surface currents etc. are replaced by the effects of increased predation on the submarine terrace down to a point somewhere near a depth of 18 m. While both of these sources of localized small-scale disturbance would be expected to influence species richness, predation is likely to be the most important (Talbot _et al_. 1978). For the sake of comparison, data from two other depth-related studies were drawn from the literature (Gosline 1965; Harmelin-Vivien 1977). In these studies, numbers of species were given for several depth ranges. In order to graph all the data together, the number of species per depth range was assigned to the mean depth of each reported range. The results (Fig. 10) proved to be remarkably consistent.

CONCLUSIONS

The coral-reef fishes on the upper reef slope at Guam exhibit seasonal variations that appear to result largely from reproductive activities which may be closely related to food resource availability. Seasonal fluctuations between carnivore and herbivore groups overlap but show depth-related temporal differences in peak abundance that may be the result of adaptations to different food resources. Climatological and oceanographic phenomena seem to play indirect, but important roles in the timing of seasonal fish abundance by their apparent influences on primary production cycles and reproductive success in fishes. The upper reef-slope fish community in general exhibits a persistent structure that has evidently evolved in response to a predictable environment of relative climatic stability. The applicability of the "intermediate disturbance hypothesis" to mobile animals is demonstrated by fishes across depth on the upper reef slope.

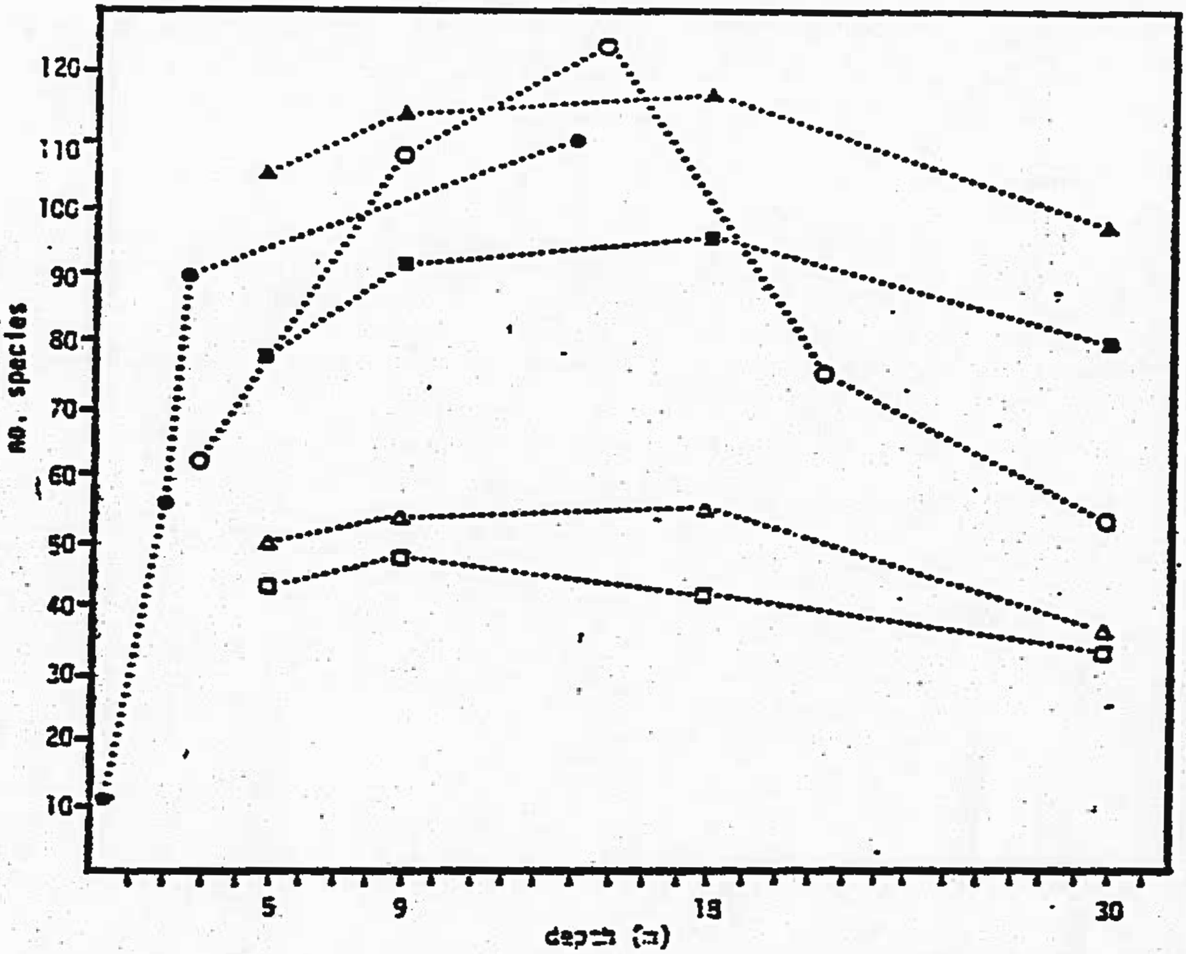

Figure 10. Actual and mean species richness (number of species) observed at Asan Pt. and Ipao Pt. study sites by depth. ■ = Asan Pt. (total no. species); ▲ = Ipao Pt. (total no. species); □ = Asan Pt. ($\bar{x}$ no. species/month); △ = Ipao Pt. ($\bar{x}$ no. species/month); ● = Oahu, Hawaii (total no. species, Gosline 1965); ○ = Tulear Reef, Madagascar (total no. species, Harmelin-Vivien 1977).

RECOMMENDATIONS

This job should be terminated with this report. The results of this study suggest several possible avenues of future investigation into the reproductive and trophic relationships among coral-reef fishes. Data presented here on several recreationally important species should be compared with DAWR creel census data in order to identify possible seasonal trends in the fisheries for these species. The information presented may be useful to fisheries biologists in managing inshore reef fisheries on both the relatively healthy and heavily impacted reefs of Guam.

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