AN ABSTRACT OF THE THESIS OF Michael E. Molina for the Master c

Science in Biology presented May 13, 1983.

Title: Seasonal and Annual Variation of Coral-Reef Fishes on tl

Upper Reef Slope at Guam.

Approved: ______________________________

Steven S. Amesbury, Chairman, Thesis Committee

Coral-reef fishes were monitored monthly at four upper reef-slop depths (5, 9, 18 and 30 m) at two locations at Guam between Septembe 1979 and November 1980. Overall fish density increased markedly a all depths during the spring and summer months, corresponding to tl onset of the rainy season and the diminishing of the tradewinds Maximum abundances were recorded between May and July. A less prc nounced increase in fish abundance occurred in the fall. Most of tl observed seasonal variation in fish abundance resulted from juvenil recruitment and the movements of subadults and adults of a relativel small group of abundant species at each depth. Planktivores, pisci vores and benthic-invertebrate feeders, primarily in deeper water were largely responsible for the spring/summer peak, while the fal increase was significantly influenced by herbivorous fishes at shal lower depths. Fluctuations of fish abundance may be related t variations in the availibility of food resources. Climatological anc

oceanographical phenomena may have favorably influenced food resour
availability as well as reproductive success during certain month
Estimates of site- and depth-related annual variation in fish abu
dance and species composition of 35 ubiquitous fish species indicat
relative constancy over extensive areas of reef. Fish species ric
ness was found to be greatest at 18 m. An explanation for this tre
in species richness based on the "intermediate disturbance hypothesi
is offered.

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SEASONAL AND ANNUAL VARIATION OF CORAL-REEF FISHES ON THE UPPER REEF SLOPE AT GUAM

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE
in
BIOLOGY

University of Guam

May 1983

ACKNOWLEDGEMENTS

I am very grateful to my committee members for their most helpfu guidance, patience and support.

I am particularly indebted to Harry T. Kami of the Division o Aquatic and Wildlife Resources, Department of Agriculture, Governmen of Guam, for providing logistical support throughout the study.

Dr. Roy T. Tsuda provided very constructive comments and valuab literature. Robert F. Myers helped identify some of the fish specie and contributed pertinent literature. Dr. Theo A. Dillaha III an Russell N. Clayshulte helped with computer programming. Tom Yoshi provided access to climatological data on Guam.

Special thanks are due to Ronald D. Strong for his assistance establishing the transect stations; and to Michael J. Wilder for th use of valuable office equipment.

I thank all my dive partners, especially R. Logan Kock, Alan Hosmer, Jr., Henry Tucker, Steve Katnik, Don Morris, Dave Hendricks Deborah Longstaff, Lynda Hilbert, and Tom Molina.

Deborah Longstaff also provided limitless encouragement an invaluable moral support.

Kathy Saison patiently typed the manuscript.

Drs. Alfred W. Ebeling and Mark A. Hixon have my supreme admira tion and gratitude for imparting to me the personal inspiration th ultimately led to this study.

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INTRODUCTION

While the study of marine reef fish assemblages has progresse rapidly within the last three decades (Harry 1953; Brock 1954; Bardac 1959; Randall 1963, 1965; Talbot 1965; Talbot and Goldman 197 Bradbury and Goeden 1974; Goldman and Talbot 1976), it has bee primarily during the past ten years that increased emphasis had bee given to studying the patterns of seasonal and annual variation c these species. Seasonality in spawning behavior among coral-ree fishes has been documented in many areas including the Caribbea (Munro *et al*. 1973; Powles 1975), Hawaii (Miller *et al*. 1979), th South China Sea (Vatanachi 1972), the Indian Ocean (Wourms and Bayr 1973), the Great Barrier Reef (Russell *et al*. 1974, 1977) and Micro nesia (Johannes 1978). Seasonal patterns in recruitment of juvenil reef fishes have been recorded in the Caribbean (Luckhurst ar Luckhurst 1977), the Gulf of California (Molles 1978), Hawaii (Watsc and Leis 1974), Guam (Kami and Ikehara 1976; Kock 1982), the Red Se (Gunderman and Popper 1975) and most intensively, the Great Barrie Reef (Sale and Dybdahl 1975, 1978; Russell *et al*. 1977; Talbot *et al* 1978; Williams and Sale 1981). Studies of the patterns of annua variability and stability of reef-fish assemblages are much mor limited in number (Smith and Tyler 1973, 1975; Thomson and Lehne 1976; Thompson and Schmidt 1977; Sale 1978, 1980a; Ebeling *et al* 1980).

The problem of accurately interpreting observed variations in th sizes of reef-fish populations was noted by Ehrlich (1975), and th value of understanding such variations in natural fish communitie from a fisheries management perspective was discussed by Cushin (1975) and Larkin (1978). Sale (1980a) discussed the current diff- culties associated with assessing the temporal persistence of cora reef-fish assemblages, and Wolda (1978) stressed the importance o investigating the patterns of annual fluctuations in abundance amon tropical populations from a theoretical point of view. Thus, studie of seasonal and annual patterns of variation in reef-fish communitie may contribute to our understanding of basic principles underlying th functioning of coral-reef ecosystems, as well as provide potentia practical insight into certain processes of fishery dynamics such a reproduction and recruitment.

During 1978 and 1979, the Guam Department of Agriculture Divisio of Aquatic and Wildlife Resources (DAWR) used a steel barge artificia reef to increase the available fish habitat near the 18-m dept contour on the upper reef slope. During that project, fish count made over a period of 20 months on the barge and along line transect permanently placed over surrounding areas of natural reef were used t monitor changes in the fish community. A result of this study was th documentation of a marked seasonal fluctuation in total fish abundanc over the natural reef areas (Kock 1982). Seasonal increases amon certain species were attributed partly to the immigration of adult and older juveniles, and partly to juvenile recruitment. Although n spawning peaks were observed, maximum settlement of juveniles occurre between March and June, and the highest overall fish abundance wa recorded in May. Lowest overall abundance occurred during the winte months and reached similar levels in both years. Annual variabilit in species composition of the fish community was not examined. Sinc it would be quite useful for fisheries managers and other ecologist to know how seasonal and annual fluctuations in fish abundance ar manifested at different depths on the upper reef slope, the presen investigation was undertaken. The objective of this study is t document the patterns of seasonal and annual variability within th conspicuous upper reef-slope fish community as they are manifeste along a depth-related environmental gradient over a 15-month tim period.

METHODS

Study Sites

Guam is located within the tropical Indo-West Pacific region ɛ lat. 13°28'N and long. 144°45'E. It is the southernmost of tł Mariana Islands and is largely surrounded by a fringing coral reeı Fishes were monitored on the upper reef slope at Asan Pt. and Ipao Pı on the leeward (western) side of the island (Fig. 1). In this study references to reef zones found on the upper reef slope follow tł definitions of Tracey et al. (1964) and include the reef fronı submarine terrace and seaward slope. In a general assessment of tł major structural elements of Guam's coastline, Randall and Hollomɛ (1974) stated that these zones in the Asan area are very similar t those found near Ipao Pt. Table 1 outlines a comparison of generɛ characteristics of the study sites based on information from thes sources, as well as from Emery (1962) and from personal observatior made during the study.

The most apparent overall structural difference noted betwee study sites was the width of the submarine terrace. This zone extenc to a greater maximum depth and is more than twice as wide at Asan Pt than at Ipao Pt. Because of this, the deepest monitoring statio (30 m) at Asan was positioned near the seaward limit of the terrace while at Ipao it was situated on the seaward slope. At both sites tł coral community showed evidence of past disturbance from Acanthaste predation.

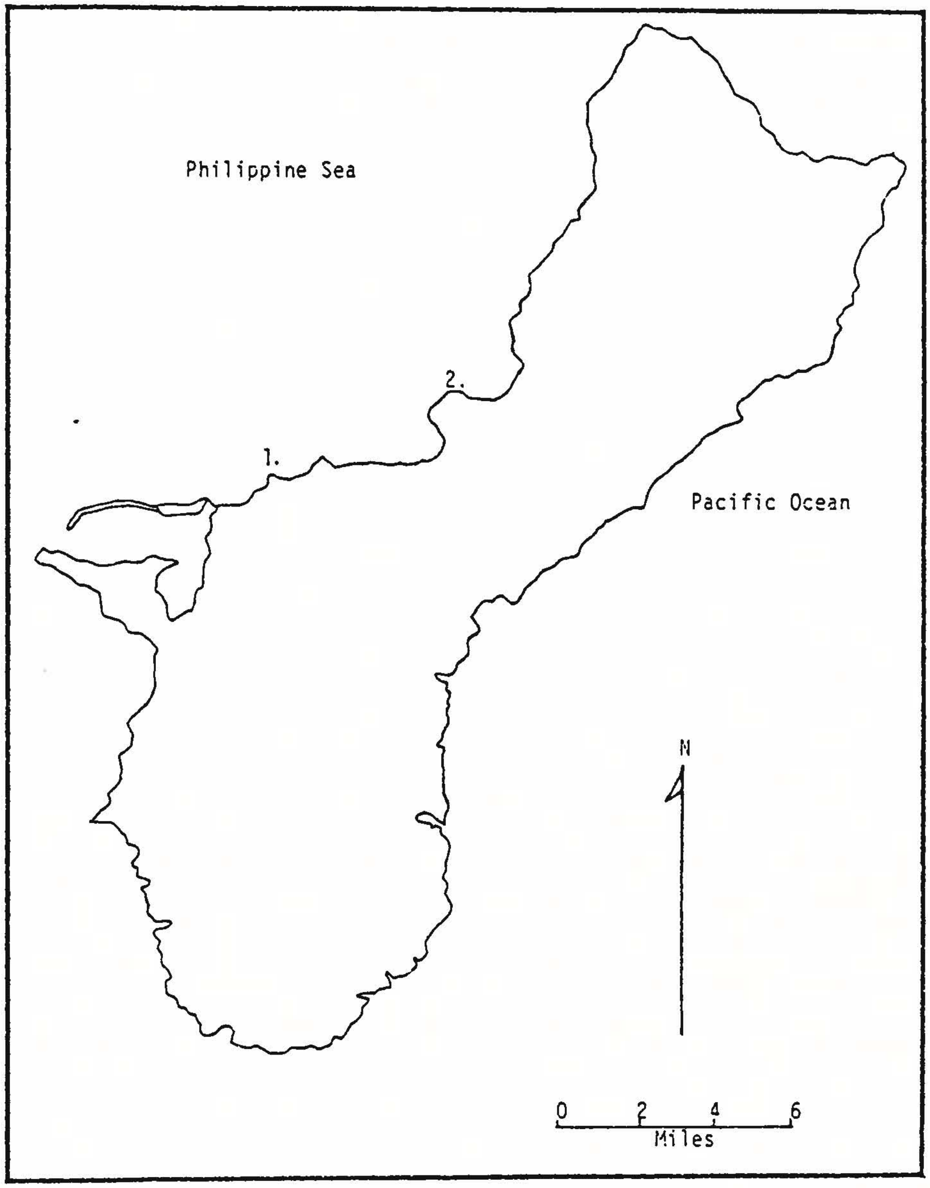

Figure 1. Map of Guam showing the locations of the Asan Pt. and Ipao Pt. study sites. 1. = Asan Pt.; 2. = Ipao Pt.

Table 1. Comparison of general study site characteristics betwee
Asan Pt. and Ipao Pt., Guam.

	ASAN PT.	IPAO PT.
Reef Flat:		
Width	Approx. 600 m	Approx. 500 m
Reef Front:		
Exposure	Approx. NNW at transects	
Width	Approx. 50 m	Approx. 80 m
Maximum Depth	Approx. 6 m	
Transect Depth	Approx. 5 m	
Relief	Submarine-channel and buttress system; channel: 2-6 m deep with holes 5-15 m dia. on inner hal: moderate relief due to scattered prominances u; to 3-4 m high on seaward half.	
Substrate	Channel floors covered by accumulations of coarse sand and gravel with scattered large boulders; buttresses covered by scattered coral heads and coral-algal knobs of moderate density with thin veneer of unconsolidated sediments and turf algae.	Channel floors covei ed by accumulations of coarse sand and gravel with scatter large boulders; but- tresses covered by coral heads, coral-algal knobs and pinnacles of moder-ate high density with isolated pock-ets of sediments an turf algae.
Submarine Terrace:		
Width	Approx. 190 m	Approx. 70 m
Maximum Depth	Approx. 35 m	Approx. 20 m
Transect Depths	Approx. 9, 18 and 30 m	Approx. 9 and 18 m
Relief	Relief due to prominances on inner half simila to seaward half of reef front; less relief on seaward half (1-2m) with a few shallow channel: (1 m deep) and occasional prominances up to 3-5 m high.	

Substrate	Inner part with coral heads and coral-algal knobs of moderate-high density; middle part with decreasing coral density surrounded by unconsolidated sediments; outer part of mostly unconsolidated sediments with widely scattered coral heads and coral-algal knobs.	Inner part with cor heads, coral-algal knobs and pinnacles of moderate density outer part with sca tered coral heads a coral-algal knobs o moderate density su rounded by flat pave ment and a few shal low channels contai ing a thin layer of sand and gravel.
Seaward Slope:		
Avg. Slope	Approx. 38°	Approx. 45°
Maximum Depth	Approx. 50 m	Approx. 35 m
Transect Depth	None	Approx. 30 m
Relief	Lower relief found on the slope than on the sub marine terrace; at Asan Pt. slope is steep and relatively featureless; at Ipao Pt. slope is steep with shallow channels (1 m deep) and a fe very widely scattered pinnacles as high as 2-3 m.	
Substrate	Mostly covered by unconsolidated sediments with occasional coral heads and/or coral-algal knobs.	Low coral growth wit scattered coral-alga knobs and occasional pinnacles, and a fev shallow channels cor tiguous with those c outer part of submarine terrace but cor taining a thicker layer of sand and gravel.

Since small channels are located on the reef flats near eac site, both locations can easily be reached by small boat. Thi facilitated data collection but also opened these areas to greate exploitation by offshore anglers and divers. Nonetheless, fishin effort observed in the vicinity of the transects during the study wa minimal. There were only two instances at Asan Pt. when actua fishing was observed. These included seeing two scuba divers wit spearguns just below the 9-m transect and seeing two divers wit handnets searching for aquarium fish at approximately 15 m. At Ipa Pt. only one instance occurred when a fisherman, using two wire fis traps, was encountered in the general area. In addition, monthly DAW interviews of offshore anglers and divers returning to the Agana Boa Basin after fishing near either study site were relatively few bot before and during the study period (unpub. data and pers. obs.) Based on these observations, the fishing pressures that occurred a both sites during the study were estimated to be relatively light an comparable in degree.

Transect Stations

During the spring of 1979, modified line transect stations wer permanently established at both study sites. At each location dupli cate 50-m transects were placed along approximate depth contours of 5 9, 18 and 30 m. A transect consisted of six unconnected rebar stakes each about 38 cm in length, embedded into reef rock at 10-m intervals A two-pound sledge hammer and a 10-cm star drill were used to star the holes for the stakes which were then hammered in tightly. Al stakes were flagged with a piece of yellow plastic marking tape t make them easier to locate on subsequent field days.

In preparation for the data collection phase of the study preliminary dives were made on the transects intermittently betwee June and August 1979. These dives enabled me to become familiar nc only with the locations of the transects and the individual stakes but also with the conspicuous fish species commonly found at eac station. This time period also provided an opportunity for me t become skilled in the use of the submersible microcassette tape dec upon which the data for the study were to be recorded. Both th plexiglass housing for the tape deck and the special scuba regulatc mouthpiece containing the remote microphone were manufactured unde the name "Wet-Tape" by Sound-Wave Systems, Inc.

Formal monthly fish counts were begun in September 1979. Dat collection was limited to the time between 1000 and 1400 hrs. Count of individuals were made for all fish species observed within tw meters above the substrate and within one meter to either side c myself as I swam from stake to stake. Dives were limited to a maximu of two depths per day, normally paired as 30 and 5 m, and 18 and 9 n On a single field day, both 50-m transects at each of the two depth were censused twice (down and back). This resulted in monthly count of fish over a combined total of 400 m^2 of reef at each depth.

Four to six field days per month were required to census th transects. A 4-m Zodiac inflatable boat with either a 6-hp or 12-h outboard engine were used throughout the study to get to and from th transect sites. Data collection was terminated with the November 19ʗ censuses.

Data Analyses

Some of the counts made at the 30-m depth had to be adjuste before analysis because of the permanent failure of the Wet-Ta recording system after August 1980. Because of the relatively sho no-decompression time limit (25 minutes) for dives to 30 meters, a since it took longer to write down observations than it did to spe them, there was sufficient safe bottom time to record data on only o pass along these transects during the last three months of the stud These counts were, therefore, adjusted to reflect the number individuals per 400 m^2 before being analyzed. Also, the recordi system failed temporarily in January 1980, resulting in the loss data and the deletion of that month from the analysis. To make t data load more manageable, a conservatively selected subset of ubiqu tous fish species was formed for closer analysis. Species composi this group were selected if they were counted on at least seven of t eight transect stations. The 35 species that qualified were used compare seasonal climatological patterns with observed season fluctuations in fish abundance.

Representative seasonal peak abundances for each of the mo ubiquitous species were identified by their maximum mean month counts. In cases where a species had maximum mean monthly coun equal in two or more months, the month flanked by the greatest repre sentation, when the data for the two flanking months were average was chosen. Depths of greatest representation were chosen for each these species based on the highest mean number per depth when th counts for all months were combined. In cases where a species had it greatest overall mean representation equal at two or more depths, th depth with the single largest mean monthly count was chosen. I addition, each of the 35 most ubiquitous species was assigned to general trophic category based on Hiatt and Strasburg (1960), Jone (1968), Randall and Klausewitz (1973), Hobson (1974), Allen (1975) and Ogden and Lobel (1978). Thus, trends in peak abundances acros depths and over months could be related to general food habits Observed changes in overall fish abundance were compared with seasona patterns of average monthly rainfall based on 24 years of Guam precip itation data from the National Oceanic and Atmospheric Administratic (NOAA) (1979, 1980) and with seasonal shifts in average monthly win patterns 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 ma 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 mos ubiquitous group, as well as additional species which occurred fre quently and were of notable abundance.

Estimates of the annual variability in fish species abundanc between consecutive years were calculated for the most ubiquitou species group according to the method of Wolda (1978). The formula i 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 ar averaged to provide an estimate of the average net change in specie abundance ($\overline{R}$) for the group as a whole. The magnitude of this chang was estimated by the variance of the log R's and is expressed a annual variability (AV) (Wolda 1978) in numbers of fish per specie between consecutive years. If nearly as many species increased a decreased in abundance between years, $\overline{R}$ would have a value near zerc and, if the magnitude of these changes was small, AV would also b relatively low.

Values of AV were calculated for each study site based on th most ubiquitous species counts which were lumped across depths. AV' were computed separately for the site-specific September, October an November data and were averaged to give a mean value per site (1600 m of reef). Annual variability (AV) at each depth was calculated usin the same 35 species by lumping the data from both sites and computin separate values for September, October and November. The resultin values of AV were averaged across months to obtain mean values p depth (800 m² of reef).

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

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

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

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

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

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

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

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

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

RESULTS

Fish counts were made during 112 dives over the 15-month perio from September 1979 through November 1980. Fishes belonging to 3 families were recorded on the transects, with 25 (76%) of them havin been represented at both study sites. Among the 200 fish specie observed at all stations, 131 (66%) were seen at both sites. Mor species were present in the Ipao counts (176) than in the Asan count (155), with 45 and 24 species restricted to each site, respectively All fish species counted during the study are listed by site and dept in Tables 2 and 3. At both study sites more species were counted a 18 m than at any other depth, but overall mean fish abundance wa greatest at 9 m.

Seasonal Variation

An increase in overall fish abundance occurred at all depth during the spring and summer months, with maximum monthly count recorded in May, June and July (Fig. 2). Maximum overall fish abun dance was encountered earlier in the year at the deeper transects (3 and 18 m counts peaked in May) than at the shallower transects (9 an 5 m counts peaked in June and July, respectively). Although ther were some variations in these seasonal trends at each depth at the tw survey areas, in general the patterns at Asan and Ipao were simila (Figs. 3 through 6). However, the fluctuations observed at the tw

Table 2. Fish species seen on Asan Pt. transects from September 19
through November 1980; * = seen only on Asan Pt. transects.

FAMILY/SPECIES	DEPTH (m) 5	9	18	30
ACANTHURIDAE (Surgeonfishes)				
Acanthurus glaucopareius 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 biocellatus 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	3(
C. traceyi (Woods & Schultz)	X			
Dascyllus reticulatus (Richardson)	X	X	X	
D. trimaculatus (Ruppell)	X		X	
Plectroglyphidodon dickii (Lienard)	X	X		
**P. imparipennis* (Vaillant & Sauvage)	X			
P. johnstonianus Fowler & Ball	X	X	X	
P. lacrymatus (Quoy & Gaimard)		X	X	)
Pomacentrus vaiuli Jordon & Seale	X	X	X	)
Pomachromis guamensis Allen & Larson	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				)
S. gibbus Ruppell		X	X	
**S. oviceps* Valenciennes		X	X	
S. psittacus Forsskal	X	X	X	)
S. rubroviolaceus (Bleeker)	X	X	X	
S. schlegeli (Bleeker)	X	X	X	)
S. sordidus Forsskal	X	X	X	)
SCORPAENIDAE (Scorpionfishes)				
**Synanceia verrucosa* Bloch & Schneider			X	
SERRANIDAE (Groupers)				
**Cephalopholis argus* (Bloch & Schneider)				)
C. urodelus (Bloch & Schneider)	X	X	X	)
Epinephelus fasciatus (Forsskal)		X	X	)
**Plectropomus melanoleucus* (Lacepede)				)
Variola louti (Forsskal)				)
SIGANIDAE (Rabbitfishes)				
Siganus argenteus (Quoy & Gaimard)			X	)
SYNODONTIDAE (Lizardfishes)				
Synodus variegatus (Lacepede)		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 (Vaillant & 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 3. Fish species seen on Ipao Pt. transects from September 19
through November 1980; * = seen only on Ipao Pt. transects

FAMILY/SPECIES	DEPTH (m) 5	9	18	30
ACANTHURIDAE (Surgeonfishes)				
Acanthurus glaucopareius 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			
CAESIONIDAE (Fusiliers)				
**Pterocaesio chrysozonus* (Cuvier)			X	X
CHAETODONTIDAE (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
CIRRHITIDAE (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	
FISTULARIIDAE (Coronetfishes)				
**Fistularia commersonii* Ruppell		X		
GOBIIDAE (Gobies)				
Nemateleotris magnifica Fowler		X	X	X
Pogonoculius zebra Fowler	X	X		
Ptereleotris evides (Jordan & Hubbs)	X	X	X	
Valenciennea strigatus (Brousonnet)	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 bandanensis (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
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		DEPTH (m) 5	9	18	30
*_E. merra_ Bloch				X	X
Variola louti (Forsskal)					X
SIGANIDAE (Rabbitfishes)					
Siganus argenteus (Quoy & 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 (Vaillant & 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	29	21	23	26	25
Total No. Species	176	105	114	117	97

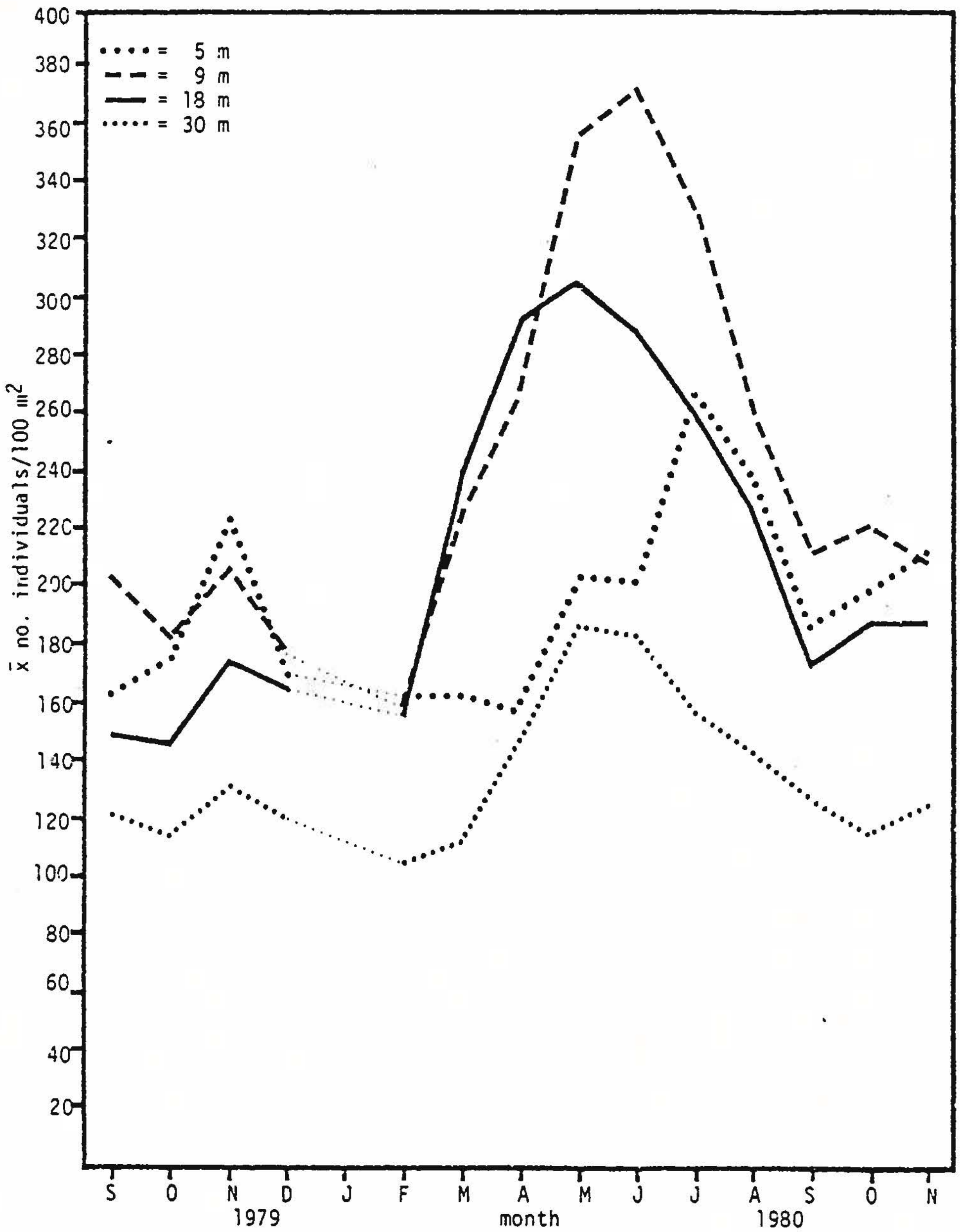

Figure 2. Monthly fluctuations in overall fish abundance (mean number of individuals/100 m²) recorded from September 1979 through November 1980 by depth.

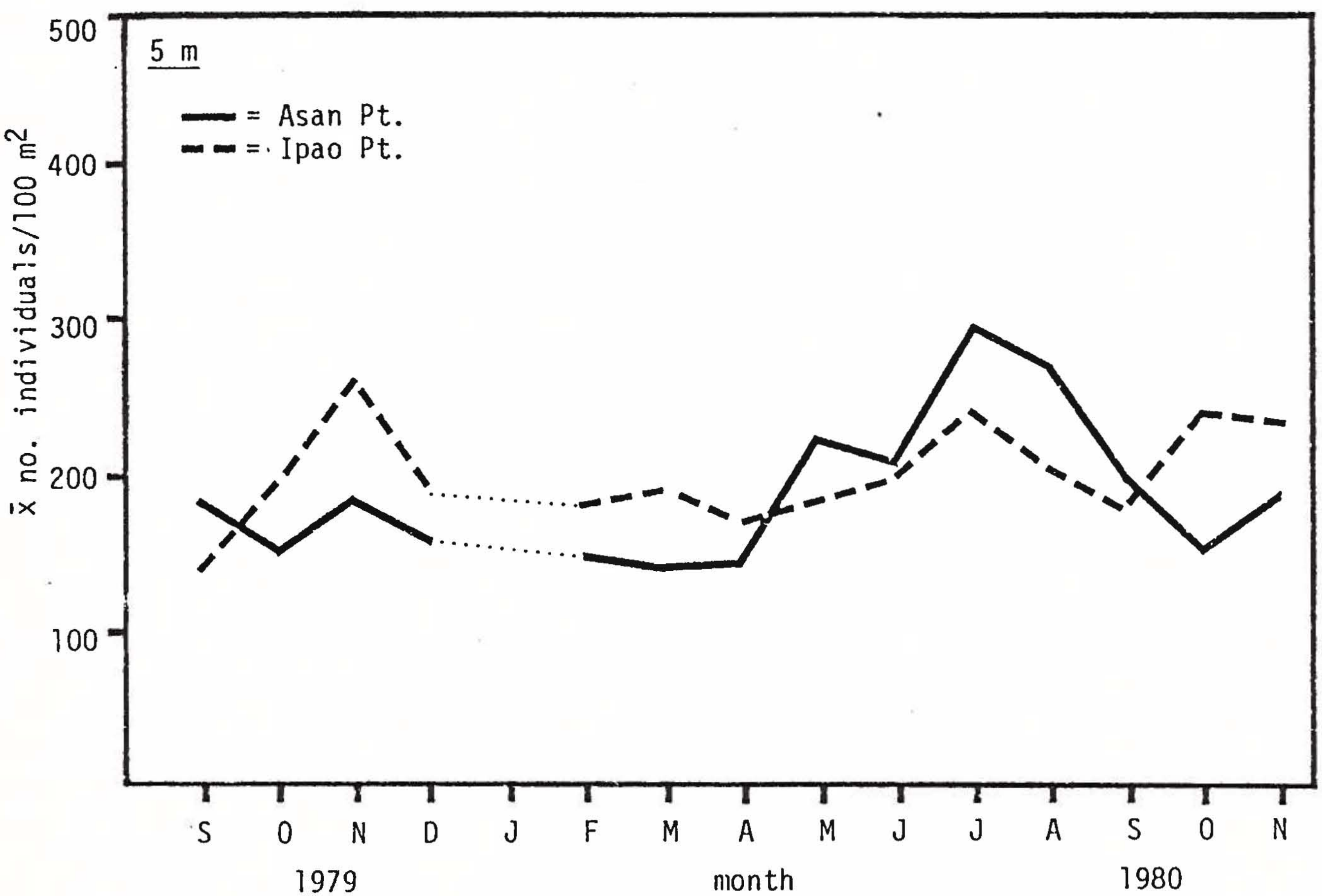

Figure 3. Monthly fluctuations in fish abundance (mean numbers of individuals/100 m²) recorded at 5-m depth by study site.

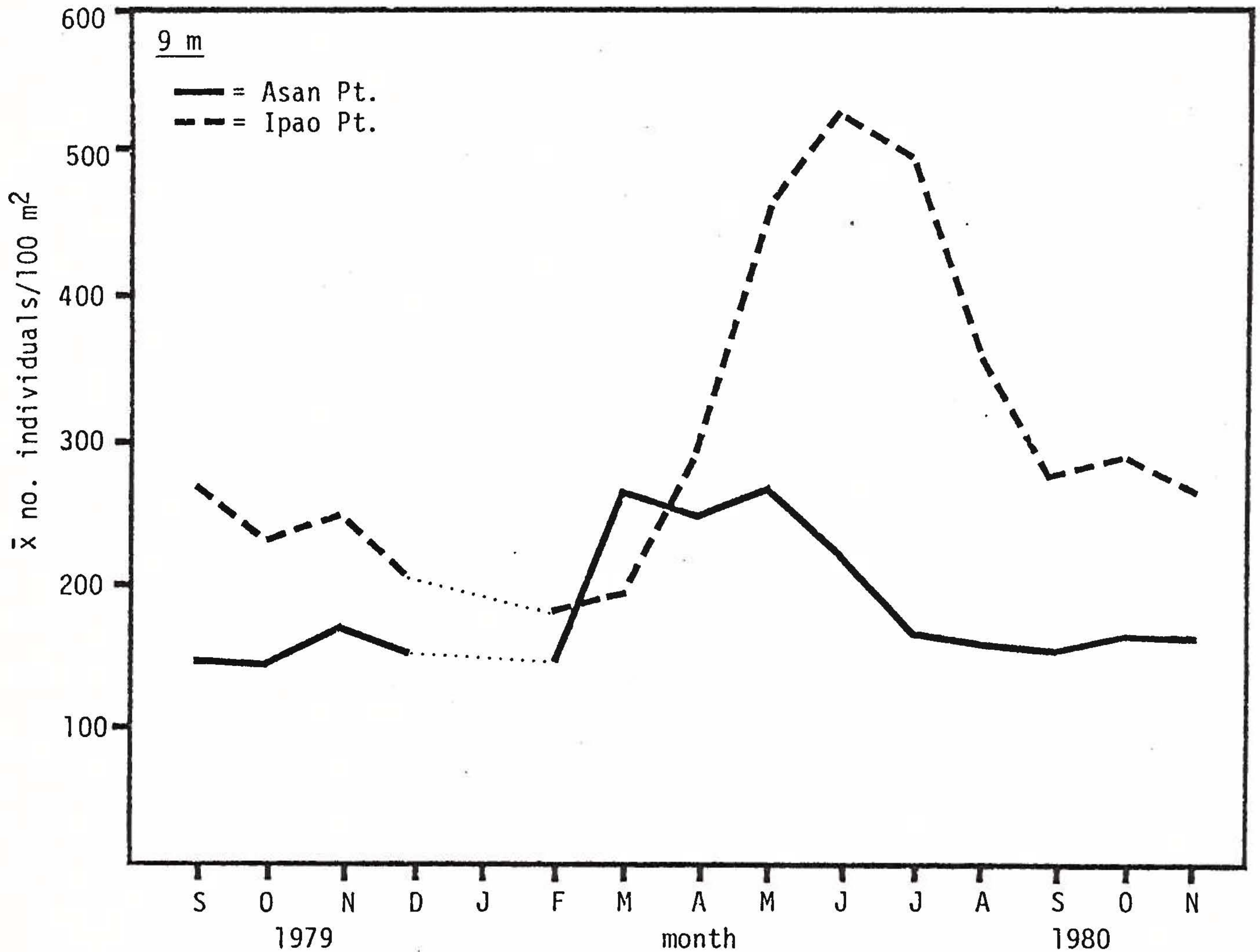

Figure 4. Monthly fluctuations in fish abundance (mean numbers of individuals/100 m²) recorded at 9-m depth by study site.

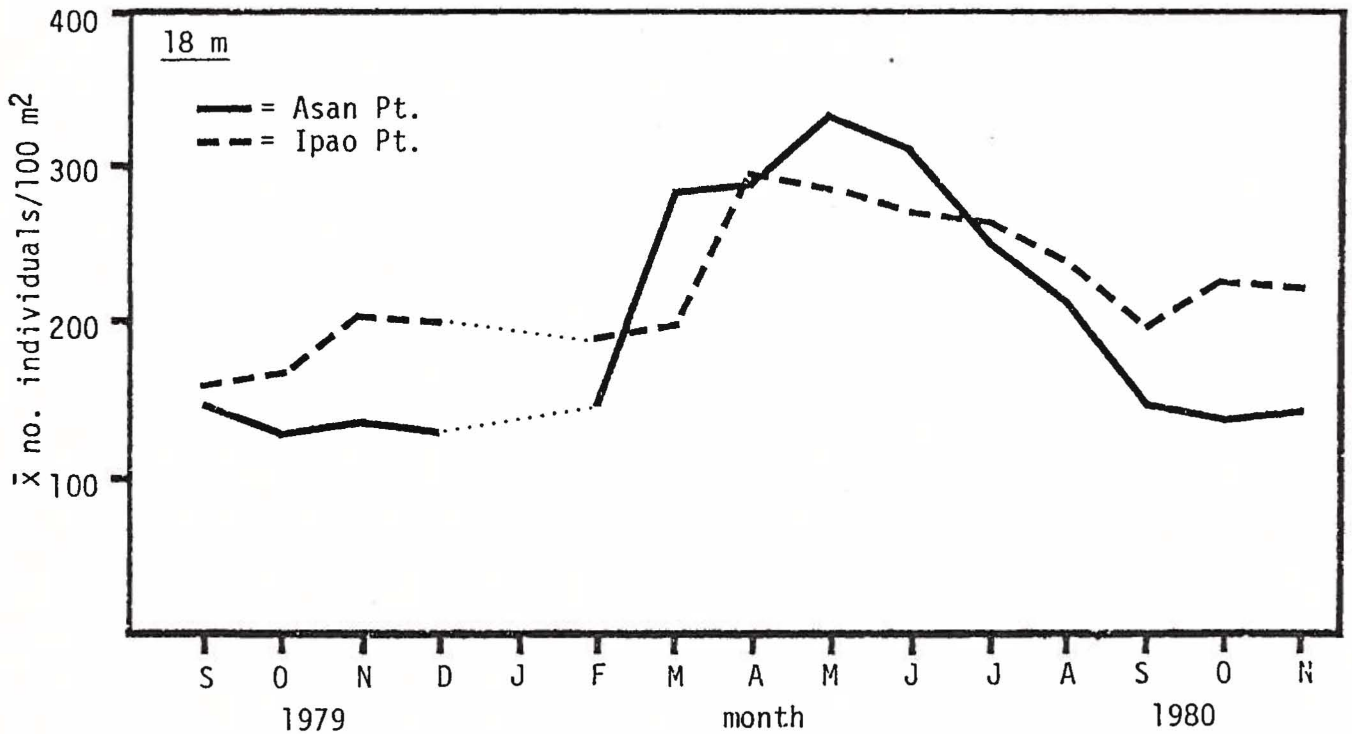

Figure 5. Monthly fluctuations in fish abundance (mean numbers of individuals/100 m²) recorded at 18-m depth by study site.

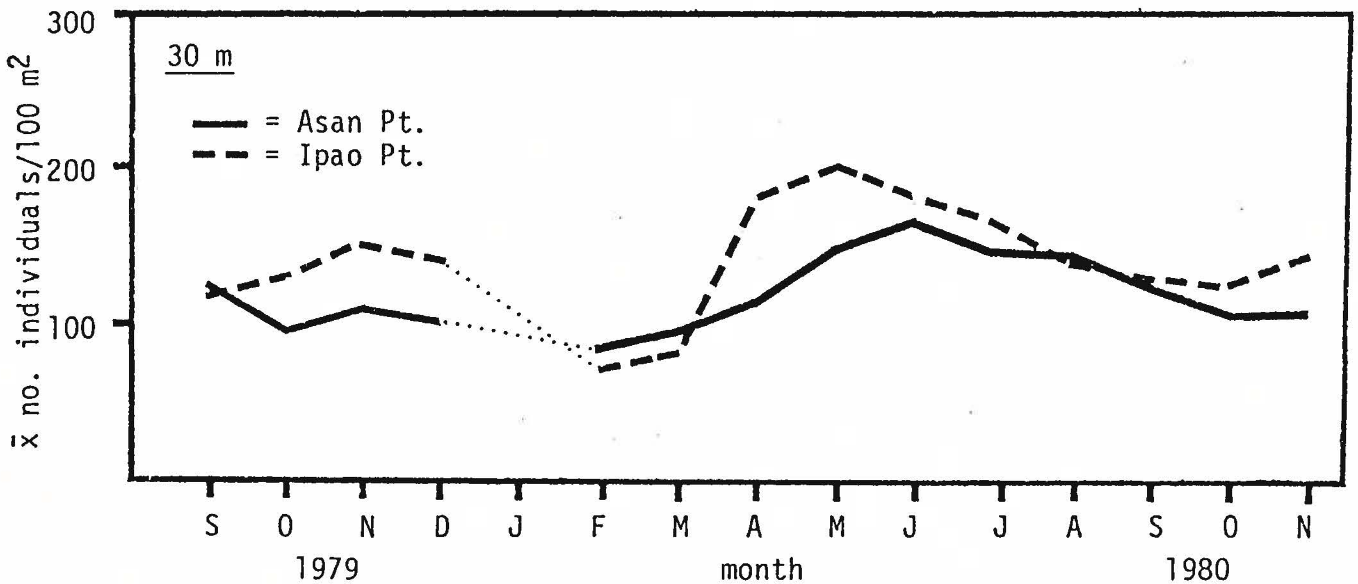

Figure 6. Monthly fluctuations in fish abundance (mean numbers of individuals/100 m²) recorded at 30-m depth by study site.

study sites were slightly out of phase with respect to each othei Ipao peaking prior to Asan at all depths.

From an examination of individual species counts, it appears thɛ most of the observed seasonal increase in fish abundance is primaril attributable to a relatively small group of species which are wel represented at each station. In every case, however, other importar but less abundant species also contributed to the overall fluctuatior To characterize the species which were most influential at each deptɦ I arbitrarily chose those species of which at least 500 individual were counted at a single station during the entire investigatic (Table 4). Fourteen species qualified at this level of abundance, 1 of which were among the 15 overall most abundant species recorde during the study (Table 5). The fourteenth species, Plagiotremu tapeinosoma, ranked number 21 in overall abundance. Ten of the 1 species contributed to the majority of the overall numerica fluctuation at each depth.

At 5 m, Chrysiptera leucopomus (Fig. 7) was the major contributing species to the spring/summer fluctuation in fish abundance Lesser contributors included Thalassoma quinquevittatum (Fig. 8) P. tapeinosoma and Stegastes fasciolatus (Fig. 9), although the latte species did not show very wide variation at this depth and tende toward slight increases in the fall. Plectroglyphidodon dickii Acanthurus nigrofuscus, and Ctenochaetus striatus (Figs. 10, 11 an 12, respectively) made relatively lower contributions during th spring and summer, as their maximum mean monthly counts were note

Table 4. Most influentially abundant fish species (≥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

Table 5. Overall most abundant fish species (listed among the top 1 most abundant species at each station) counted during th study in order of total abundance.

SPECIES	Total No. Counte
Chrysiptera traceyi	8799
Pomachromis guamensis	8137
Pomacentrus vaiuli	7387
Dascyllus reticulatus	7047
Stegastes fasciolatus	6598
Thalassoma quinquevittatum	5543
Cirrhilabrus sp.	5513
Acanthurus nigrofuscus	3880
Plectroglyphidodon dickii	3154
Chrysiptera leucopomus	3083
Plectroglyphidodon lacrymatus	2467
Scarus sordidus	1811
Ctenochaetus striatus	1744
Plectroglyphidodon johnstonianus	1691
Scarus psittacus	1009
Meiacanthus atrodorsalis	871
Scarus schlegeli	858
Naso lituratus	841
Nemateleotris magnifica	778
Paracirrhites arcatus	715
Plagiotremus tapeinosoma	661
Cirrhitichthys falco	577
Acanthurus triostegus	574
Halichoeres biocellatus	557
Macropharyngodon meleagris	529
Centropyge shepardi	507
Acanthurus glaucopareius	492
Dascyllus trimaculatus	462
Parupeneus trifasciatus	434
Chaetodon citrinellus	416
Thalassoma lutescens	404
Canthigaster solandri	391
Zanclus cornutus	359
Plectroglyphidodon imparipennis	354
Sufflamen bursa	347
Parapercis clathrata	337
Chaetodon punctatofasciatus	288
Cheilinus unifasciatus	274
Acanthurus pyroferus	221

Total No. Species = 39

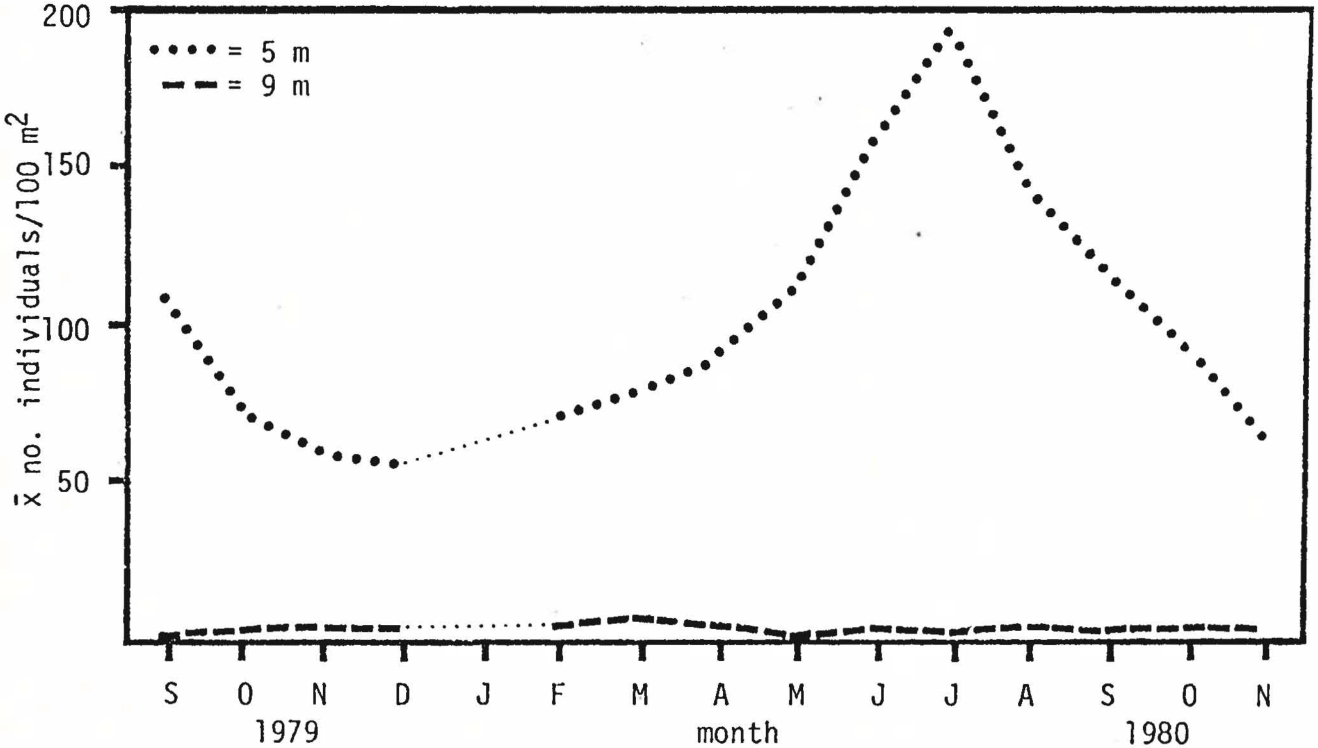

Figure 7. Monthly fluctuations in abundance (mean number of individuals/100 m²) of *Chrysiptera leucopomus* recorded from September 1979 through November 1980 by depth.

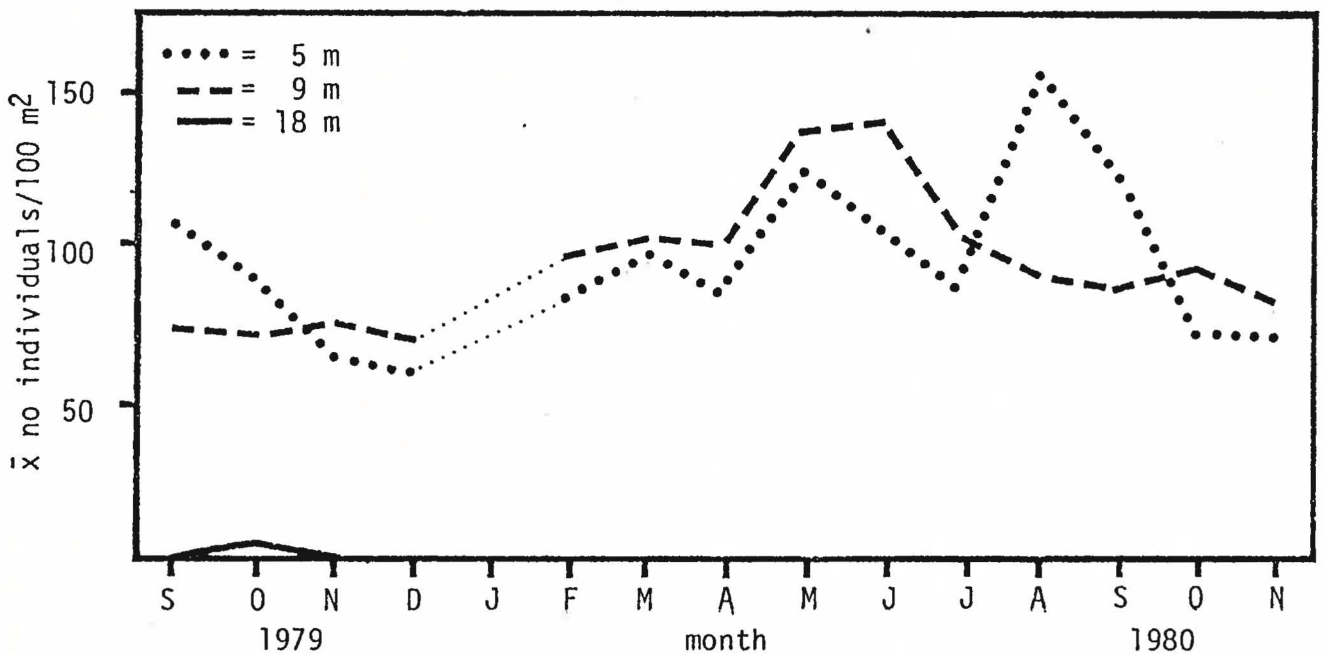

Figure 8. Monthly fluctuations in abundance (mean number of individuals/100 m²) of Thalassoma quinquevittatum recorded from September 1979 through November 1980 by depth.

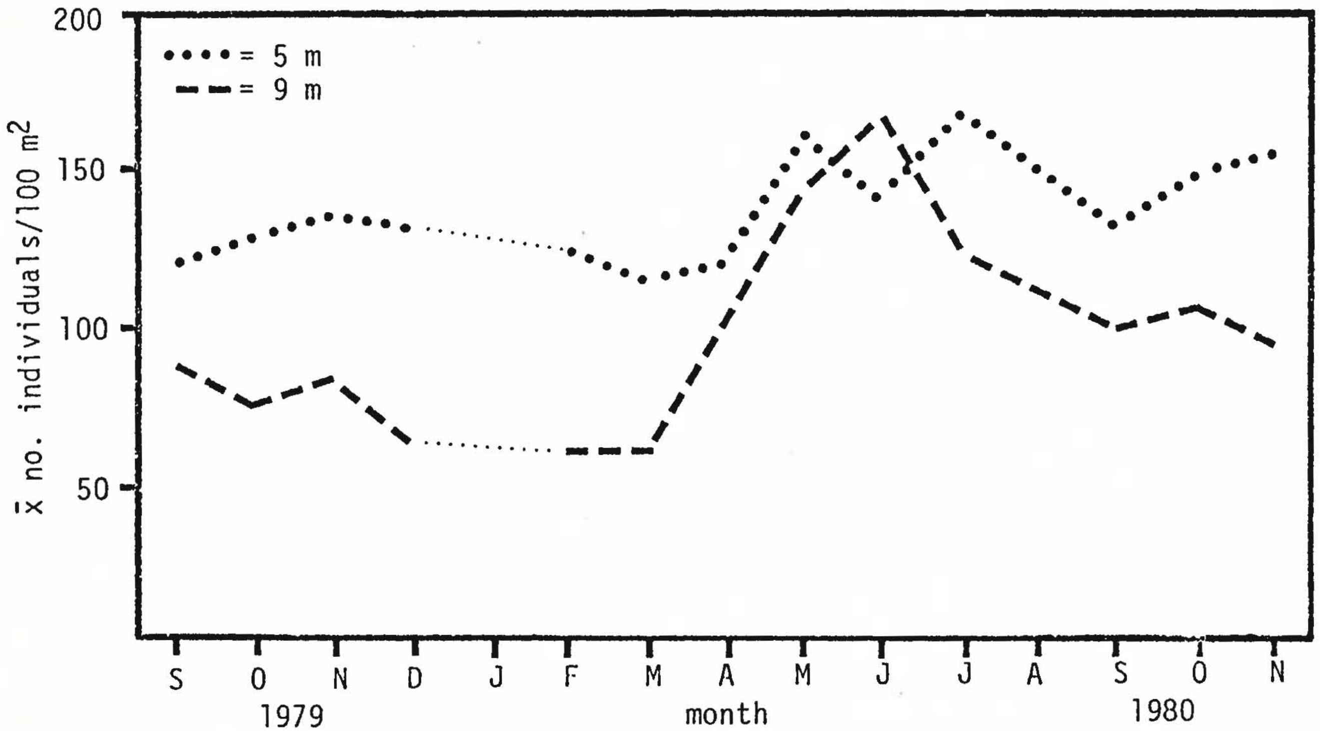

Figure 9. Monthly fluctuations in abundance (mean number of individuals/100 m^2) of <u>Stegastes</u> <u>fasciolatus</u> recorded from September 1979 through November 1980 by depth.

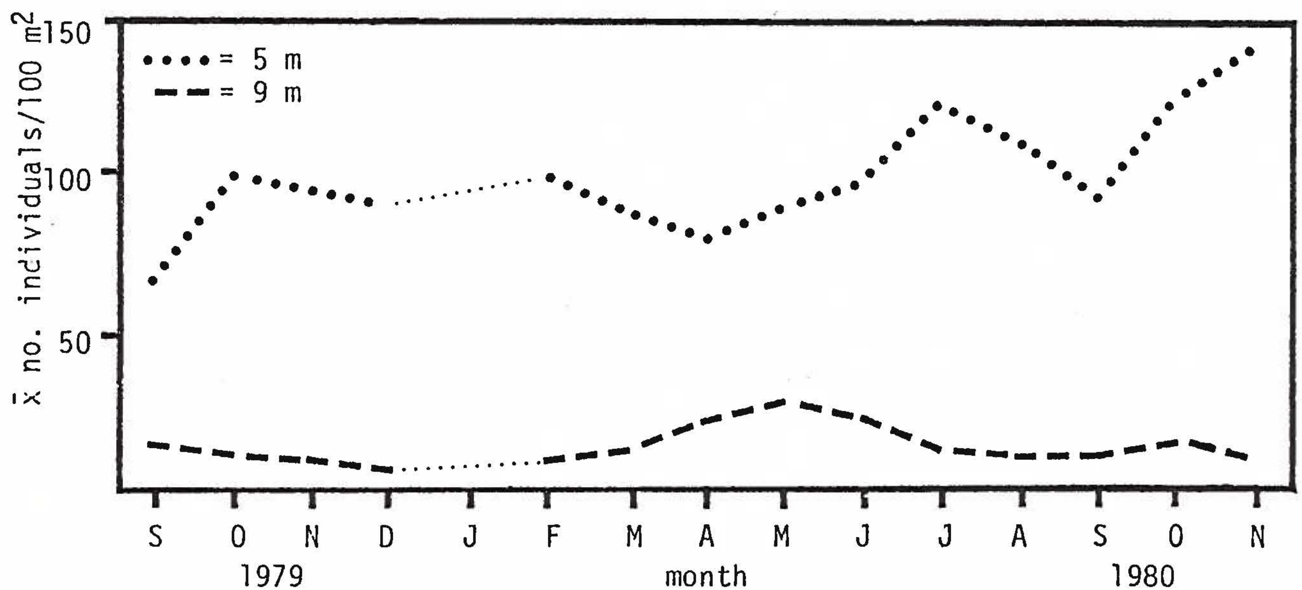

Figure 10. Monthly fluctuations in abundance (mean number of individuals/100 m²) of Plectroglyphidodon dickii recorded from September 1979 through November 1980 by depth.

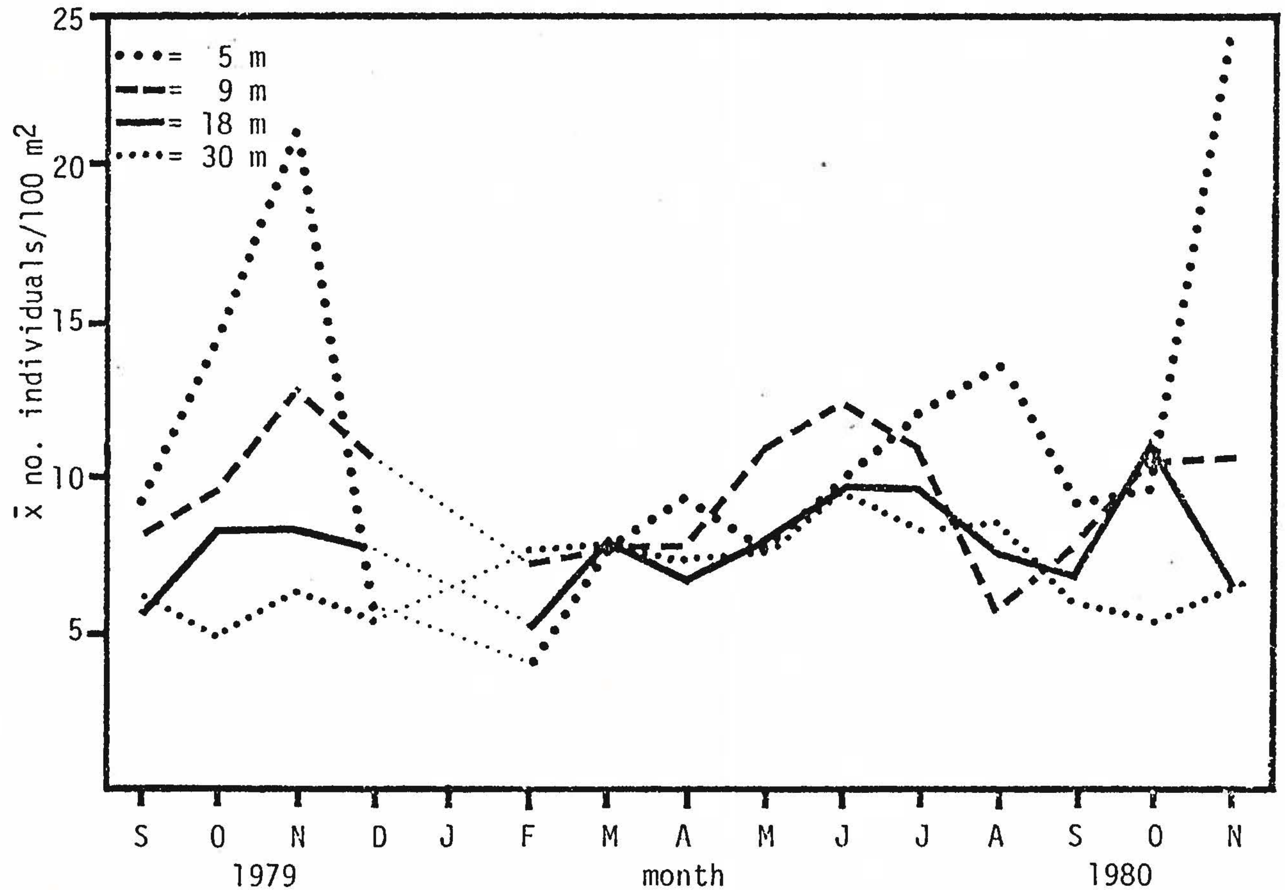

Figure 11. Monthly fluctuations in abundance (mean number of individuals/100 m²) of Acanthurus nigrofuscus recorded from September 1979 through November 1980 by depth.

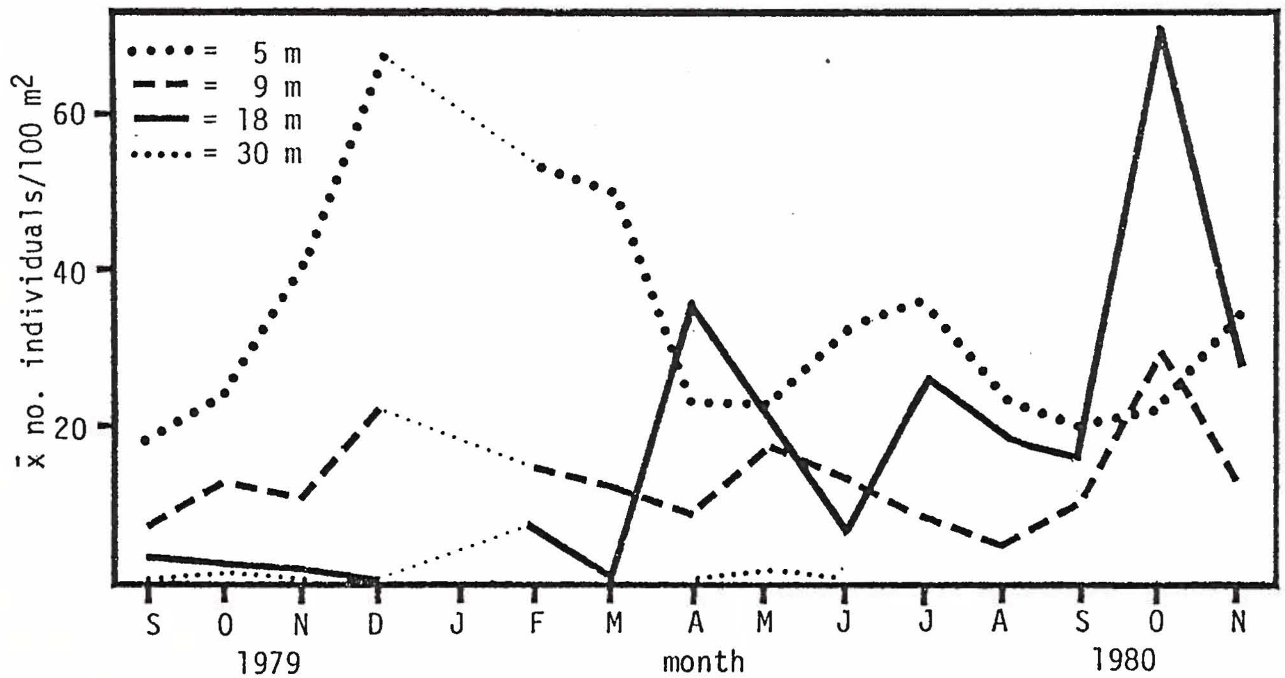

Figure 12. Monthly fluctuations in abundance (mean number of individuals/100 m²) of Ctenochaetus striatus recorded from September 1979 through November 1980 by depth.

from November to December. Although much less abundant, Scaru psittacus (Fig. 13) and S. sordidus (Fig. 14) also showed increases a this depth in November.

The widest variation in fish abundance was observed on the 9- transects. The strongest contributors to this variation wer Pomachromis guamensis (Fig. 15) and Dascyllus reticulatus (Fig. 16) Lesser contributors included Cirrhilabrus sp. (Fig. 17) S. fasciolatus, T. quinquevittatum and Plectroglyphidodc johnstonianus. Although A. nigrofuscus added slightly to the ob served spring/summer increase, its peak abundance at this depth wa recorded in November.

P. guamensis and Cirrhilabrus sp. were responsible for much c the fish abundance variation at 18 m, while Pomacentrus vaiuli (Fig 18), Chrysiptera traceyi (Fig. 19), D. reticulatus, an Plectroglyphidodon lacrymatus (Fig. 20) contributed substantially, bu to lesser degrees. A. nigrofuscus was found to add relatively less t the overall spring/summer increase in abundance at this depth alsc while again its peak representation was recorded in the fall.

C. traceyi and P. vaiuli clearly dominated the counts at 30 m and were largely responsible for the seasonal increase in fish abun dance observed during the spring and summer at that depth. In general a small number of very abundant species had a strong influence on th overall seasonal fluctuation observed at all depths.

A closer examination of the 35 most ubiquitous species (Table 6 revealed a bimodal pattern of season of peak abundance (Fig. 21) More of these ubiquitous species peaked in May and November (7 [20%]

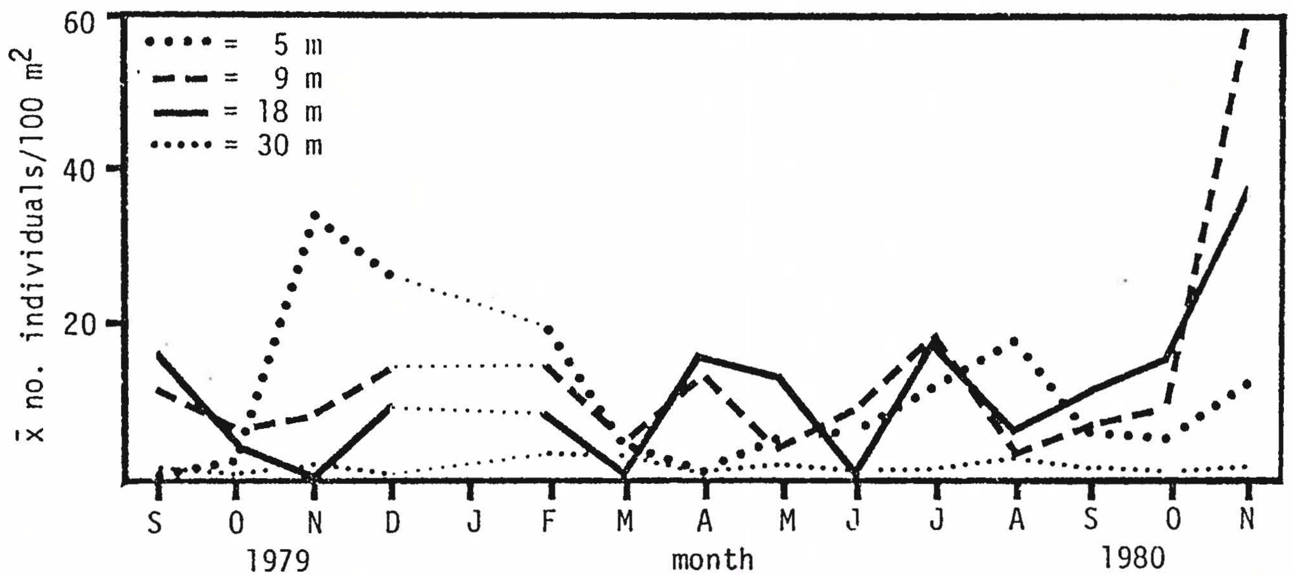

Figure 13. Monthly fluctuations in abundance (mean number of individuals/100 m²) of Scarus psittacus recorded from September 1979 through November 1980 by depth.

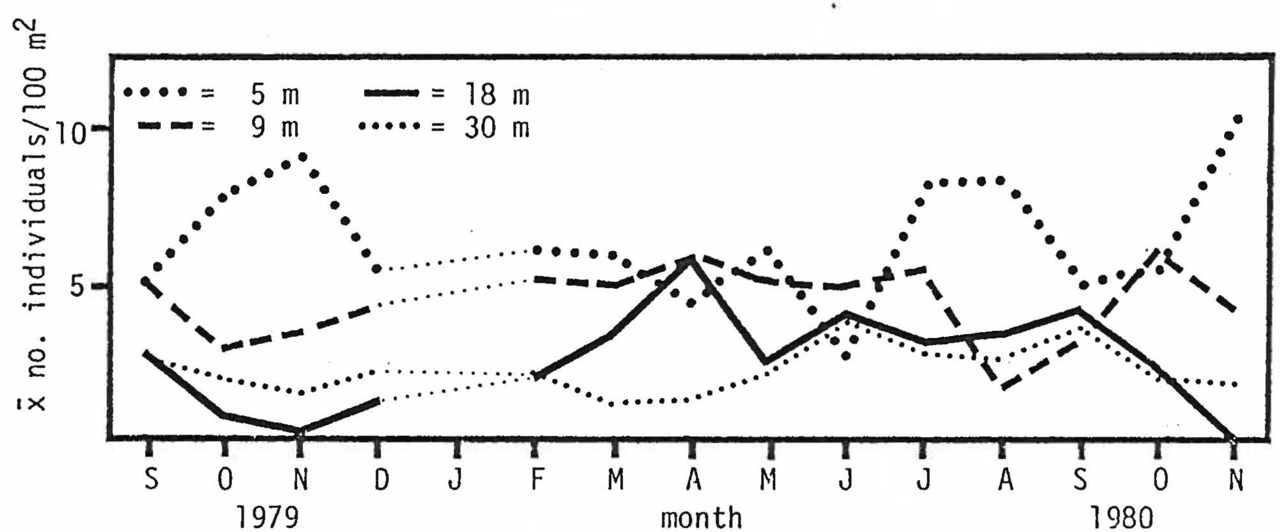

Figure 14. Monthly fluctuations in abundance (mean number of individuals/100 m^2) of Scarus sordidus recorded from September 1979 through November 1980 by depth.

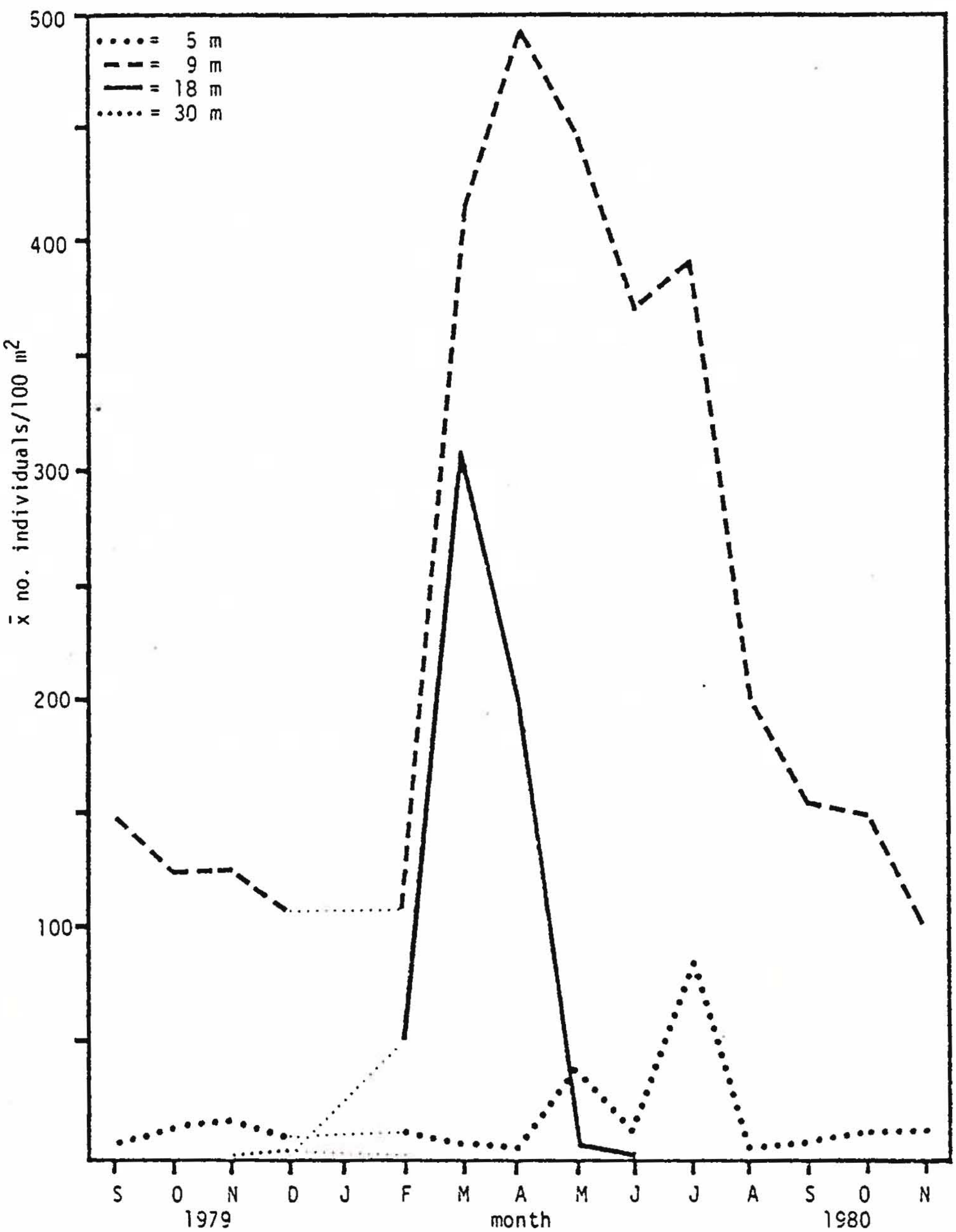

Figure 15. Monthly fluctuations in abundance (mean number of individuals/100 m²) of <u>Pomachromis guamensis</u> recorded from September 1979 through November 1980 by depth.

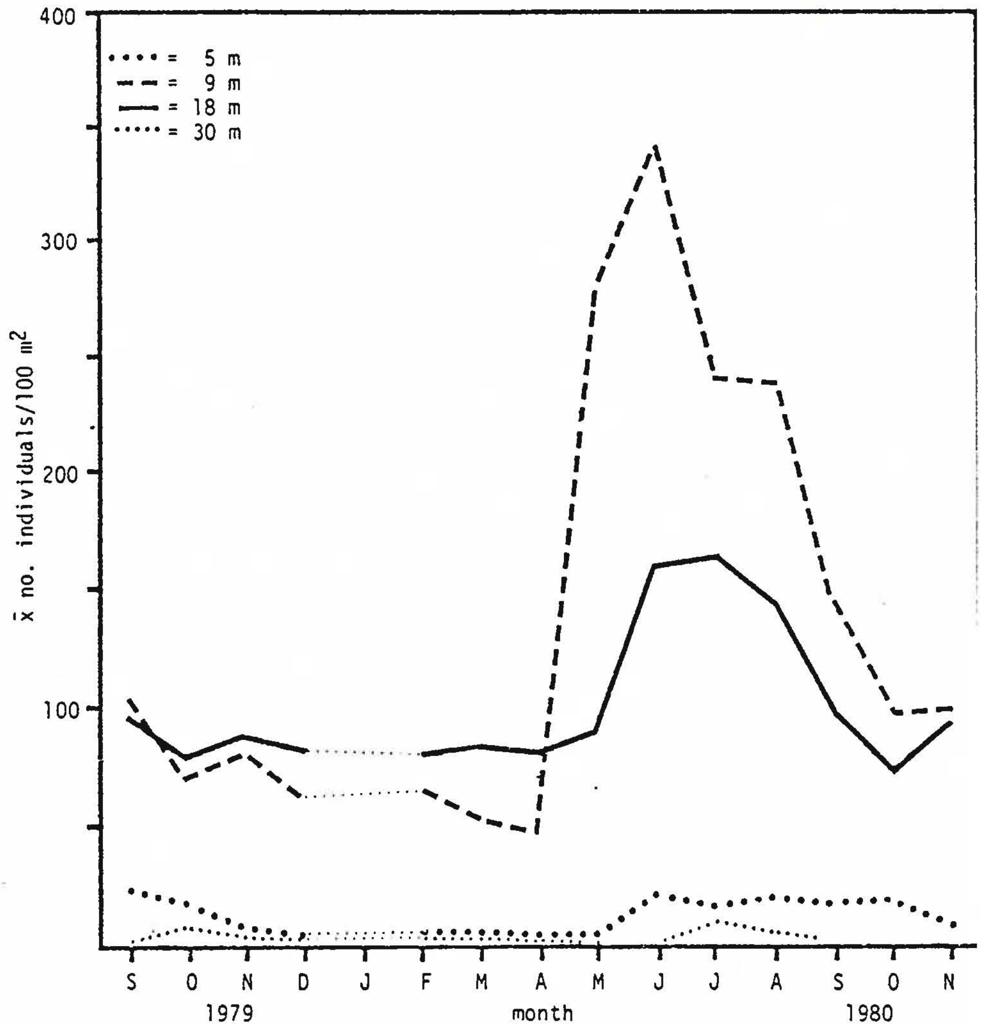

Figure 16. Monthly fluctuations in abundance (mean number of individuals/100 m²) of Dascyllus reticulatus recorded from September 1979 through November 1980 by depth.

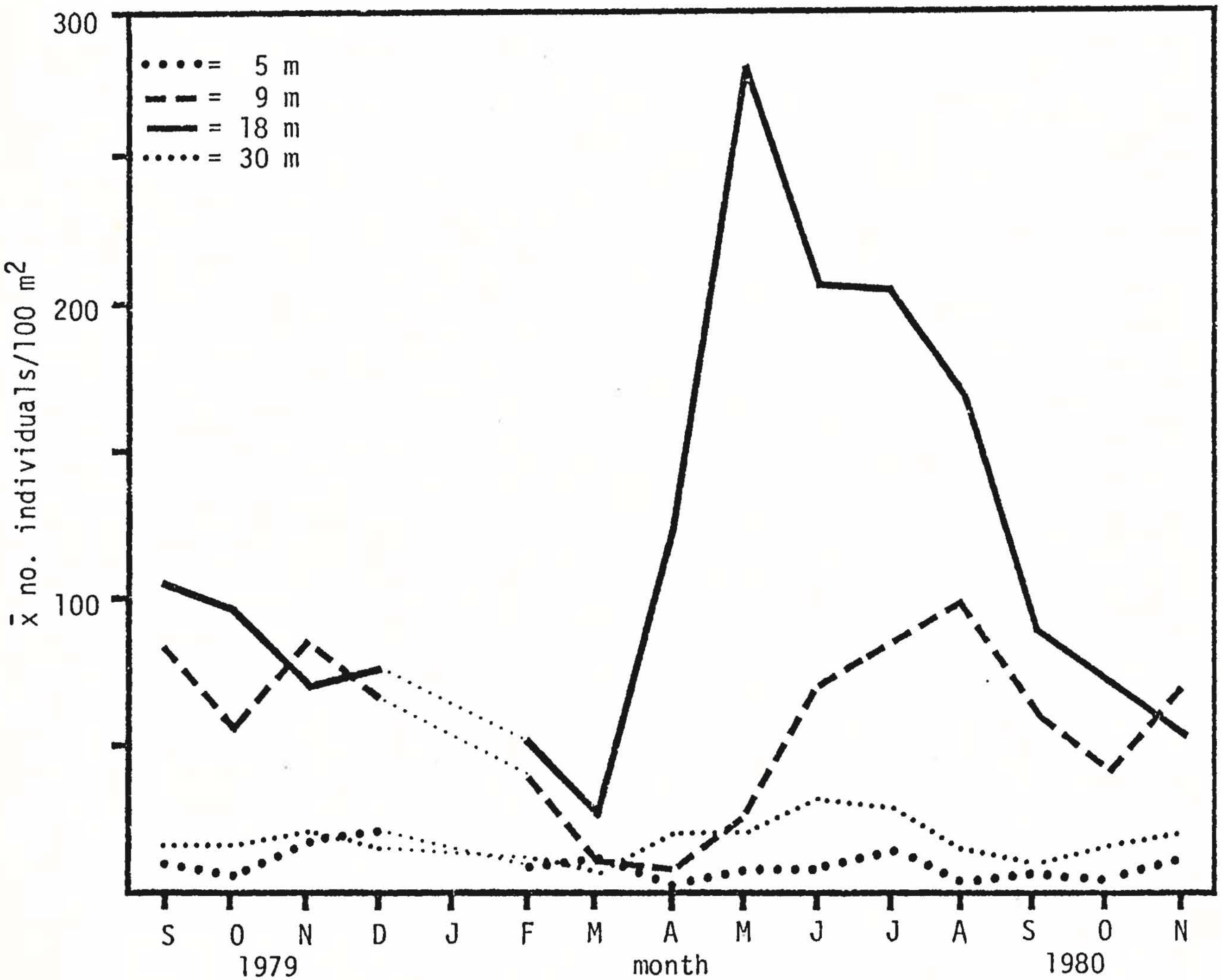

Figure 17. Monthly fluctuations in abundance (mean number of individuals/100 m²) of Cirrhilabrus sp. recorded from September 1979 through

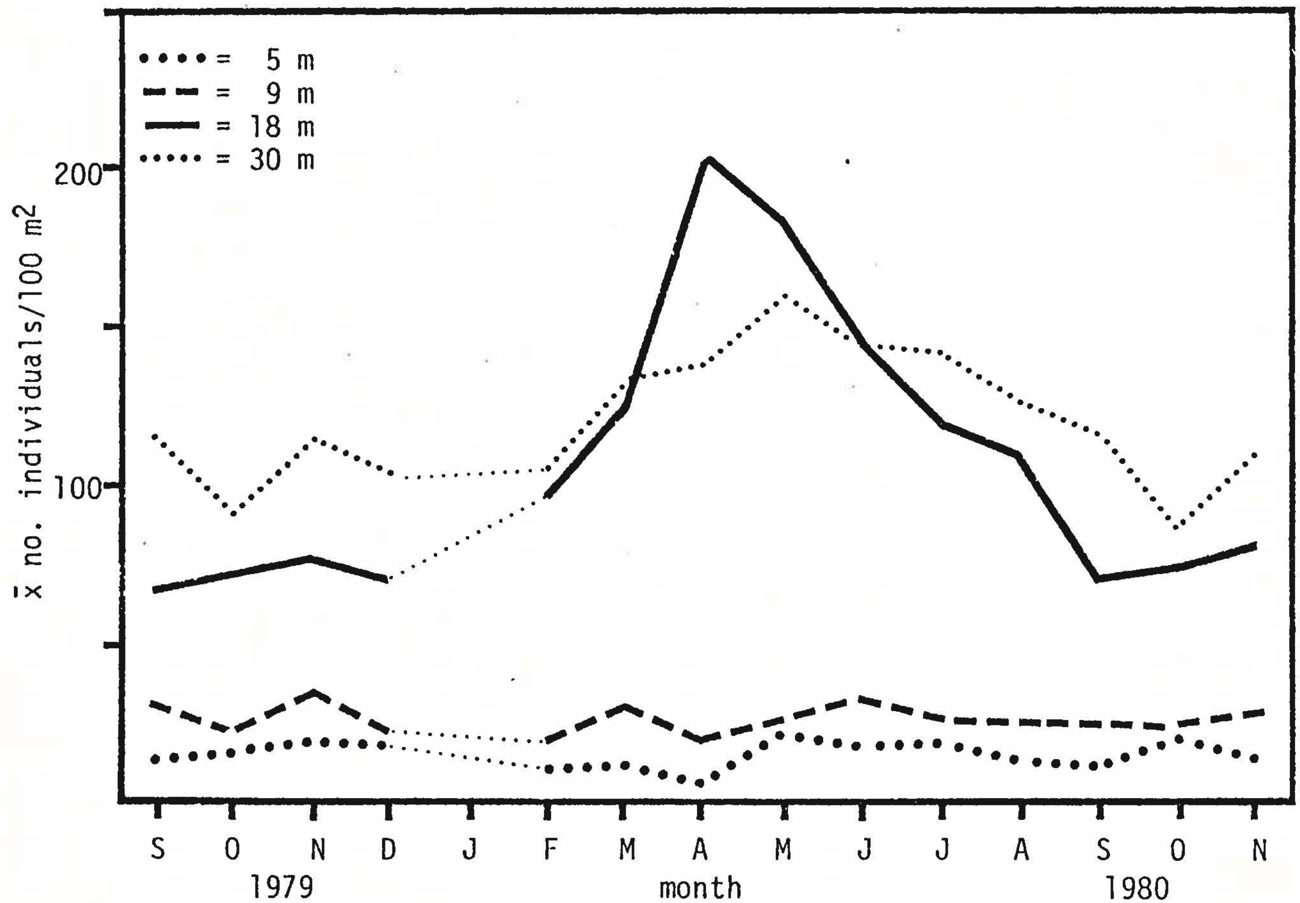

Figure 18. Monthly fluctuations in abundance (mean number of individuals/100 m²) of Pomacentrus vaiuli recorded from September 1979 through November 1980 by depth.

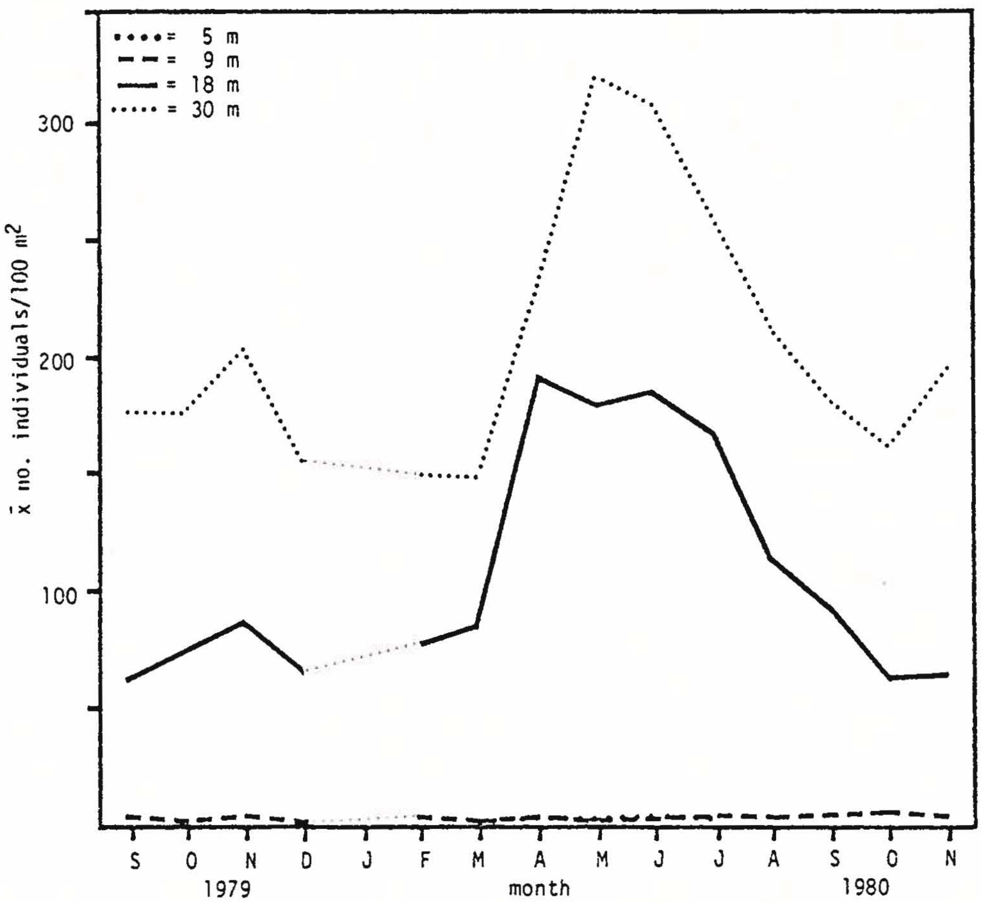

Figure 19. Monthly fluctuations in abundance (mean number of individuals/100 m²) of <u>Chrysiptera</u> <u>traceyi</u> recorded from September 1979 through November 1980 by depth.

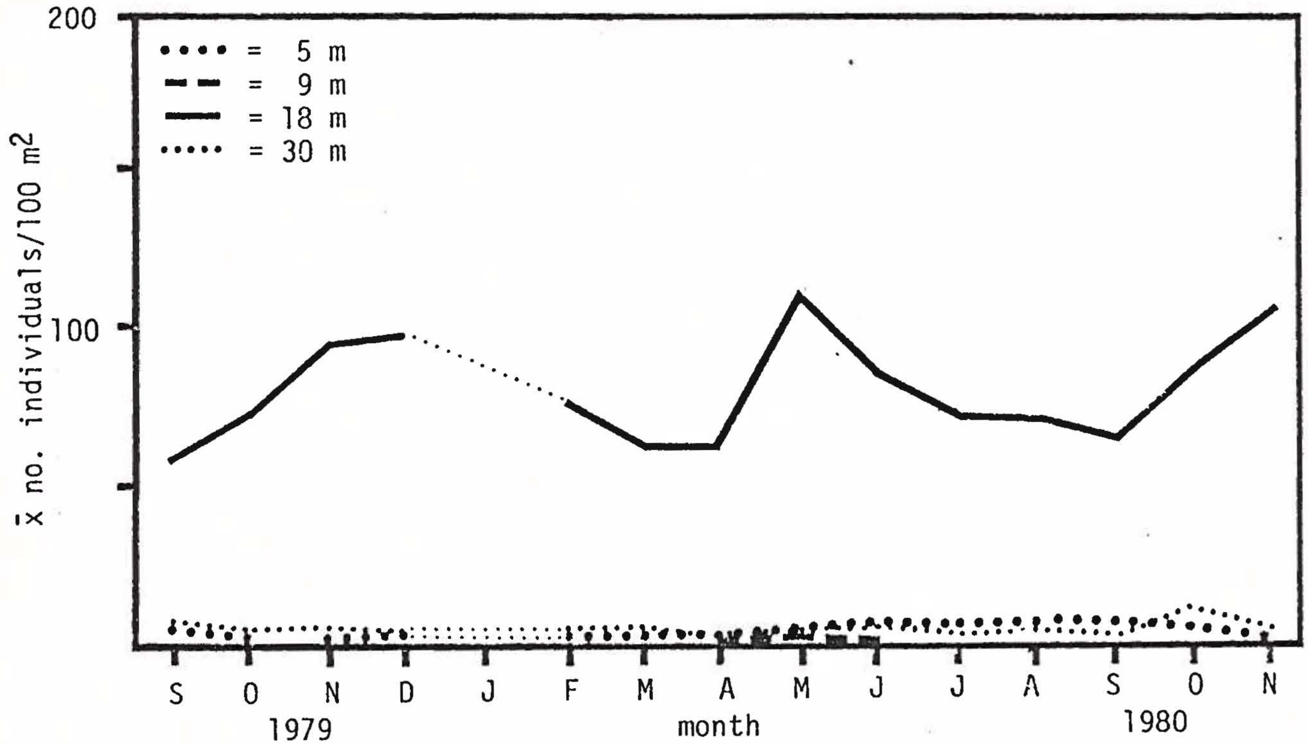

Figure 20. Monthly fluctuations in abundance (mean number of individuals/100 m²) of Plectroglyphidodon lacrymatus recorded from September 1979 through November 1980 by depth.

Table 6. Most ubiquitous fish species (counted at 7 or 8 transec stations) seen during the study in order of total abundance

SPECIES	No. Stations	Total No. Counte
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
Meiacanthus atrodorsalis	7	871
Scarus schlegeli	8	858
Naso lituratus	8	841
Acanthurus glaucopareius	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 urodelus	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 chryserydros	8	51

Total No. Species = 35

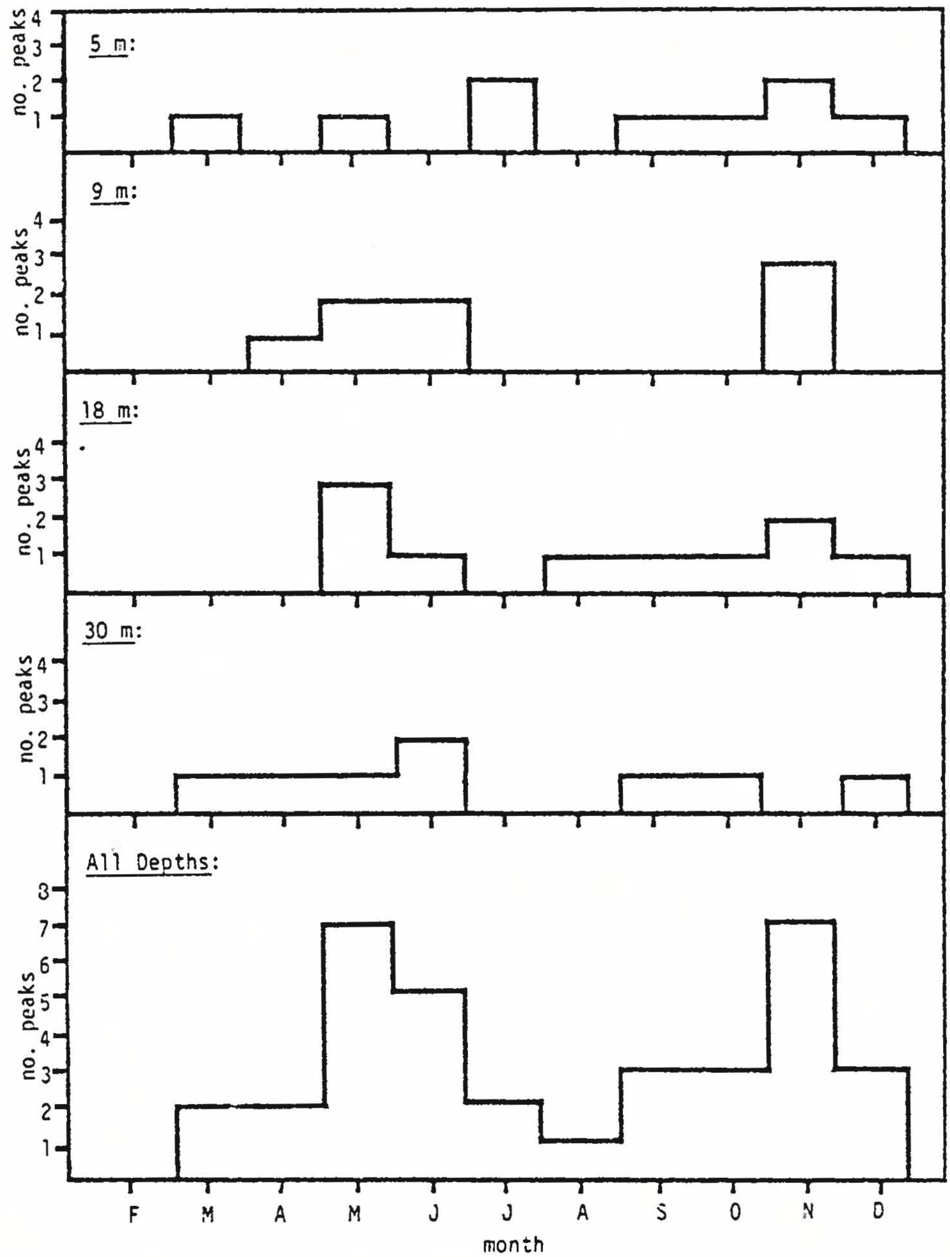

Figure 21. Number of representative peak abundances recorded each month (based on maximum mean monthly counts) within the most ubiquitous species group.

in each month) than in any of the other months. Also, the majority the May peaks (57%) occurred at 18 and 30 m, while 71% of the Novemb peaks were recorded at 5 and 9 m. In addition, five of the ni labrids (56%) peaked in May and June, while three of the fo acanthurids (75%) peaked in November and December. These results te to enhance the significance of the timing in peak abundance of t more influentially abundant species occurring at 5 m (Table 4), whe five of seven species were herbivores, and four of these either peak or showed increases between October and December.

Among the 35 most ubiquitous species, 19 were assigned to general carnivore group which included benthic invertebrate-feeder piscivores and planktivores; nine were listed as herbivores; and sev were categorized as omnivores (Table 7). Among the carnivore grou 13 species (68%) were observed to peak in abundance at either 18 or m (Table 8). Not surprisingly, most of the herbivores (8 spp, 89 peaked at 5 and 9 m, while the recorded peak abundances among t omnivores were almost equally distributed (3 spp [43%] at 5 and 9 m; spp [57%] at 18 and 30 m). The monthly fluctuations in numbers peaking species per trophic category, shown in Fig. 22, strong suggest a temporal partition in peak abundance between the carnivo and herbivore groups. When these two groups were expanded to inclu 28 species apiece (Tables 9 and 10), the resulting overall pattern temporal partitioning remained just as strong (Fig. 23).

Although the relationships were less clear at 5 m, fluctuatio in overall fish abundance (Fig. 2) seemed to be positively correlat with rainfall (Fig. 24) and negatively correlated with windspe

Table 7. General trophic categories to which the members of the mo ubiquitous species group were assigned. Species are list in decreasing order of total abundance relative to ea category.

CARNIVORES	HERBIVORES	OMNIVORES
Cirrhilabrus sp.	*Acanthurus nigrofuscus*	*Pomacentrus vaiuli*
Meiacanthus atrodorsalis	*Scarus sordidus*	*Dascyllus reticulatu*
Parupeneus trifasciatus	*Ctenochaetus striatus*	*Chaetodon citrinellu*
Thalassoma lutescens	*Scarus psittacus*	*Canthigaster solandr*
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 chryserydros		
No. Species/Group = 19	9	7
Total No. Species = 35		

Table 8. Number of species per general trophic category (within th most ubiquitous species group) that peaked in mean abundanc at each transect depth.

Trophic Category	Transect Depth				Total No. Specie
	5m	9m	18m	30m	
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

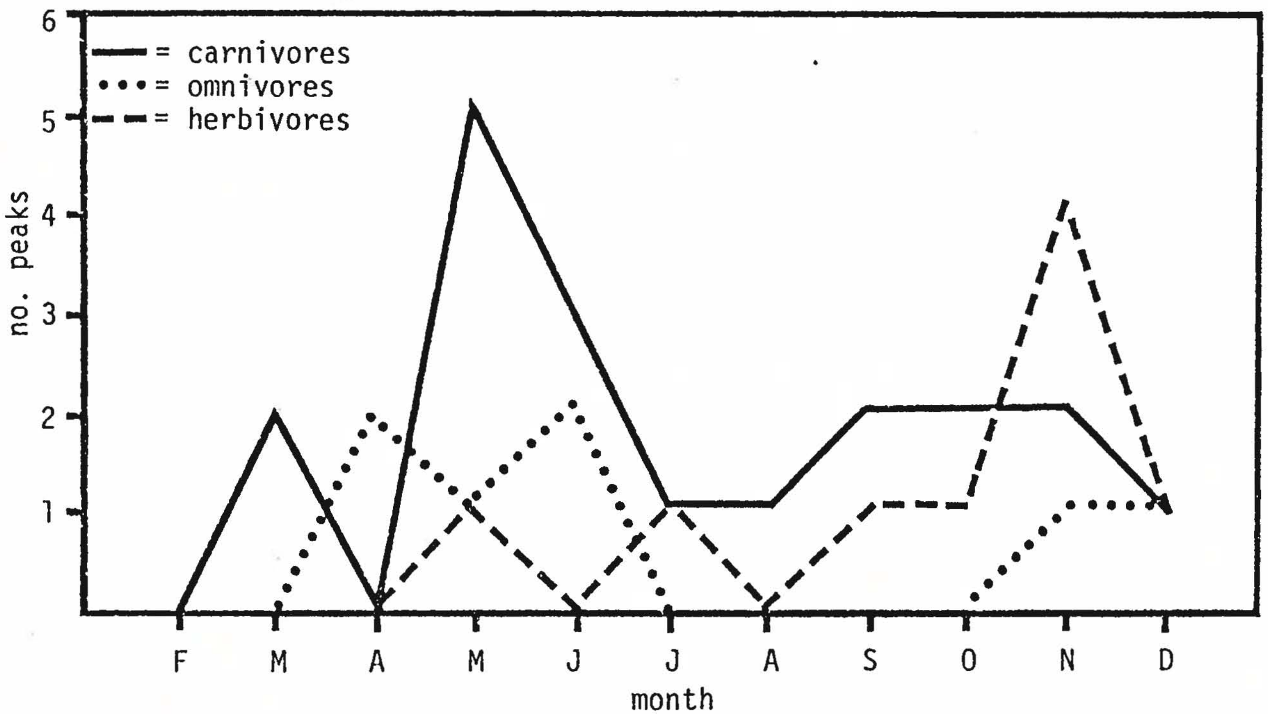

Figure 22. Number of representative peak abundances recorded each month (based on maximum mean monthly counts) among carnivores, herbivores and omnivores within the most ubiquitous species group. Total number of species = 35.

Table 9. Expanded list of carnivores counted during the study base on ubiquity across all transect stations, and listed i order of total abundance. Months of maximum mean monthl count (peak month) and depths (m) of greatest representatic (peak depth) are given for each species. Number of pea months per quarterly interval are shown below.

SPECIES	Number Counted	Number Stations	Peak Month	Peak Dept
Thalassoma quinquevittatum	5542	5	May	5
Cirrhilabrus sp.	5513	8	May	18
Meiacanthus atrodorsalis	871	8	Jun	30
Paracirrhites arcatus	644	6	Aug	9
Macropharyngodon meleagris	529	6	Apr	9
Parupeneus trifasciatus	434	8	Oct	30
Thalassoma lutescens	404	7	Nov	18
Zanclus cornutus	359	8	Oct	18
Sufflamen bursa	347	8	Mar	5
Parapercis clathrata	337	8	May	18
Stethojulis bandanensis	292	8	Jun	9
Labroides dimidiatus	280	8	May	5
Cirrhitichthys falco	277	6	Jun	18
Cheilinus unifasciatus	274	8	Jun	18
Sufflamen chrysopterus	214	7	Nov	9
Cephalopholis urodelus	201	7	May	9
Paracirrhites forsteri	162	6	Apr	9
Halichoeres hortulanus	156	7	Mar	30
Forcipiger flavissimus	124	7	Dec	30
Halichoeres marginatus	88	8	May	18
Ostracion meleagris	85	6	Feb	5&9
Epibulus insidiator	74	8	Sep	30
Gomphosus varius	61	6	Feb	5
Cheilinus trilobatus	59	8	Aug	18
Parupeneus bifasciatus	56	7	Jul	5
Parupeneus chryserydros	51	8	Sep	18
Coris gaimard	39	6	Apr	9&18
Epinephelus fasciatus	39	6	Jun	9

Feb-Mar	Apr-Jun	Jul-Sep	Oct-Dec	TOTAL
4	14	5	5	28

Table 10. Expanded list of herbivores counted during the study base on ubiquity across all transect stations, and listed i order of total abundance. Months of maximum mean monthl count (peak month) and depths (m) of greatest representatic (peak depth) are given for each species. Number of pea months per quarterly interval are shown below.

SPECIES	Number Counted	Number Stations	Peak Month	Peak Dept
Stegastes fasciolatus	6598	4	Jun	5
Acanthurus nigrofuscus	3880	8	Nov	5
Plectroglyphidodon dickii	3134	4	Jul	5
Chrysiptera leucopomus	2885	4	Jul	5
Plectroglyphidodon lacrymatus	2395	5	May	18
Scarus sordidus	1811	8	Jul	5
Ctenochaetus striatus	1744	7	Dec	5
Plectroglyphidodon johnstonianus	1658	6	Jun	9
Scarus psittacus	1009	8	Nov	9
Scarus schlegeli	858	8	May	9
Naso lituratus	841	8	Nov	18
Centropyge shepardi	500	5	Jun	30
Acanthurus glaucopareius	492	8	Sep	5
Acanthurus triostegus	428	3	Nov	5
Acanthurus pyroferus	216	6	Oct	30
Scarus brevifilis	200	5	Dec	9
Acanthurus olivaceus	124	4	Mar	18
Chaetodon reticulatus	104	8	Nov	5
Acanthurus mata	91	4	Nov	5
Centropyge flavissimus	71	8	Oct	5
Centropyge heraldi	67	5	May	30
Acanthurus lineatus	62	3	Nov	5
Zebrasoma flavescens	56	5	Oct	18
Scarus rubroviolaceus	49	6	Aug	9
Naso brevirostris	48	6	Aug	18
Naso unicornis	21	4	Nov	5
Cetoscarus bicolor	10	6	Aug	9
Zebrasoma veliferum	9	3	Oct	18

Feb-Mar	Apr-Jun	Jul-Sep	Oct-Dec	TOTAL
1	6	7	14	28

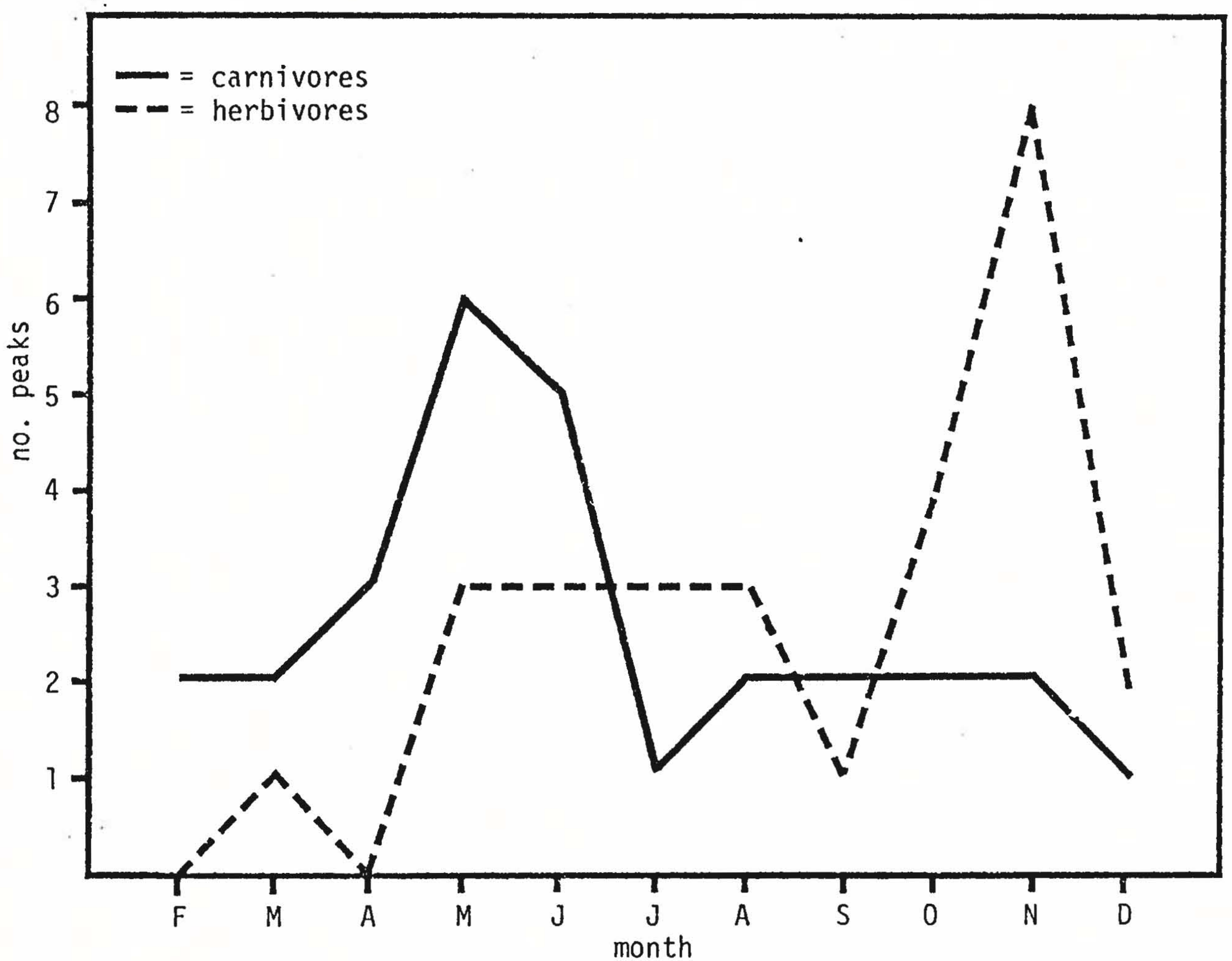

Figure 23. Number of representative peak abundances recorded each month (based on maximum mean monthly counts) among equal numbers of carnivores and herbivores within an expanded ubiquitous species group. Total

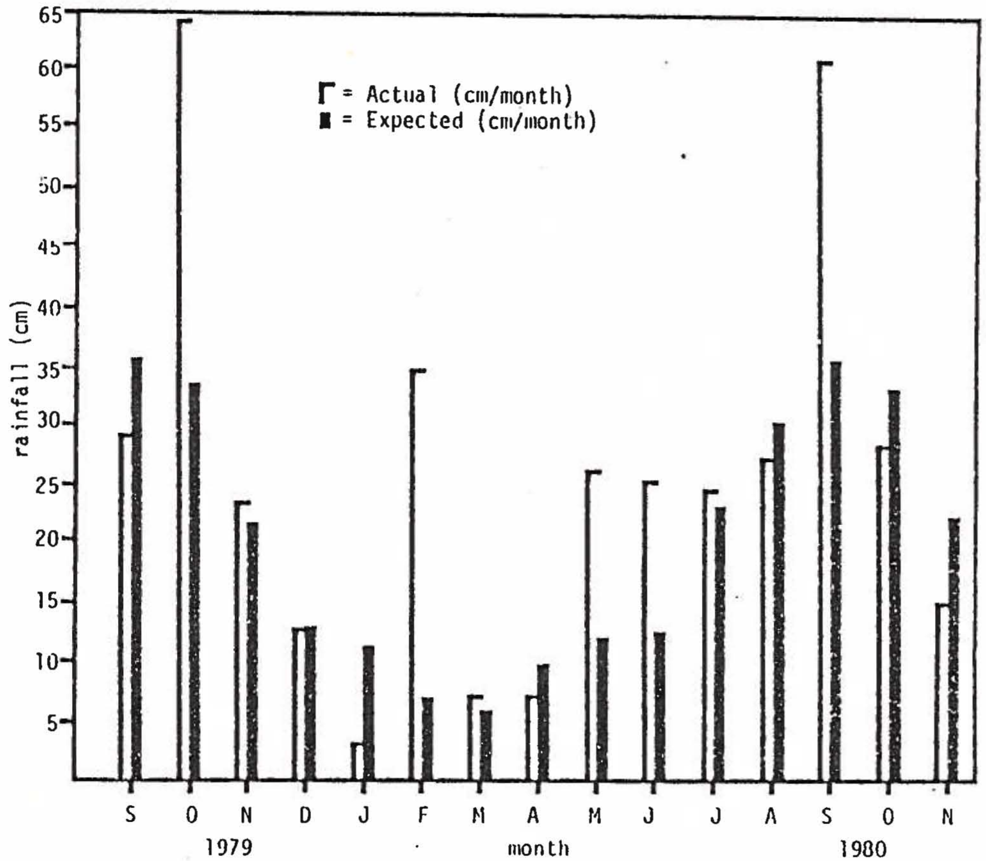

Figure 24. Actual and expected (based on 24 years of data) monthly rainfall on the island of Guam for the months of September 1979 through November 1980 recorded by the National Oceanic and Atmospheric Administration, U. S. Naval Air Station, Guam.

(Fig. 25). The expanded carnivore and herbivore data were tested · see if rainfall might be a factor influencing the timing of tl observed peak abundances. While the combined fish abundance of bo trophic categories was significantly greater (chi-square for a 2 X contingency table, $p < 0.01$) during the wet season (Table 11), it wa fishes within the expanded herbivore group that were the major contr butors (chi-square for 2 classes, $p < 0.01$) to this increase (Tabl 12). Chi-square tests for more than two classes also supporte (herbivores, $p < 0.05$) this result (Table 13). When the carnivore ar herbivore data were segregated into quarterly intervals (Tables 9 ar 10), it was found that these periods were not homogeneous (G-statisti $[G_H]$, $p < 0.025$) in their expected ratios of numbers of species peak per trophic category; and that it was the October-December period tha was significantly different (G-statistic [G], $p < 0.05$) (Table 14) Therefore, although the overall fish abundance represented by bot trophic groups was greatest during the rainy season, the abundanc fluctuations between the two groups were found to be partitione temporally. While the expanded carnivore group increased early an peaked before the month of maximum rainfall (Fig. 21), the expande herbivore group did not increase significantly until later in th season, and peaked only after the rainiest month had passed. Thus the seasonal fluctuations among the more ubiquitous and abundant fis species appeared to follow a depth-related pattern that was probabl related to food resources.

The first species noted to recruit in appreciable numbers durin 1980 was the planktivore P. guamensis (Fig. 15), which settle

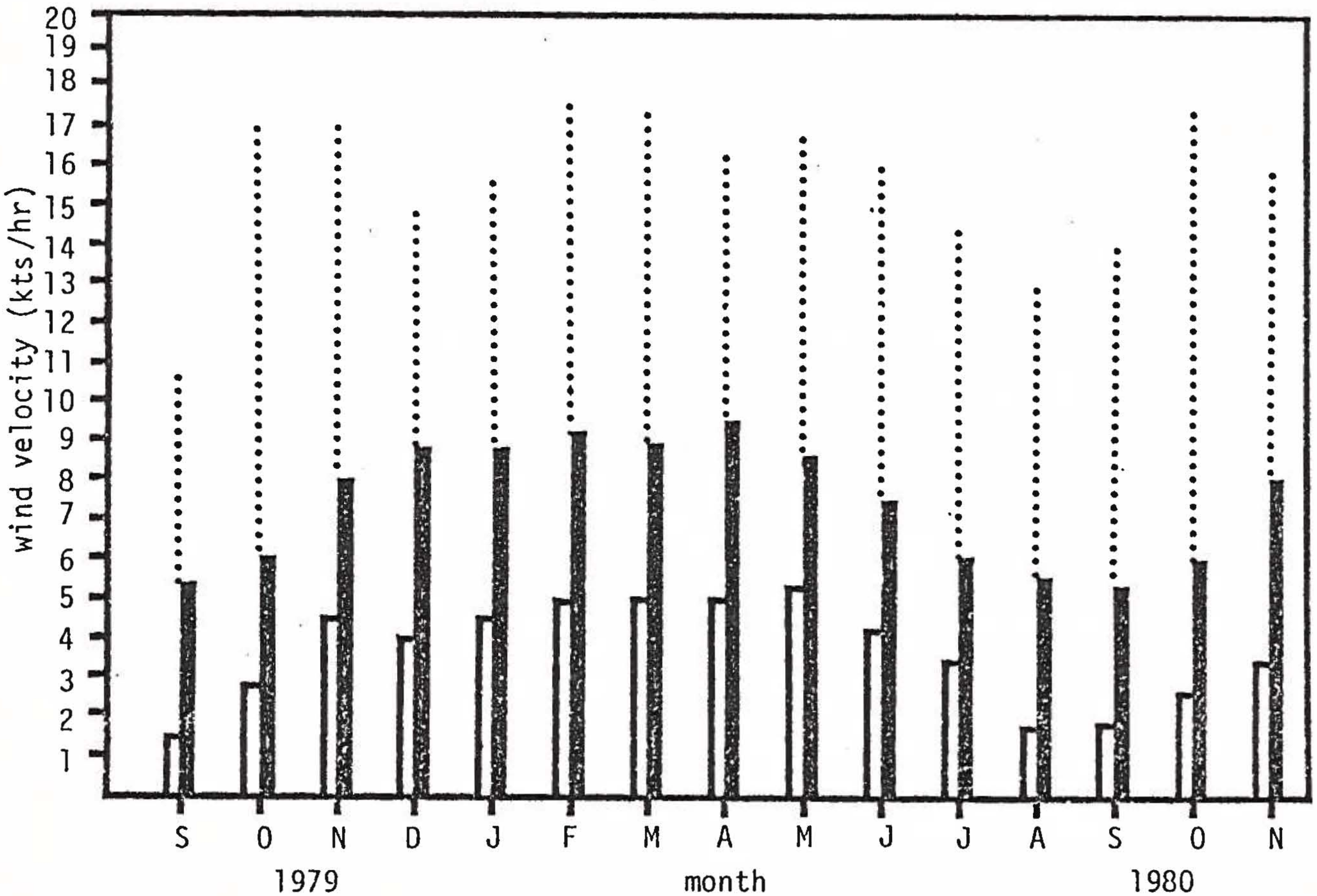

Figure 25. Actual and expected (based on 21 years of data) mean monthly windspeed on the island of Guam for the months of September 1979 through November 1980 recorded by the U. S. Naval Oceanography Command Detachment, U. S. Naval Air Station, Guam. **:** = actual $\bar{x}$ maximum sustained high-hour wind velocity (kts/hr); **▛** = actual $\bar{x}$

Table 11. Two-by-two test of independence using X^2 (Sokal and Roh' 1969) to determine if overall fish abundance of equal nu bers of carnivores and herbivores was significantly great during the wet season ($\bar{x}$ rainfall $\geq$ 12.5 cm/month). Fi abundance is based on numbers of maximum mean monthly coun within each trophic group. Data not collected duri January.

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

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

$$= 6.842^{**}$$

** = $p < 0.01$

Table 12. Two class tests of independence using X^2 (Sokal and Rohl 1969) to determine if either carnivores or herbivores wer significantly more abundant during the wet seasc ($\bar{x}$ rainfall ≥ 12.5 cm/month). Fish abundance is based c the numbers of maximum mean monthly counts of 28 carnivore and 28 herbivores. Data not collected during January.

CARNIVORES:

	f	$\hat{f}$	$f-\hat{f}$	$(f-\hat{f})^2$	$\frac{(f-\hat{f})}{\hat{f}}$
Dry Season (Jan-May)	13	14	-1	1	0.07
Wet Season (Jun-Dec)	15	14	1	1	0.07
Σ	28	28			

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

$$= 0.142 \text{ ns}$$

HERBIVORES:

	f	$\hat{f}$	$f-\hat{f}$	$(f-\hat{f})^2$	$\frac{(f-\hat{f})}{\hat{f}}$
Dry Season (Jan-May)	4	14	-10	100	7.14
Wet Season (Jun-Dec)	24	14	10	100	7.14
Σ	28	28			

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

$$= 14.286^{**}$$

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

Table 13. Tests of independence for greater than two classes using (Sokal and Rohlf 1969) to determine if fish abundance either carnivores or herbivores was significantly greate during quarterly periods of the year. Fish abundance based on the numbers of maximum mean monthly counts of carnivores and 28 herbivores. Data not collected duri January.

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	7.636	-0.636	0.404	0.053
Oct-Dec	14	7.636	6.364	40.500	5.304
Σ	28	27.999			

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

$$= 8.994^*$$

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

Table 14. Two-by-two test of independence using the G-statistic (Soka and Rohlf 1969) to determine if fish abundance of equal num bers of carnivores and herbivores was significantly greate during quarterly periods of the year. Fish abundance i based on numbers of maximum mean monthly counts within eac trophic group. Data not collected during January.

MONTHS	CARNIVORES	HERVIVORES	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

$$G_H = 2\ [119.905 - 186.603 - 153.725 + 225.419]$$

$$= 9.994^{**}$$

$$G_P = 2\ [186.603 + 19.408 + 19.408 - 225.419]$$

$$= 0$$

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

strongly in March at 9 and 18 m. Other relatively abunda plankton-feeders that recruited between March and June included t omnivores D. reticulatus, P. vaiuli and C. traceyi (Figs. 16, 18 a 19, respectively), all of which consume significant amounts zooplankton. Together, these plankton-feeders were the four overa most abundant species counted during the study (Table 5), and alo with other less abundant planktivores, such as Nemateleotris magnifi and Ptereleotris evides, probably represented a significant fo resource for several piscivores. In fact, maximum mean monthly coun of the groupers, Cephalopholis urodelus and Epinephelus fasciatus, t hawkfishes, Cirrhitichthys falco and Paracirrhites forsteri, the sa perch, Parapercis clathrata, and the wrasses, Cheilinus trilobatus a C. unifasciatus, were all recorded between February and June (Tab 9). Piscivore increases observed during these months were mainly d to the appearances of subadults and adults and additionally includ sporadic sightings of larger groupers, snappers and wrasses, such Variola louti, Lutjanus bohar and Cheilinus undulatus. These latt species are deeper water predators that may have undergone a season vertical migration in response to increased prey abundance on t upper reef slope (Kock 1982).

Several benthic invertebrate-feeders also exhibited peak abu dances during the same period. Increases among these species we primarily due to juvenile recruitment, but older juveniles and adul were also commonly encountered. They included the boxfish, Ostraci meleagris, the triggerfish, Sufflamen bursa and the wrasses, Cor gaimard, Gomphosus varius, Halichoeres hortulanus, H. marginatus

Macropharyngodon meleagris, Stethojulis bandanensis ar T. quinquevittatum (Fig. 8), amidst others. These species also ma have peaked during a time of expanding food resources since the stron planktivore fluctuation suggested the presence of abundant plankton upon which many 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 durir the October-December period (Table 10), eight (Acanthurus lineatus, A nigrofuscus [Fig. 11], A. triostegus, A. pyroferus, Naso lituratus, N unicornis, Zebrasoma flavescens and Z. veliferum) were browsing ar two (A. mata and Ctenochaetus striatus [Fig. 12]) were grazing sur geonfishes; two (Scarus brevifilis and S. psittacus [Fig. 14]) wer grazing parrotfishes; and one each (Centropyge flavissimus an Chaetodon reticulatus) were browsing angelfish and butterflyfish respectively.

Altogether, ten (71%) of the 14 ubiquitous herbivores are browsers, eight of which 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 larges increases in surgeonfish abundance were due to the presence o subadult/adult mixed-species foraging aggregations that appeared to b most numerous and most frequent during the fall. The most conspicuou species included Acanthurus glaucopareius, A. nigrofuscus A. triostegus, and N. lituratus. In contrast, the majority of th newly recruited juvenile browsers observed during this study wer territorial damselfishes that generally peaked in overall abundanc during the spring/summer months on the reef front and upper submarin terrace. The most important of these species included C. leucopomu (Fig. 7), S. fasciolatus (Fig. 9), P. dickii (Fig. 10), P. lacrymatu (Fig. 20) and P. johnstonianus. Juvenile parrotfishes were en countered at a rather moderate frequency, often in small groups (10-2 individuals) or as part of larger (100-200 individuals) mixed-specie foraging aggregations. However, there were no strong relationship between parrotfish abundance and specific depths or reef zones Scarus brevifilis and S. psittacus peaked during the October-Decembe period, while, peak abundances were recorded for Cetoscarus bicolor Scarus rubroviolaceus, S. schlegeli and S. sordidus (Fig. 13) betwee May and August. The latter species, however, showed strong increase in the fall, and along with S. psittacus and S. schlegeli often forme substantial portions of foraging aggregations. Since the reef slop algal biomass did not fluctuate noticably during this study, ther seems to be no direct relationship between fluctuations in herbivorou fish abundance and food resources on the upper reef slope. But agai data directly supporting this was not collected during th investigation.

Annual Variation

Annual variation in the counts of the 35 most ubiquitous fis species was estimated with data collected during the months of Septem ber, October and November, 1979 and 1980. The counts of these specie were lumped across depths and analyzed by site. Values of mean log ($\bar{R}$) calculated from the September data show that net decreases i abundance occurred between years in most species at both sites; bu based on the October and November data sets these values showed ne increases between years at both sites. Values of AV calculated fc both sites were generally low, ranging from 0.06 to 0.17, indicatir that relatively little overall change in ranked fish abundances ha occurred between years. Within the 1600 m² area surveyed at eac site, the most ubiquitous upper reef slope fishes show fairly stabl 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 deptr specific data across sites. The mean log R's ($\bar{R}$) among months for th 35 ubiquitous species show net decreases to have been prevelar between years in the September data, while net increases are found i the October and November data sets. Comparisons of the mean log R' ($\bar{R}$) among depths indicate that the most widespread increases i abundance between years occurred at 18 m. The calculated values of A range from 0.03 to 0.23, with consistently higher values at 18 m Table 15 summarizes the values of $\bar{R}$ and AV calculated for each stuc site and depth for each pair of months. The results show that on relatively broader scale of analysis (1600 m² of reef), AV's calcu lated by site are comparatively low and not very different from eac other. Values of AV are generally higher when calculated for specifi depths and depth-month combinations (800 m² of reef). The mean valu for all depths ($\bar{x}$ AV = 0.13) is similar to that for both study site ($\bar{x}$ AV = 0.10), indicating low annual variation in abundance over th extensive reef areas analyzed. In addition, trends in the calculatec

Table 15. Annual variation (AV) in ranked fish abundances of the : most ubiquitous fish species observed at Asan Pt. and Ipa Pt. Calculations are based on data collected during Septer ber, October and November, 1979 and 1980. $\bar{R}$ and AV ar explained in text and in Wolda (1978).

Study Site	Transect Depth (m)	September	October	November	$\bar{}$
$\bar{R}$:					
Asan	All	-0.08	0.06	0.04	0.(
Ipao	All	-0.04	0.08	0.03	0.(
Both	5	0.03	0.01	-0.02	0.(
Both	9	-0.18	0.08	0.10	0.(
Both	18	0.02	0.09	0.09	0.(
Both	30	-0.02	-0.08	0.03	-0.(
AV:					
Asan	All	0.09	0.06	0.17	0.1
Ipao	All	0.10	0.10	0.07	0.(
Both	5	0.14	0.10	0.07	0.1
Both	9	0.14	0.14	0.10	0.1
Both	18	0.15	0.18	0.23	0.1
Both	30	0.04	0.15	0.12	0.1

values of AV across depths seem to be loosely correlated with th depth-related trends in observed species richness (Tables 2 and 3).

Yearly changes in species composition among the 35 most ubiquitous species as estimated by the J and R indices of resemblance sho the same trend (Tables 16 and 17). Study sites (all depths combined show greater species constancy (i.e., higher index values) than individual depth zones indicating that species composition is mor stable over broader areas than within narrower zones. The mean value of each index for all depths combined, excluding 30 m, were simila ($J = 0.84$; $R = 0.91$) and relatively high, indicating the presence of fairly constant ubiquitous species composition. Yearly differences i the numbers of species observed at 30 m is misleading since twice th amount of census time was expended at that depth in 1979. Consequently, the 30-m data was not used in computing the mean similarit values.

Table 16. Annual variation in species composition of the 35 mos ubiquitous fish species observed at Asan Pt. and Ipao Pt. a estimated by the Jaccard Coefficient (J). Calculations ar based on data collected during September, October ar November, 1979 and 1980. J is explained in text and Sokal and Sneath (1963).

Study Site	Transect Depth (m)	September	October	November	)
Asan	All	0.97	0.91	0.94	0.[illegible]
Ipao	All	0.97	0.97	0.91	0.[illegible]
Both	5 m	0.81	0.87	0.88	0.[illegible]
Both	9 m	0.82	0.85	0.85	0.[illegible]
Both	18 m	0.74	0.88	0.88	0.[illegible]
Both	30 m	0.82	0.66	0.72	0.[illegible]

Table 17. Annual variation in species composition of the 35 mo ubiquitous fish species observed at Asan Pt. and Ipao Pt. a estimated by the Resemblance Index (R). Calculations a based on data collected during September, October a November, 1979 and 1980. R is explained in text and Smith (1973).

Study Site	Transect Depth (m)	September	October	November	
Asan	All	0.98	0.96	0.97	0.9
Ipao	All	0.96	0.98	0.98	0.9
Both	5 m	0.90	0.93	0.93	0.9
Both	9 m	0.90	0.92	0.92	0.9
Both	18 m	0.85	0.93	0.94	0.9
Both	30 m	0.91	0.78	0.84	0.8

DISCUSSION

The changes in overall fish abundance observed during this stu((Fig. 2) conformed to a general pattern consistent with recent wo done at Guam (Kock 1982), Micronesia (Johannes 1978), Hawaii (Wats(and Leis 1974), the Caribbean (Luckhurst and Luckhurst 1977) and tl Great Barrier Reef (Russell <u>et al</u>. 1977; Talbot <u>et al</u>. 1978; Willian and Sale 1981), in which fish abundance fluctuations were found to t highly seasonal and largely related to reproductive activities. Tl results of this investigation also suggest that within the overal upper reef slope fish community, there is a temporal partitioning i peak abundance across depth, possibly resulting from a more specifi temporal partitioning among general trophic groups. Stror planktivore recruitment at 9 and 18 m in March appeared to initiat the observed seasonal increase in overall fish abundance. This earl planktivore recruitment was followed closely by increases among othe abundant plankton-feeders, primarily at 18 m, through June. Pea abundances among the most ubiquitous carnivores were conspicuousl clustered between April and June, with major piscivore increases beir especially prominant during these months at 9 and 18 m. In contrast recorded peak abundances among the most ubiquitous herbivores wer clumped between October and December, at 5 m.

While increases among the plankton-feeders were primarily due t juvenile recruitment, piscivore increases resulted from the appear ances of subadults and adults. Benthic invertebrate-feeders increase as a result of juvenile recruitment and the immigration of subadul· and adults. The herbivore increases, on the other hand, we attributed to juvenile recruitment and sightings of subadult/adu mixed-species feeding aggregations that appeared to be more numero and more frequently encountered in the fall.

The initial planktivore influx, as well as juvenile recruitme in general, might have been influenced by several factors promoti successful larval survival. These may have included decrease predation, favorable ocean current patterns and increased larval fo availability, among others. Once recruited, successful settlement the reef may be influenced by food and space availability, a variations in competition and predation pressures. If peak juveni recruitment is the result of seasonally intensified reproduction th is timed to coincide with factors favorable for larval survival a juvenile settlement, the above factors may be considered examples "ultimate" causes of seasonal peak fish abundance. However, if fi reproduction is relatively constant through the year, seasonality recruitment may be the result of intermittently enhanced survival d to these factors and, in this case, they might be regarded "proximate" causes of seasonally maximum fish abundance.

Since spawning activity was not observed during this study, have no data directly supporting the hypothesis that reef fish repr duction is seasonally intensified. Similarly, this study did n examine the possibility of differential larval survival throughout t year or the effects of predation and competition on newly settle recruits. However, because this investigation did yield dat indicating that different trophic groups exhibited different patterr of seasonal abundance, it is possible that food availability may be ε important proximate or ultimate cause influencing the observe seasonal peaks in overall fish abundance.

While recognizing that seasonal variation in overall fish abur dance at Guam is manifested through a variety of patterns, Kock (198ż proposed that seasonally abundant planktonic food may be important i timing the initiation of strong juvenile recruitment on the upper ree slope. In doing so, he cited the post-reproductive loosening ar fragmentation of *Boodlea composita* beginning in February (R. T. Tsudε pers. com.) and the desiccation of *Caulerpa racemosa* (Peterson 197ż beginning in March, as examples of reef-flat algae that are trans ported offshore during the midday low tide season. Accordingly, i was inferred that the suspended particulate material resulting fr(these and other species of dead algae may somehow indirectly contri bute to the nourishment of pelagic fish larvae, and that the adde benefit of this condition is ultimately manifested in the form (maximum juvenile settlement between March and June.

Although the diurnal low spring tide season at Guam may beg around March, there is evidence that effective reef-flat algal desi(cation may not occur until later in the season. Tsuda (1974) hε shown that the algae which are most seasonal at Guam are intertidε species, the majority of which are most abundant between January ar June. The algae in the upper intertidal zone are the first to di: appear--at least a month before those in the lower intertidal zon(He also emphasized that the desiccation of intertidal algae regulated by the critical factors of time of day and duration of exposure (Doty 1946; Lawson 1957) which are effectively met at 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 195? 1975), approximately the time of the initial planktivore influ observed during this study.

The much greater than average rain experienced in February (Fig 24) may have added additional nutrients through rain-induced terres trial run-off. The addition of detrital material after April due t the developing seasonal reef-flat algal kill may also be influential Although peak abundances among the most ubiquitous carnivores did no show a significant relationship with the rainy season (Table 11), is reasonable to conclude from the observed trends that increase availability of food in a variety of forms could have played a important role in their fluctuations. At the very least, the dat clearly suggest that many of the planktivores, piscivores and benth invertebrate-feeders within the fish community are capable of takir advantage of seasonal increases in their food supplies. Beside conferring potential growth benefits to recruiting juveniles, repro duction coincident with maximum levels of fluctuating food resource may allow adults to meet more successfully the increased energ demands spawning places upon them. Therefore, the relationsh between food resource availability and fish abundance for spawners a well as recruits may have significance from both "proximate" physio logical (Lagler et al. 1962) and "ultimate" evolutionary (Fisher 193(perspectives.

Data on the herbivorous segment of the fish community led to th same general conclusion based on the intimate association recognize between these fishes and the high benthic algal production common found on shallow coral reefs (Odum and Odum 1955; Hiatt and Strasbu 1960; Randall 1961; Bakus 1964; Birkeland 1977; Wanders 1977; Bro 1979). Since these fishes have generally low assimilation efficie cies (Odum 1970; Chartok 1972), and retain food for only a few hou (Ogden and Lobel 1978), they also have relatively large food bioma requirements (Bardach 1961). As a result, the majority of the herb vorous fish community predominates in shallower water since mari benthic algae and seagrasses are most productive at depths less th 20 m (Ogden and Lobel 1978). Foraging groups consisting primarily parrotfish and surgeonfish species that feed intensely even in t shallowest reaches of the intertidal zone during high tide (Bak 1967) may also be major agents in the cycling of nutrients across t reef flat (Smith and Marsh 1973; Marsh 1974).

In Guam, both adults and juveniles of several surgeonfish a parrotfish species commonly seen on the upper reef slope, are known frequent the reef flat (Amesbury 1978; Amesbury and Myers 1982; Katni 1982; Myers 1982), especially during high tides. Foraging groups a largely composed of grazers (chiefly parrotfishes and a few surgeo fish species) which rasp sand, rubble and other hard substrate su faces for detritus, diatoms, blue-green algae and other organi materials, and browsers (chiefly several surgeonfish species) whic bite and consume leafy, fleshy or filamentous algae without scrapi the substrate (Bakus 1967; Jones 1968). After studying the foo habits of surgeonfishes in Hawaii and Johnston Island, Jones (196 concluded that the algal genera _Ectocarpus_, _Sphacelaria_, _Cladophora_ _Polysiphonia_, _Gelidium_, _Centroceras_, _Ceramium_ and _Microcoleus_ were th most important food items eaten by browsing species of *Acanthurus* ar *Zebrasoma*. Browsing species of *Naso* were found to feed heavily (*Lobophora*, *Dictyota* and *Sargassum*. Since all of these algal gener are commonly found at Guam (R. T. Tsuda, pers. comm.), they presumab represent an important food resource for many of the same species (browsers studied by Jones (1968) which also exist here (Shepard ar Myers 1981; Tables 1 and 2). When the relatively extensive reef-fla area that exists at Guam (Randall and Eldredge 1976) is considered, is easy to imagine how beneficial the additional algal biomas associated with this zone might be to the shallow-water herbivorou fish community. However, in order to utilize even a limited amount (the energy stored in this biomass, many herbivorous fishes have had t adapt to a distinctive type of production cycle largely controlled b solar radiation, tide and rainfall.

As the diurnal low spring tide season develops, both grazers ar browsers are excluded from foraging on the reef flat during certai hours of the day (Bakus 1967). Since most herbivorous fishes ar nocturnally inactive (Hobson 1965, 1972; Starck and Davis 1966 Rosenblatt and Hobson 1969), this low-tide restriction of diurna reef-flat foraging might be viewed as a condition less favorable t maximum growth, especially among juvenile browsers. Widesprea reduction in food resources due to desiccation (Tsuda 1974) during th fully developed diurnal low spring tide season also may be highl stressful to foraging herbivore populations, and in particular t those browsers most intimately associated with the reef flat. Th severity of this form of environmental stress is compounded b seasonally high rainfall (Fig. 24) which serves to extend the tin period of algal reduction by preventing the reef-flat community frc starting to reestablish itself as soon as the critical midday low-tic season ends. Rainfall continuing into the later months of the yeε could produce reef-flat salinities low enough to delay tł reappearance of upper intertidal algae until January (Tsuda 1974).

For the most part, peak abundances among the ubiquitous shallow water browsers were recorded only after the passage of September Guam's rainiest month (Fig. 24). Thus, while there may be a stror positive relationship between fish abundance and rainfall among mar of the species censused, there are at least some species, especiall at 5 m, for which this relationship does not hold. Furthermore, Fig 2 indicates that in both 1979 and 1980 the fall increase in fish abur dance, most evident at 5 m, did not occur until after the actua seasonal peak rain month had passed. Although this suggests tł existence of a mechanism enabling certain herbivores to respond t environmental cues by adjusting reproductive effort to coincide wit increasing food supplies, it is purely speculative at this point Nevertheless, while the upper intertidal algae may not become reestab lished until January, it is likely that the reestablishment process c the reef flat as a whole would occur progressively earlier from th reef margin toward shore as diurnal low tides and peak rainfal diminish over time. The increase in fish abundance that occurred mos notably in shallower water during the fall may have been related t reproduction among grazers in response to lengthening diurnal foragin time on the reef flat, and among browsing surgeonfishes in response t the reestablishment of the reef-flat algal community.

Because of the rather ubiquitous nature of their food source ar their wide-ranging foraging habits, parrotfishes may be less depender than browsing surgeonfishes upon the reef flat, and they may also b relatively less affected by the seasonal diurnal restriction c reef-flat foraging. This may be supported by the comparatively lowe juvenile representation of the latter species observed during thi study, which also suggests that reproduction among browsing surgeor fishes may be more responsive to changes in reef-flat algal biomass The herbivores that peaked in abundance earlier in the year wer mostly territorial damselfishes that commonly inhabit the reef fror and submarine terrace. Others included deeper-water angelfishes parrotfishes and surgeonfishes. The effects of seasonally reduce reef-flat algal biomass might be felt indirectly by the damselfishe and angelfishes in the form of temporarily increased interspecifi competition for food (Barlow 1974), particularly since subtidal alga appear to flourish year round (Tsuda 1974). Thus far, the importanc of food resource availability has been stressed as being a significar motivating force in producing the seasonal variation in fish abundanc recorded during this study.

Certain nonherbivorous fish species may also take advantage c reproducing during the fall for a similar reason, since increasin plankton, algal production and detritus accumulations on the reef fla may support a significant biomass of benthic invertebrates as well Estimates of larval lives ranging from a few weeks to a few months ar reported for many fish species including gobies, blennies, butterfl) fishes and wrasses (Sale 1980a). However, reproduction during tl fall may be of secondary importance to these species since they ar not as directly dependent as herbivores on reef-flat algal biomas: Thus, nonherbivorous species may spread their reproductive activitie over a longer period of time which may partially explain why pea abundances within the most ubiquitous carnivore group analyzed in thi study did not prove to be significantly correlated with the April t June period (Tables 13 and 14).

Despite numerical variations in seasonal abundance, the fis community in general seems to exhibit a fairly predictable annua cycle, returning to initial levels after a 12-month period. Th resulting low values of AV (Table 15) characterize the fish communit on the upper reef slope as being relatively persistent. The values c AV calculated for upper reef-slope fishes at Guam may be compared wit those calculated for organisms in less climatically stable region (Table 18). The values for Guam are slightly lower but similar t those for marine fishes in southern California (Ebeling _et_ _al_. 1980) and they are lower than those for marine fishes in northern Californi (Miller and Geibel 1973; Burge and Schultz 1973) and for estuarin fishes in northern Florida (Livingston 1976).

The high annual constancy in species composition found durin this study also indicates the presence of a fairly persistent fis community on the scale analyzed (Tables 16 and 17). These result generally agree with other studies of fish assemblages made o

Table 18. Comparison of annual variation (AV) in ranked specie abundances calculated for some organisms living in differer geographical areas and climatic regimes. AV values measur the scope of yearly changes in species abundances, wher 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 197
0.17*	Marine Fishes	Monterey Bay, Calif.	Miller & Geibel 197
0.15	Arthropods	Humid, stable climate	Wolda 1978
0.15	Marine Fishes	Santa Cruz Is., Calif.	Ebeling _et al_. 198
0.11	Marine Fishes	Naples Reef, Calif.	Ebeling _et al_. 198
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)

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 1980b) and artificial reefs (Russell *et al*. 1974, 1977; Talbot *et al*. 1978). Some authors have suggested that the differences in the spatial scales used among these studies may be sufficient to result in the observed differences in variations in fish abundance and species composition (Gladfelter *et al*. 1980; Sale 1977, 1980a, 1980b). Others have proposed that 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 collected on larger spatial scales and after longer 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 2 and 3) 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 disturbanc primarily in the form of predation (Talbot et al. 1978) are expect to more frequently or more intensely interrupt the competitive proce by nonselectively removing members from the community, there enabling a greater number of species to coexist. This would occur a depth above which the disturbances may become so frequent or inten that species diversity becomes limited by severe environmental cond tions. In this form of the "intermediate disturbance hypothesi (Connell 1978), it may be that the frequency and intensity of natur disturbances at the surface due to storms, large waves, surfa currents etc. are replaced by the effects of increased predation the submarine terrace down to a point somewhere near a depth of 18 While both of these sources of localized small-scale disturbance wou be expected to influence species richness, predation is likely to the most important on the upper reef slope in general (Talbot et a 1978). For the sake of comparison, data from two other depth-relat studies were drawn from the literature (Gosline 1965; Harmelin-Vivi 1977). In these studies, numbers of species were given for sever depth ranges. In order to graph all the data together, the number species per depth range was assigned to the mean depth of each report ed range. The results (Fig. 26) proved to be remarkably consistent.

In summary, the coral-reef fishes on the upper reef slope at Gu exhibit seasonal variation that appear to result largely from repr ductive activities which may be closely related to food resour availability. Seasonal fluctuations between carnivore and herbivo

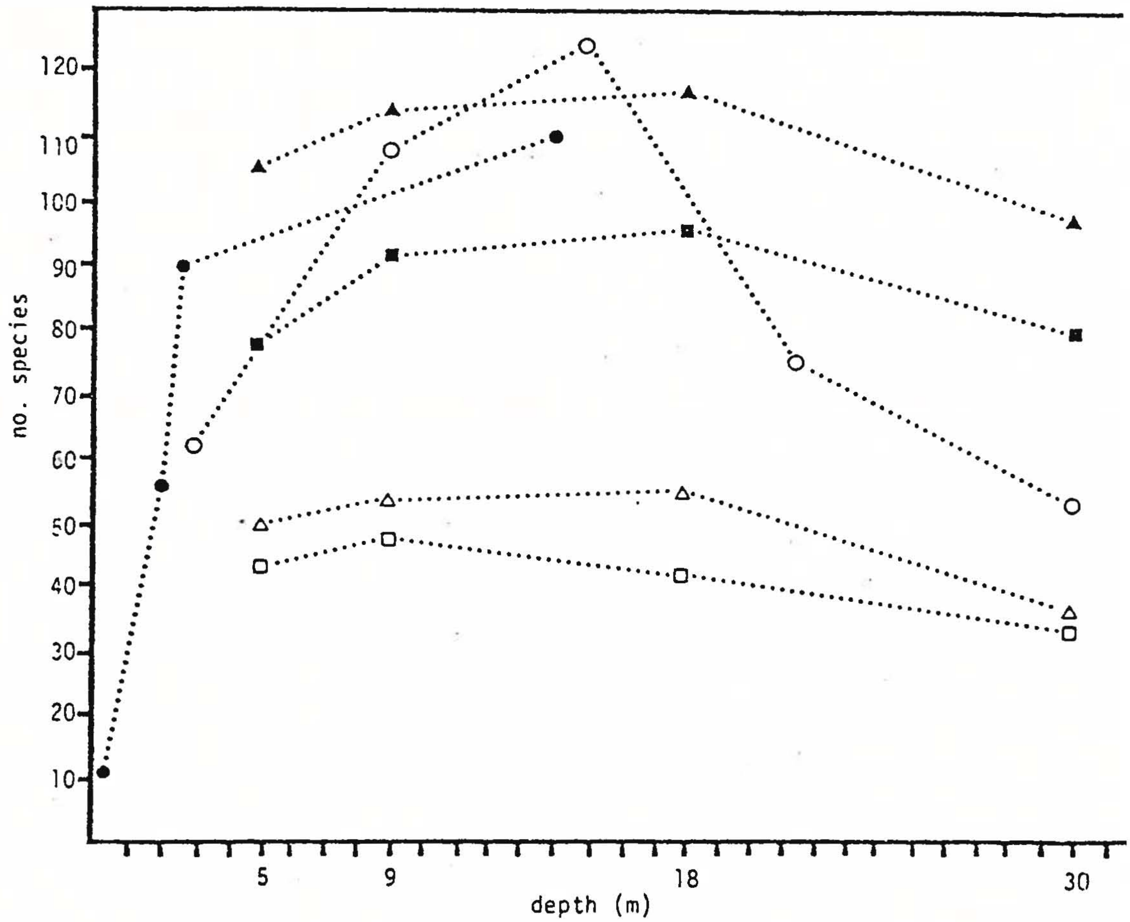

Figure 26. Actual and mean species richness (number of species) observed at Asan Pt. and Ipao Pt. study sites by depth. ■ = Asan Pt. (total no. species); ▲ = Ipao Pt. (total no. species); □ = Asan Pt. ($\bar{x}$ no. species/month); △ = Ipao Pt. ($\bar{x}$ no. species/month); ● = Oahu, Hawaii (total no. species, Gosline 1965); ○ = Tulear Reef, Madagascar (total no. species, Harmelin-Vivien 1977).

groups overlap, but show depth-related temporal differences in pe abundance that may be the result of adaptations to different fo resources. Climatological and oceanographic phenomena seemed to pl indirect but important roles in the timing of seasonal fish abundan by their apparent influences on primary production cycles and repr ductive success in fishes. The upper reef-slope fish community general exhibits a persistent structure that has evidently evolved response to a predictable environment of relative climatic stabilit The results of this study suggest several possible avenues of furthe investigation into the reproductive and trophic relationships amo coral-reef fishes. The applicability of the "intermediate disturban hypothesis" to mobile animals is demonstrated by fishes across dept on the upper reef slope. The information presented may be useful t fisheries biologists in managing inshore reef fisheries on both rela tively healthy and heavily impacted reefs at Guam (Amesbury 1978 Johannes 1979; Katnik 1982).

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