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POPULATION BIOLOGY OF STOLEPHORUS HETEROLOBUS (PISCES: ENGRAULIDAE) IN PALAU, WESTERN CAROLINE ISLANDS

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ABSTRACT

This study sought to assess the biological and fishery parameters which affect the population dynamics of S. heterolobus in order to evaluate management alternatives for the bait fishery in Palau. Monthly pooled length frequencies from samples of the commercial bait catches from December 1971 to June 1973 yielded estimates of growth, recruitment, and mortality. The von Bertalanffy growth equation for standard length in millimeters, L_t, at time t months was: $L_t = 91.1 (1-\exp(-0.174(t+0.150)))$. Counts of daily growth rings on the otoliths from 13 fish agreed with the growth pattern derived from the length frequencies. The length-weight relationships for males and females were similar and the combined relationship for adults was: $W = 7.61 \times 10^{-6} L^{3.09}$. The sex ratio did not significantly differ from 1:1. The average total mortality, Z = 0.65 per month, was estimated from catch curves based upon the combined length frequencies. Biweekly tows from each of the four sectors of the baiting area, for eggs and zooplankton, identified the primary locus of spawning as the open lagoon. Spawning was correlated to salinity. Time series analysis suggested three months between successive spawnings. Mature eggs were found in females whose ovaries comprised over 2% of their body weight. The smallest female containing mature eggs was 51.7 mm SL. The relative fecundity was 450 mature eggs per gram of body weight and the absolute fecundity was given by: $F = 457\ W + 2.70$ where W is the body weight in grams. Few recruits were observed in the bait samples during the drought in the spring of 1973 which prompted the inclusion of a rainfall term in the Ricker stock and recruitment model. The inclusion

of a rainfall term produced a satisfactory fit to the recruitment data (r^2 = 0.56). A rough estimate of 1% larval survival to recruitment at age three months came from a relative life table depicting the equilibrium state of the population. A second life table was prepared using only the natural mortality, M = 0.37 per month, which indicated that one effect of the increased mortality from fishing has been to decrease the number of repeat spawners.

Fishing logs from the first day of fishing in August 1964 through December 1974 were tallied and analyzed. The mean annual catch was 72,161 buckets per year with an effort of 1607 boat nights per year. The average catch per effort was 44.9 buckets per boat night. Since the bait are nightlighted, fishing mortality was estimated with the swept area concept applied to the volume of illuminated water. The average catchability was 0.0012 per lift and the average fishing mortality for 232 lifts per month was 0.28 per month. The exponential yield model and the dynamic pool model suggested that the present fishery is operating near its optimum fishing intensity. Simulations with a population projection matrix, integrating the life table information and the stock and recruitment model, suggested that variations in recruitment explained the increased catch rates in 1969 and the decreased catch rates in the latter half of 1970 and in 1973. The low catches in 1971 were a combination of the earlier poor recruitment coupled with high fishing during the spring and summer months. Judging from the 1972 and 1974 catch rates, the bait fishery is resilient.

Recommended management techniques included continuing the policy of limited entry and possibly augmenting this with a closed season during March and April. It was further recommended that these findings be periodically reviewed as more information accumulates on the bait fishery.

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LIST OF ABBREVIATIONS AND SYMBOLS

SYMBOL		DEFINITION
A		Cross sectional area of illuminated water
a	1.	Annual mortality rate
	2.	Constant
B	1.	Population biomass
	2.	Bait load in buckets per boat
BN		Effort expended by one boat fishing one night
b	1.	Regression coefficient
	2.	Constant
C		Catch
CV		Coefficient of variation
D		Zooplankton displacement volume
df		Degrees of freedom
d_{max}		Maximum difference between cumulative percentages in Kolmogorov-Smirnov test
E		Effort
F	1.	Absolute fecundity
	2.	Instantaneous fishing mortality rate
	3.	Ratio of two variances
FL		Fork length
I	1.	Percentage of gonad weight to body weight
	2.	Light intensity
K	1.	Growth rate in von Bertalanffy equation
	2.	Extinction coefficient of light in water
	3.	Carrying capacity of the environment

LIST OF ABBREVIATIONS AND SYMBOLS (Continued)

SYMBOL		DEFINITION
K	4.	Constant
L	1.	Standard length
	2.	Lifts of the bait net
$L\infty$		Asymptotic length
l_t		Standard length at time t months
l_x		Number of fish aged x months
ln		Natural logarithms
M		Instantaneous natural mortality rate
m_x		Age specific fecundity
n	1.	Number of variates
	2.	Subscript in the yield per recruit model
N_L		Number of fish of standard length, L
N_t		Number of fish aged t months
NMFS		National Marine Fisheries Service
P	1.	Probability of accepting the null hypothesis
	2.	Precipitation in millimeters
p		Probability of a fish being caught in one lift of the net
q		Instantaneous mortality rate associated with one unit of effort
R^*		Reproductive potential of a cohort
R	1.	Recruitment
	2.	Radius of illuminated water
	3.	Refractive index
	4.	Intrinsic growth rate of the population

LIST OF ABBREVIATIONS AND SYMBOLS (Continued)

SYMBOL		DEFINITION
r	1.	Correlation coefficient
	2.	Raising factor from number in a sample to number of fish caught
	3.	Intrinsic rate of increase of the population
r^2		Amount of variance of the dependent variable explained by the regression
S	1.	Salinity
	2.	Spawning stock
	3.	Survival rate
S_m		Spawning stock size producing the maximum number of recruits
S_r		Spawning stock size producing an equal number of recruits
$\hat{s}$		Survival rate estimate
S.D.		Standard deviation
S.E.		Standard error of the mean
SL		Standard length
T		Skipjack tuna catch in metric tons
t	1.	Time in months
	2.	t statistic for comparing two means
V	1.	Variance
	2.	Volume
W	1.	Coefficient of concordance
	2.	Body weight in grams
	3.	Average number of buckets of bait in a sector on one night
	4.	Wattage of underwater lights

LIST OF ABBREVIATIONS AND SYMBOLS (Continued)

SYMBOLS		DEFINITIONS
W_∞		Asymptotic weight
w		Bait sample weight in grams
X	1.	Coded age of a fish
	2.	Horizontal distance
Y	1.	Yield
	2.	Variable
Z	1.	Instantaneous total mortality rate
	2.	Depth in meters
	3.	Settled volume of zooplankton in $cm^3/100\ m^3$

INTRODUCTION

Stolephorus is an Indo-Pacific genus of anchovy (Engraulidae) with species occurring from East Africa (Losse 1966) to almost the eastern tropical Pacific (Hida 1973). In Southeast Asia, _Stolephorus_ spp. are important food fish; for example, an estimated 10,000 metric tons are caught each year in the Philippines (Tham 1974). In addition to being a source of protein for humans, several species of _Stolephorus_ are used as bait in pole and line skipjack fisheries in the central and western Pacific: _S. purpureus_ in Hawaii (June 1951, Nakamura 1970), _S. devisi_ and _S. heterolobus_ in Papua New Guinea (Kearney et al 1972, Lewis et al 1974), _S. buccaneeri_ and _S. heterolobus_ in Fiji (Lee 1973), and _S. heterolobus_ in Palau (Uchida 1970, Wilson 1970).

The development and continuance of the skipjack tuna fishery in Palau depends upon an adequate bait resource, i.e., efficient utilization of the _S. heterolobus_ population. In 1968, the First Marine Resources Conference of the Trust Territory of the Pacific Islands recommended conducting a bait survey. A second conference, in 1969, reiterated the need for an assessment of the bait supply. A noticeable decline in the bait catch per effort in 1970 brought to light the paucity of quantitative information on _Stolephorus_, and at the request of the Trust Territory Government, this study was initiated in 1971 to assess the population biology of _Stolephorus heterolobus_ (Rüppell) in Palau and its interaction with the skipjack fishery.

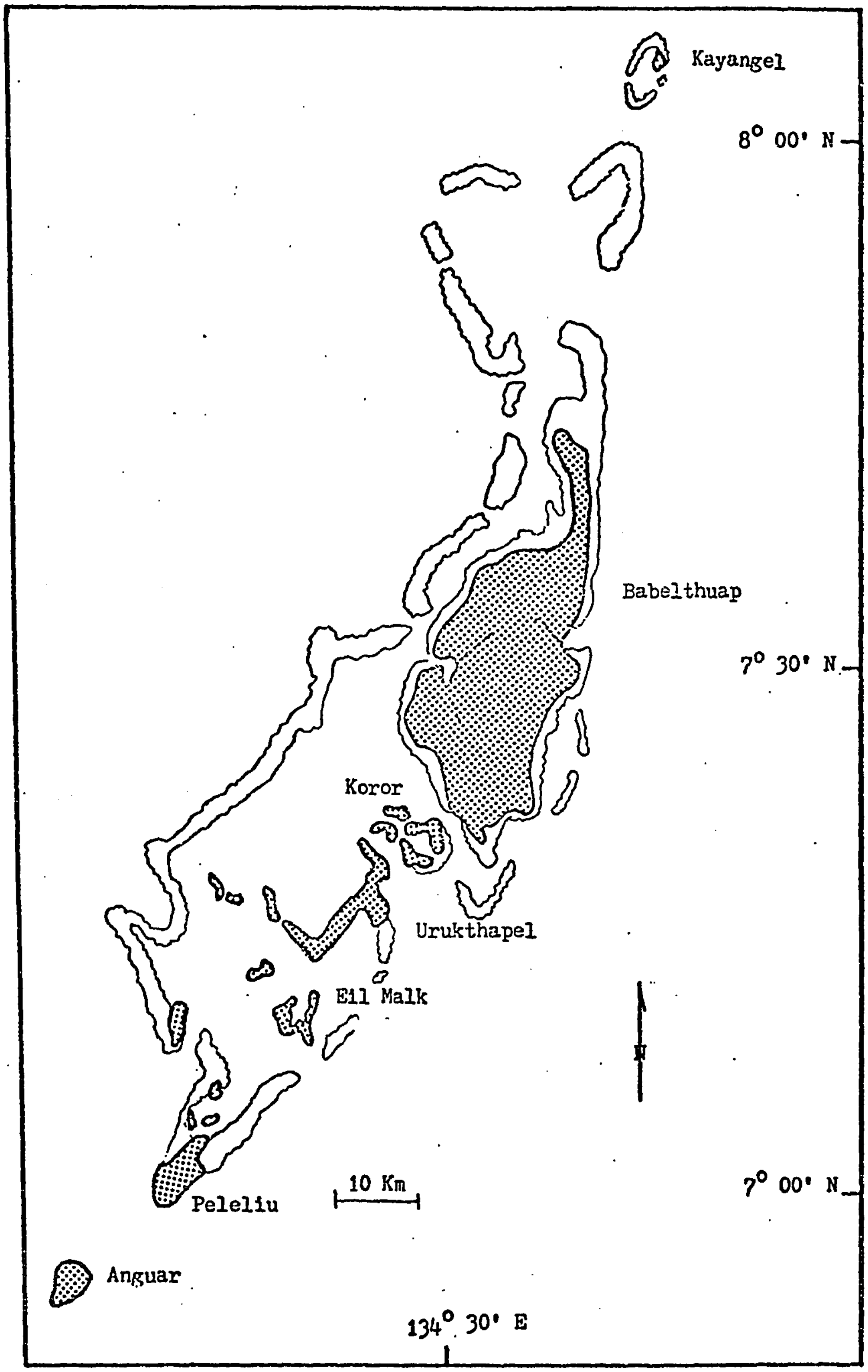
Description of Palau Islands

The Palau Islands (6° 53'N to 8° 12'N and 134° 8'E to 134° 44'E) are situated at the eastern boundary of the Philippine Sea along the crest of the Palau - Kyushu Ridge (Dickinson 1973) and extend for approximately 150 km (Figure 1). The Palau Trench with a depth of 8200 m is approximately 50 km to the east of the island chain. Prevailing oceanic currents offshore are the North Equatorial Current and the Equatorial Countercurrent (Bryan 1944).

The NE trade winds prevail from December to March and the SW monsoons from June to October. The winds are more variable during the other months. Rainfall averages 400 mm a month except during the dry months of February through April when the monthly average decreases to approximately 200 mm per month. The mean temperature is 27^{o} C with only about 1^{o} C variation during the year, but the diurnal temperature variation is about 6^{o} C (U.S. Dept. Commerce 1971).

The Palau chain consists of over 200 islands partially enclosed by a barrier reef. The islands range in size from Babelthuap, the largest island in the Trust Territory at 285 km^2, to stacks only a meter or so across. Babelthuap and areas of Koror are volcanic while the other islands are either uplifted blocks of limestone or mounds of coral rubble and sand (Corwin 1951). The uplifted block islands or "Rock Islands" are up to 200 m high and are typically steep sided and heavily vegetated. These limestone islands have rich deposits of phosphate and the more acessible islands were mined extensively, first by the Germans and later by the Japanese (Mason 1955). Mason found deposits of phosphate on Urukthapel, an island adjacent to the main baiting area, with phosphate concentrations exceeding 37%.

Figure 1. The Palau Island chain.


Kayangel
8° 00' N
Babelthuap
7° 30' N
Koror
Urukthapel
Eil Malk
N
10 Km
7° 00' N
Peleliu
Anguar
134° 30' E

The main lagoon and the baiting area are between the islands of Koror and Urukthapel and the barrier reef to the west. The lagoon water is a mixture of oceanic water and rain runoff from the islands. Water exchange in the lagoon is via two passages in the barrier reef and by flow across the reef during the semi-diurnal high tides. Sheet runoff of rainfall occurs even in heavily wooded areas (Corwin 1951) and this runoff carries decaying vegetation, bird wastes, and phosphate into the lagoon. Motoda (1969) found that the primary productivity in the lagoon, 80 mgC m^{-2} d^{-1}, was twice that of the oceanic water beyond the reef.

Literature Review

Stolephorus heterolobus

The literature of *Stolephorus heterolobus* (Rüppell) has been concerned primarily with its taxonomy and to a lesser extent its zoogeography. Rüppell (1837) described it as *Engraulis heteroloba* from collections made at Massuwa, Ethiopia on the Red Sea. Gunther (1868), in cataloguing fish collections in the British Museum, identified his specimens, which were obtained from Rüppell, as *Engraulis heterolobus*. Just prior to Gunther's work, Bleeker (1866), redescribed this species as *Stolephorus heterolobus* on the basis of the ventral scutes.

Both Bleeker (1868 - 1870) and Weber and deBeaufort (1913) recognized five species of *Stolephorus* in the Indo-Australian archipelago. Delsman (1931) and his assistant Hardenberg found more than five types of *Stolephorus* eggs in their extensive collections of fish eggs and larval fish from the Java Sea. They found two types of eggs for the fish identified as S. heterolobus: one type of egg had a minute oil globule and the other egg type did not. On the basis of ovarian work, the egg type with the oil globule was ascribed to S. heterolobus and the fish whose egg lacked the oil globule was described as a new species, Stolephorus pseudoheterolobus Hardenberg (1933 a). As a result of the egg and larvae studies, Hardenberg increased the number of Stolephorus species to nine (1933 b, 1934).

Since most of the early work on Stolephorus was from a single area, the Java Sea, the taxonomic literature was insufficient to separate and identify the Stolephorus species in the Philippines (Tiews et al 1970). Consequently, I.A. Ronquillo has undertaken a revision of the genus. While specimens from many sources were examined, the type specimen of S. pseudoheterolobus was no longer available, possibly having been destroyed during World War II (Whitehead 1965). Since specimens of S. pseudoheterolobus fit the earlier descriptions of S. heterolobus, the latter name was restored and the similar fish whose eggs have oil globules was temporarily called Species A. Ronquillo's revised key to the genus Stolephorus was published by Whitehead (1967) and also by Tiews et al (1970). Tham (1974) summarized the taxonomy of Stolephorus and recommended the adoption of Ronquillo's key.

Much of the information on the natural history of S. heterolobus comes from Tham's work in the Singapore Straits. In 1948, he established a station for collecting hydrographic, chemical, and biological data (1953). A specific objective was to determine the feeding relationships in this region. Significant partial correlation coefficients were obtained for the catch of Stolephorus spp. and the chlorophyll content and also with the catch of Scombermorus. A possible relationship was found between Stolephorus spp. and copepod abundance. He concluded that S. heterolobus (S. pseudoheterolobus in this early work) was an important link in the food chain, feeding upon small crustacea and phytoplankton, and, in turn, being fed upon by carangids and scombrids (Tham 1950). Tham further noted that S. heterolobus do not spawn in the Singapore Straits, but that young and adult fish aggregate to feed in the maze of channels separating the numerous islands (1953). Tham later determined a von Bertalanffy growth equation from the length frequency data (1966, 1969) and published a synopsis of the biological data of S. heterolobus (1970).

Palau Islands

The Palao Tropical Biological Station was established in 1934 by the Japan Society for the Promotion of Scientific Research (Hatai 1937). The station's policy was to encourage Japanese scientists to investigate specific aspects of the coral reef ecosystem. Some of the topics which were pertinent to this study included hydrography (Matsuya 1937), submarine illumination (Motoda 1939), plankton productivity (Motoda 1941, 1969), settled plankton volumes (Tokioka 1942), and a comparison of the lagoon, bay, and open sea with respect to transparency, pH, oxygen, and temperature (Motoda 1940). Abe (1939) studied the fish fauna of Palau and reported four species of Stolephorus: S. heterolobus, S. zollingeri (= S. buccaneeri according to Whitehead, 1965), S. indicus, and S. tri.

The first bait fish surveys in Palau were made in conjunction with the annual fishing surveys beginning in 1925 (Anon. 1937). Several species of bait fish were used in the early tuna fishery and the boats changed baiting grounds frequently because of temporary depletions of bait.

After World War II, the U.S. Government surveyed the fisheries potential of the former Japanese mandated islands (Smith 1947). Soon afterwards, Smith and Schaefer (1949) conducted exploratory fishing in the western Pacific including Palau. Seines in shoal waters yielded *Spratelloides delicatulus* and *Pranesus pinguis* primarily. In 1956, Wilson conducted a bait survey for Hawaiian Tuna Packers (mimeo) and another survey later for the Trust Territory (MS Marine Resources Division, Saipan, Mariana Islands). The main bait species identified by Wilson was *Stolephorus heterolobus* with *Spratelloides delicatulus* and *Pranesus pinguis* being of secondary importance. Incidental bait species include carangids, apogonids, and larval sphyraenids.

Description of the Bait Fishery

The bait fishery and the skipjack fishery resumed operations in August 1964 with six Okinawan style fishing boats. Since the bait are transferred from the lift net to the baitwells in buckets, the bucket has become the standard unit of measurement. Each bucket contains approximately 2 kg of bait. One measure of effort in this bait fishery is the number of boats baiting each night or the boat night. The average bait catch rate in 1964 was 40.3 buckets per boat night. The highest annual catch and catch rate occurred in 1969 with 111,103 buckets and 69.9 buckets per boat night respectively. The catch rate dropped in 1970 from 86.4 buckets per boat night in August to 38.1 buckets per boat night in December. The decline continued into 1971 reaching an all time low rate of 8.3 buckets per boat night in February. Since 1965, the fleet size has hovered around eight boats. Prompted by the high tuna catches of 1969 and 1970, mother ships and their catcher boats were brought into Palau increasing the fleet size from eight to 15 boats by March and to 20 boats by June 1971. Thus, at the time of the record low bait catches, the fleet size was doubled. Low bait catches continued through 1971 and by November 1971, the extra boats had left Palau. The present study began in late 1971.

The process of catching bait is straightforward. Each tuna boat has an outboard powered bait skiff with a diesel generator. The baitman goes to the baiting area in the later afternoon in the skiff while the tuna boat is still offshore fishing. After dusk, the generator is started and a 1000 W underwater light is suspended about 2 m below the anchored skiff. Later, after the tuna boat has returned to the freezer plant in Malakal to offload its catch and resupply, it will find its baitman in the baiting area. When sufficient bait have aggregated around the light, the baitman will gently scull the skiff, with its suspended light, to over the middle of the net which has been set out from bamboo poles attached to the tuna boat. The baitman dims the light and watches the bait through a look-box. When the bait have formed a tight school around the light, the baitman gives the signal for the crew to haul the net. The net is dried up until only a small portion remains in the water. The concentrated bait are maneuvered into buckets and transferred into the baitwells on the tuna boat. The buckets are counted during the transferal process. If more bait is captured than can be accomodated in the baitwells, the surplus is stored in a floating receiver called a "kowarie" and left in the baiting area.

Presently, most of the baiting occurs in the system of channels between the numerous islands to the west of Urukthapel Island. This area is favored because it is located only about 12 km from the freezer plant, the passages in the reef are convenient, and the area is protected from the winds regardless of their direction. However, in the first few months of the fishery, the boats baited throughout the lagoon, and even now if bait is scarce the boats will bait elsewhere.

OBJECTIVES

The objectives of this study are threefold. The first objective is to estimate the life history parameters of Stolephorus heterolobus, specifically growth, fecundity, spawning, and mortality. The second objective is to discover the dynamics of the bait fishery by incorporating the biological findings with an analysis of the fishery statistics. The final objective is to explore management techniques in the bait fishery.

MATERIALS AND METHODS

Study Area

The 20 month field study, beginning in October 1971, concentrated on the main baiting area (Figure 2). The water depth here averages 30 m with a 15 m shelf in part of the inside sector. The tidal currents, ranging up to 0.3 m sec^{-1}, varied with the tides. Tropic tides (Sverdrup et al 1942, p. 561) exceeded 2 m.

The main baiting area and its adjacent lagoon were divided into four sectors: north, inside, south, and outside. The north and south sectors are intermediate between the semi-enclosed inside sector and the open lagoon or outside sector. Little or no baiting occurs in the outside sector because it can become quite choppy very quickly. The more protected sectors support the bait fishery.

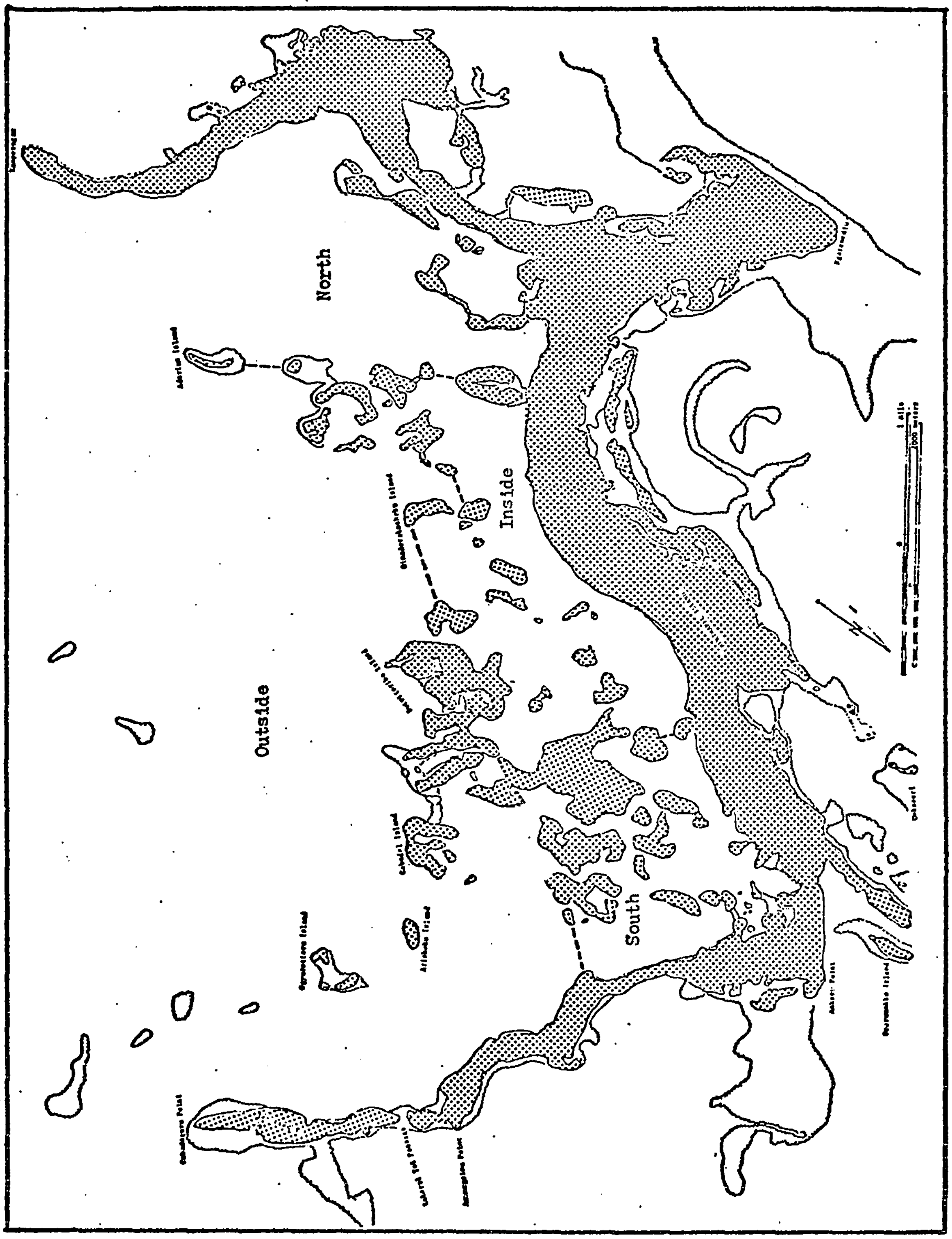
Sampling

Bait Catches

Twice weekly, two bottles containing 250 ml of 10% formalin, buffered with sodium tetraborate, were supplied to baitmen who collected bait samples from the commercial fleet. During the transfer of bait from the lift net to the tuna boat's baitwells, the baitman would dip net a sample. Usually both samples were collected the same night by different boats.

A small lift net was used to supplement the bait samples from the fleet and also for exploratory bait fishing. This net was 2.3 m in diameter and designed to be assembled, set, hauled, and disassembled in a 4 m skiff. The net was made from a panel of ¼-inch knotless

Figure 2. The main baiting area near Urukthapel Island.


North
Inside
Outside
South

netting with a floor of the same material. A collapsible frame was made from four sections of ¼-inch spring steel galvanized rods. Two 12V, 50 amp hr batteries, connected in parallel, powered the 100 W and 25 W underwater lights. On several occasions, a 200 kHz depth recorder was used to estimate relative bait abundance.

In the laboratory, the fish in the samples were identified and the standard length (SL) of S. heterolobus was measured to the nearest 0.1 mm with a dial caliper. The weight of S. heterolobus and the weight of the entire sample was determined to the nearest 0.1 g.

In addition, length frequency data on S. heterolobus obtained by National Marine Fisheries Service (NMFS) personnel between June 1965 and May 1968 in Palau were made available to me. The length in these data was expressed as fork length, and I converted these data to standard length by a linear regression of standard length, SL, on fork length, FL, based on measurements from 32 of my specimens

$$SL = 0.962\ FL - 0.544$$

$$r = 0.999,\ df = 30,\ P<0.001 \qquad (1)$$

Stolephorus eggs and zooplankton

Originally, eggs and zooplankton were sampled biweekly in the protected sectors only; however, after March 1972, the outside sector was also included. Usually, two, two minute circular surface tows were made in each sector with a 75 cm diameter, 283 μ mesh net. The volume of water filtered was determined from an asymmetrically placed flow-meter. Short duration tows were necessary to avoid clogging the net (Smith et al 1968). The tow contents were transferred to 500 ml polypropylene bottles and preserved with 10 ml of buffered formalin. Usually, the tows were made between 0900 and 1400 hrs.

Zooplankton abundance in each sector was estimated as the settled volume of zooplankton in 100 ml oil testing tubes. A sample bottle was shaken and its contents poured into two oil tubes simultaneously. After the plankton had settled in the tubes for a half day, the tubes were gently agitated and the plankton allowed to resettle. The double settling minimized differences in interstitial water. Since there were two tows per sector and each tow was split into two tubes, the four readings per sector were averaged and expressed as cm^3 plankton per 100 m^3 sea water filtered.

After the zooplankton volumes had been determined, all the _S. heterolobus_ eggs and larvae in the entire sample were counted and standardized to number per 100 m^3 sea water filtered.

Environmental data

Wherever possible, after the tows were completed in the sector, the skiff was secured to the frame of a bait receiver for the remainder of the sampling. The low freeboard of the skiff allowed the observer to record the surface temperature to the nearest 0.1° C while holding the thermometer in the water. Salinity was determined with a refractometer from a water sample taken from a depth of 20 cm. Although the refractometer had a salinity scale, the increments were sufficiently large, 2 per mil, that more precision was obtained by recording the refractive index and then calculating the salinity with an empirical relationship

$$S = 5645\ R - 7527 \qquad (2)$$

where S is salinity per mil and R is the refractive index. Secchi depth was recorded to the nearest 0.1 m.

Rainfall and wind information were obtained from the U.S. Weather Station on Koror. The station is located on a hill about 6 km from the study area and although weather phenomena in Palau can be localized, the topographical similarity leads me to believe that the differences are small.

Primary productivity was measured using the C^{14} uptake method following the procedures in Strickland and Parsons (1968). Subsurface samples from a depth of 2 m were poured into four 300 ml BOD bottles, two of which were painted black and taped with electrical tape. Two light bottles and one dark bottle were inoculated with labeled carbon from 2 ml, 1 μCi ampoules; the other dark bottle was an unlabled blank. All four bottles were incubated _in situ_ at 2 m for two hours. Incubation was terminated by the injection of 1 ml of buffered formalin. Back in the laboratory, the samples were filtered and stored in a dessicator. Later in Hawaii, the samples were counted on a geiger counter which had been calibrated by liquid scintillation. The counts per minute were converted to mgC $m^{-3}\ hr^{-1}$.

Dissolved oxygen concentrations in the upper 20 meters were measured on two occasions with a YSI oxygen meter.

Data analyses

Growth

Standard length frequencies from the commercial bait samples, tallied in 2 mm increments (Gulland 1966), were pooled monthly. To de-emphasize the larger samples, the pooling procedure downweighted the larger samples to 100 fish and used the raw frequencies of those samples with less than 100 fish. All the samples in a given month were summed by size for the monthly pooled length frequency.

Probability plots (Harding 1949, Cassie 1954) of the monthly pooled length frequencies yielded the number of modes and their means and standard deviations. This method assumes that the size frequency of a given cohort, i.e., fish of the same age group, is normally distributed. This assumption was validated by those catches which were mostly composed of recruits having a normally distributed size frequency. An example of this normal distribution is the size frequency for October 1972 in Figure 10 (p. 52). If the number of modes was not readily apparent from the size frequency, then I used the fewest modes which still yielded a low X^2.

In addition to the probability plots, the pooled length frequencies were analyzed using the computer program, NORMSEP (Abramson 1971, LeGuen and Sakagawa 1973). NORMSEP uses Hasselblad's (1966) method for separating normal distributions from polymodal frequency data by calculating truncated normal distributions based upon supplied cutoff points and a range of mean values. The first normal distribution is removed from the frequency and the process is repeated for the remaining modes. The goodness of fit of the overall calculated length frequency to the actual length frequency was tested with a X^2 for each combination of means. The final set of means selected was that set with the lowest X^2. In this study, probability plots supplied the necessary information for NORMSEP.

After identifying the monthly modes, the modes for successive months were compared for possible linkages believed to approximate the growth pattern of S. heterolobus. In determining the actual links, I have assumed that there is no negative growth and that the smaller mode in a later month represents new recruits. There are no links for an elapsed time greater than one month. The initial mean length, the corresponding subsequent length, and a time interval of one month for each link was used in a computer program by Fabens (1965) to least squares fit the data to the von Bertanlanffy growth model (Bertalanffy 1957).

Counts of otolith rings were used to corroborate the growth estimates derived from length frequencies. Otoliths from 13 fish, 30.4 mm to 76.1 mm SL, which had been preserved in buffered formalin were excised and the right sagittae were mounted with euparol. After a clearing period of one month, the rings were counted six times at 400 x. I have assumed that these marks on the sagittae were deposited daily as has been shown recently for S. purpureus, an ecological vicariate of S. heterolobus, in Hawaii (Strusaker and Uchiyama 1976).

Fecundity

The fecundity of S. heterolobus was determined from 10 fish, 52 mm to 90 mm SL, which were selected to represent the size range of mature fish. Randomly selected fish in this size range were weighed and their ovaries excised and weighed. A simple index of gonad development was calculated as the percent ovarian weight to total body weight (Vladykov

1956). S. heterolobus ovaries contained three types of cells: spherical cells (< 0.2 mm), small elliptical eggs (0.2 mm - 0.38 mm major axis), and larger elliptical eggs (> 0.38 mm major axis). The spherical cells were not counted because the oocytes could not be distinguished from follicular cells in the routine counts. All of the elliptical eggs were counted and the major axis of approximately 150 eggs in each ovary were measured either with an ocular micrometer or with a microprojector.

Total mortality

Estimates of total mortality for two periods in the history of the bait fishery were calculated from catch curves (Ricker 1958, Chapman and Robson 1960, Beverton 1963). The number of fish is inversely related to age. Thus, the term total mortality is a collective term used to describe the combined effects of the factors tending to reduce the bait population. Further, to yield an estimate of total mortality from a catch curve, it is necessary to assume that the recruitment and mortality have been constant over the time represented. While recruitment in Palau is not constant, this assumption was fulfilled partially by combining frequencies from several months to give an average value for mortality.

Since the bait samples were not aged but merely recorded as length frequencies, it was necessary to convert the sample length frequencies to the number of fish caught in each age category by a boat on the night of the sample. The first step was to raise the sample length frequency to the number of fish caught in each size category by a boat on the night of the sample. Gulland (1969) gave a simple raising factor, r, as the ratio of the average catch of bait per boat night expressed in grams per boat night to the sample weight in grams

$$r = (2000\ W)/w \qquad (3)$$

where W was the number of buckets per boat night for the sector on the night being sampled, w was the sample weight in grams, and 2000 is a bucket to gram conversion factor. The raised length frequencies for a given month were then summed by size.

The second step converted the raised length frequencies to aged frequencies using the von Bertalanffy growth equation. An age-length key was constructed by assuming that fish 15 days to 45 days old were one month old; fish 46 days to 75 days were two months old and so on. The lengths corresponding to these ages were calculated from the von Bertalanffy equation and the monthly raised length frequencies were regrouped into monthly age frequencies. The initial age in the key is two months even though the fish are not fully recruited into the bait fishery until they are three months old.

Catch and effort statistics

In addition to obtaining information on the life history of S. heterolobus during the 20 month stay in Palau, the daily catch reports from the Palauan tuna fishery (Figure 3), beginning with the first day of fishing in August 1964, were gathered and tallied to give monthly totals for the bait catch in buckets, the tuna catch in metric tons, the number of boats operating during the month, the number of

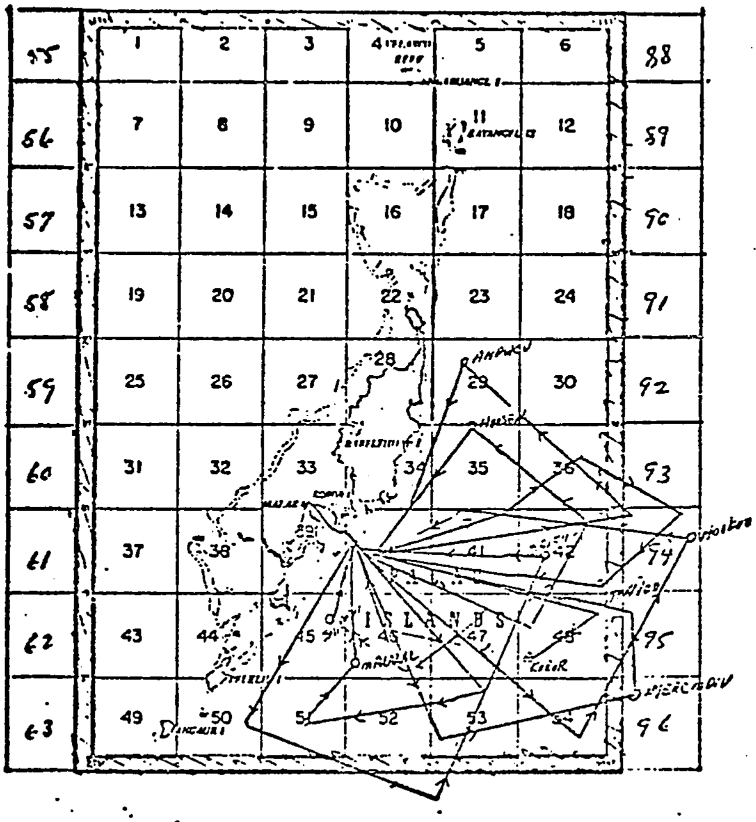
Figure 3. Standard form of Marine Resources Division for reporting daily catch information on tuna and bait for the tuna fleet.

Front

MARINE RESOURCES DIVISION HEADQUARTERS
Koror, Palau
Western Caroline Islands 96940

SKIPJACK AND LIVE BAIT CATCH DATA

Boat Name VAN CAMP   Date DEC 17 1974



	Bait Area	BAIT Receiver		Skipjack		Time of set	Catch 1st set	Catch 2nd set	Catch to Receiver		Skipjack Area		Skipjack Landed
BOAT	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
MALAK	[illegible]	34	100	45	[illegible]			11.00	[illegible]	[illegible]	17		
SAIP	[illegible]	34	[illegible]	45	[illegible]			[illegible]	[illegible]		22		
KELOR	1035	34	120	[illegible]	[illegible]			11.50	"	"	22		
HESEA	[illegible]	34	[illegible]	[illegible]	[illegible]			[illegible]	"		1	[illegible]	
NAUL	[illegible]	34	70	45	[illegible]			[illegible]	"	"		17	
ANPK	[illegible]	34	40	[illegible]	[illegible]			[illegible]	"	"	1	15	
NGER	[illegible]	34	[illegible]	[illegible]	[illegible]			[illegible]	"	"	7		17
SEIK	1055	34	30	45	[illegible]			17.30	"	"	3	15	
HEKEO	1055	34	45	[illegible]	[illegible]			17.45	"	"	1	[illegible]	

Back

Bait information

BOAT	AREA	RECEIVE	SET	TIME OF SET	1ST	2ND	DEPARTURE
MALAKAL	2	100	2	03:30	100		04:30
SAIPAN	1	58	1	04.00	58		04:45
KELOR	4	120	1	04.00	120		05:00
HESEAL	1	65	1	04.30	65		04.30
NAUMEO	1	70	1	02.30	70		05.00
ANPOKU	1	40	1	04.00	40		04:45
NGERCHEMAU	1	60	1	03.00	60		04:30
SEIKAI	1	30	1	04.00	30		05.00
HEKEO	1	45	1	04.00	45		04:50

baiting trips, and the number of tuna trips. During the last 10 years, there have been many changes in the fleet, such as increasing the vessel size and range, but the process of baiting has remained relatively unchanged. All the boats use the "Stick Held Dip Net" of 1/8 inch hard cloth approximately 13 m on a side. There was a gradual changeover from 350 W to 1000 W underwater lights in 1968. To make the earlier bait catch data comparable to the more recent data, I have scaled the earlier catch data by the ratio of the fishing mortality associated with a 1000 W light to that associated with a 350 W light. The appendix gives the details of calculating the fishing mortality as a function of the underwater light source.

Beginning in July 1970, the catch reports included the location and bait catch for each lift of the net. Thus, two measures of effort are available for this bait fishery: the previously mentioned boat night or the number of boats baiting each night and the lift. Frequently in fisheries literature, the catch per unit effort is used as a relative index of abundance (Gulland 1963). This usage assumes that the fishermen are not operating in exceptional areas and that the catchability of each unit of effort remains constant. The first assumption is valid for Palau (see Table 19, p. 111) because the location of baiting is selected for the reasons mentioned earlier such as proximity to the freezer plant, etc. The second assumption of constant catchability is fulfilled more by the lift than by the boat night. The boat night is unable to discriminate between 100 buckets obtained after three lifts and a single lift during the night of 100 buckets. Minor differences in bait abundance can be masked by varying the number of lifts during the night. The value of the boat night is that it is available from the first day of fishing and so it provides a complete historical record of the bait fishery even though this picture will have less variability than what actually occurred in the bait population. The catch per boat night, while not being sensitive to subtle changes in bait availability, does respond to the more persistent changes. The alternative index, the catch per lift, is only available since July 1970 and it is subject to differences in turbidity and moon phase as will be shown later. I will use both indices, where appropriate, in discussing the interactions between the fishery and the bait population.

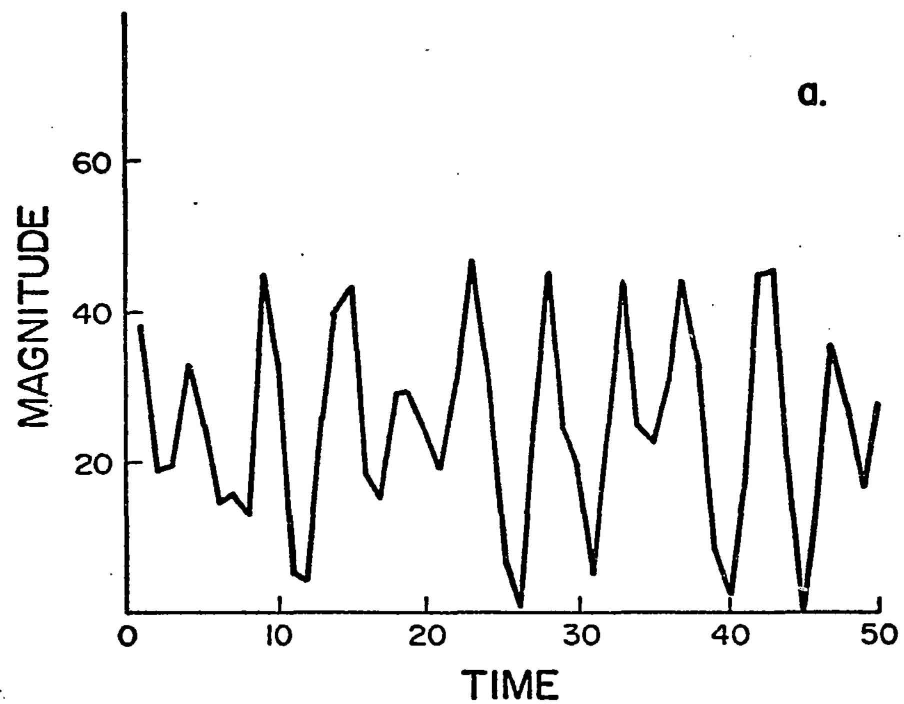
Statistics

Routine statistics such as means, standard errors, analyses of variance, etc., were calculated using Hewlett-Packard library computer programs whenever possible. If a desired program capability for more specialized analyses such as the various fishery production models was not available, I programmed these in BASIC.

One of the specialized programs determined the periods of cyclic data using periodograms (Enright 1965). Periodograms were formed by partitioning the data into cycles with an assumed period and then calculating the average amplitude for each phase. The root mean square of the average amplitudes, A_p, was plotted for a sequence of periods. A peak in the graph indicated the period of a cycle. The underlying principle is that A_p will tend to zero in a very long data record if an incorrect period is used.

Figure 4 a. Test data generated from three superimposed time series: a sine wave with a period of 6.8 time units, a cosine wave with a period of 4.7 time units, and a random pattern scaled between 0 and 10.

Figure 4 b. Periodogram of the above data for those periods between 4 and 8 time units. A_p is the root mean square of the average amplitude for period, p. The peaks at 4.7 and 6.8 time units correspond to the cosine wave and the sine wave respectively.


a.
MAGNITUDE
60
40
20
0
10
20
30
40
50
TIME

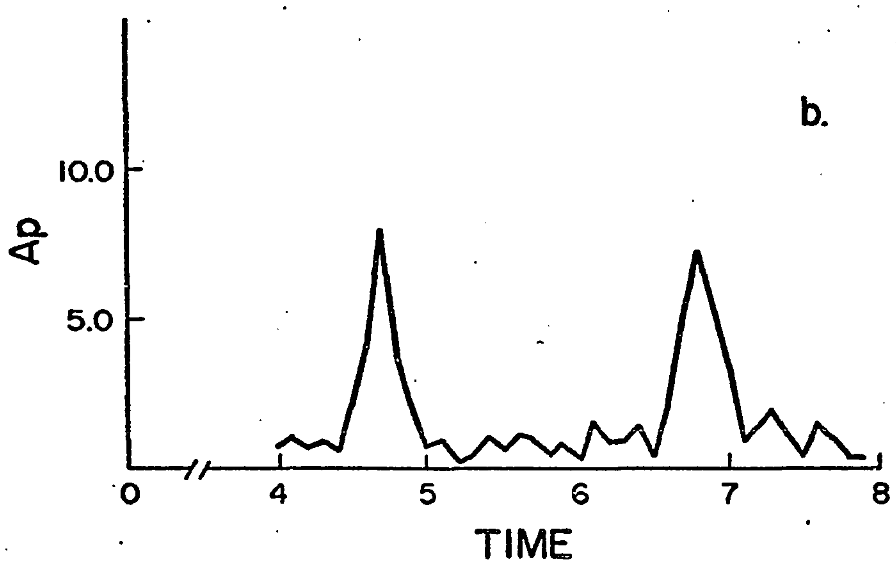

b.
Ap
10.0
5.0
0
4
5
6
7
8
TIME

Figure 4a shows a portion of the test data used in verifying the computer program for developing periodograms. The test data was generated from equation (3)

$$X_t = 10 \sin (2\pi t/6.8) + 15 \cos (2\pi t/4.7) + R + 20 \qquad (4)$$

where X_t is the dummy variable at time t, t is in time units from 1 to 100, R is a random number between 0 and 10, and the 20 scales the resulting curve such that X_t is non-negative. Essentially the test data is composed of two curves, one with a period of 4.7 time units and the other with a period of 6.8 time units, and random background noise. The periodogram (Figure 4b) produced from the test data does indeed show pronounced peaks at 4.7 and 6.8 time units.

RESULTS AND DISCUSSION

Stolephorus species in Palau

On the average, 91% by weight of the bait sampled during the 19 months of field work was *S. heterolobus* (Table 1). In addition to *Spratelloides delicatulus* and *Pranesus pinguis*, which were previously mentioned as being important in the incidental catches, four other species of *Stolephorus* were encountered. The fish called *S. Species A* by Ronquillo (Whitehead 1965) was caught intermittenly throughout the study but at no time was it ever dominant in the bait catches. B.R. Smith (personal communication) identified specimens of *S. Species A* as *S. devisi*. *S. buccaneeri* was caught in a single sample in November 1972 and there were frequent offshore sightings of this fish by fishermen during that month. *S. indicus* and *S. tri*, also, were taken in a single sample, as was the remaining Palauan engraulid, *Tryssina*

Table 1. Composition of the bait samples separated by weight into *Stolephorus heterolobus* and other species.

Month	No. Samples	*S. hetero.* Weight (g)	Other	Total	% Other
December 1971	9	1311.6	154.4	1466.0	10.5
January 1972	8	898.9	0.0	898.9	0.0
February	13	1814.4	0.0	1814.4	0.0
March	14	2000.5	56.7	2057.2	2.8
April	15	2173.2	3.4	2176.6	0.2
May	14	2185.3	30.2	2215.5	1.4
June	16	2103.5	220.9	2324.4	9.5
July	16	2467.9	181.8	2649.7	6.9
August	7	557.7	0.0	557.7	0.0
September	14	1461.8	192.3	1654.1	11.6
October	8	880.9	31.4	912.3	3.4
November	10	1720.4	276.4	1996.8	13.8
December	12	2024.8	307.7	2332.5	13.2
January 1973	12	2271.6	228.4	2500.0	9.1
February	16	3033.3	820.1	3853.4	21.3
March	10	1817.4	247.8	2065.2	12.0
April	12	2309.0	182.1	2491.1	7.3
May	8	1127.0	218.9	1345.9	16.3
June	13	1735.3	295.5	2030.8	14.6
Totals	227	33894.5	3448.0	37342.5	9.2 mean

baelema.

Environmental factors

Table 2 contains the monthly precipitation values from 1964 to 1974 expressed in millimeters (U.S. Dept. Commerce 1964 - 1974). Rainfall in Palau averages 3600 mm per year. The months of January through April are quite variable. The rainy season usually begins in May with the onset of the SW monsoon winds and continues through October. The dry season, averaging over 200 mm of precipitation per month, extends from February through April. In 1973, the dry season was severe. Rainfall during February 1973 was the lowest monthly total, 31 mm, recorded since the U.S. Weather Bureau began keeping records in Koror in 1947.

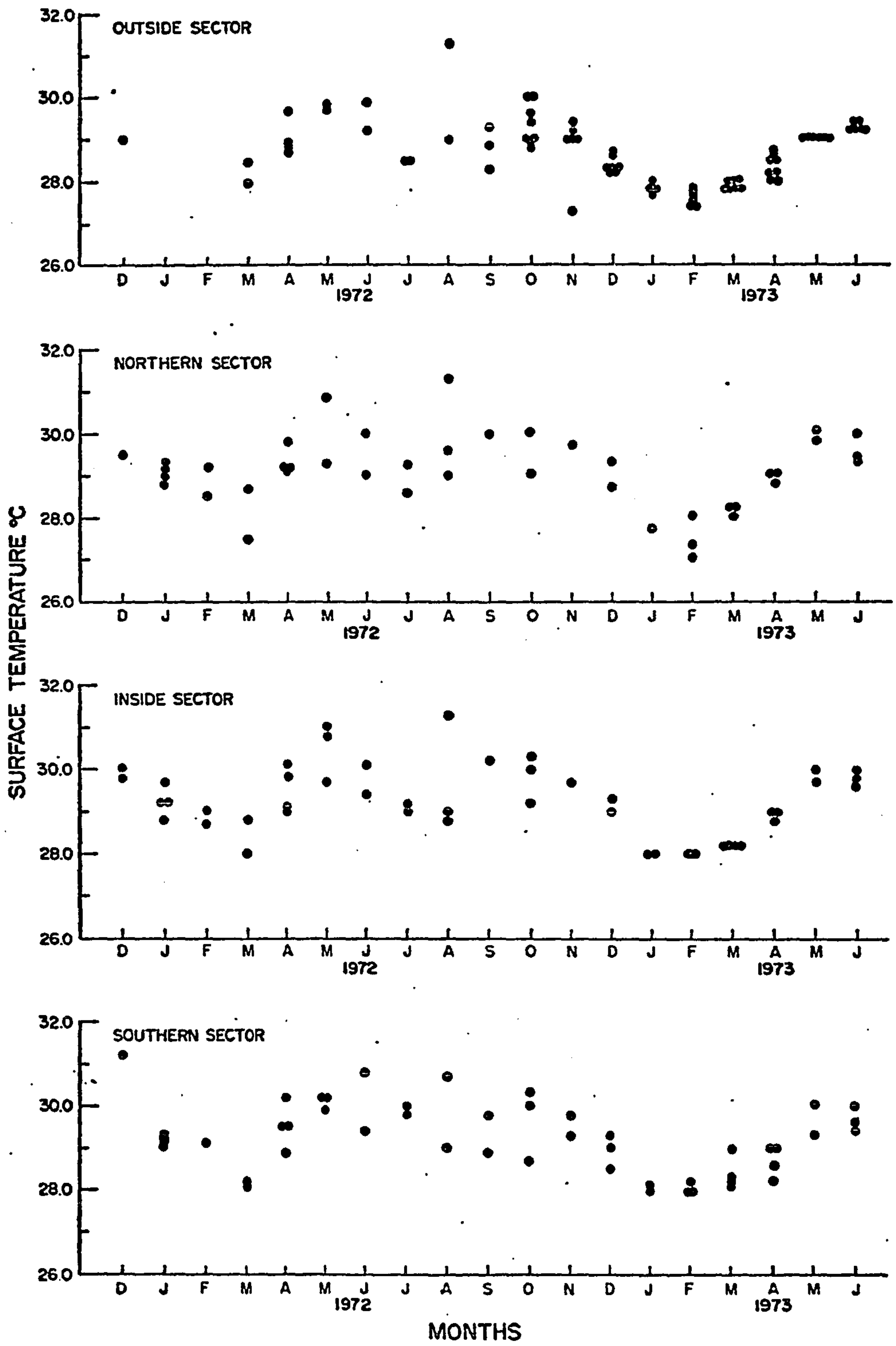
Monthly surface temperatures by sector are given in Figure 5. The minimum temperatures in all sectors were observed during February 1973. The maxima were more variable. The differences between means by month and sector were tested with Kendall's non-parametric rank concordance test, W, (Tate and Clelland 1957). The outside sector was cooler ($W = 0.40$, $P < 0.01$) than the more protected areas. Tokioka (1942) reported slightly cooler surface temperatures in the exposed anchorage as compared with the enclosed bays. January through March 1973 were cooler than the other months ($W = 0.89$, $P < 0.01$).

Closely related to rainfall and surface temperatures were the monthly salinities, Figure 6. Salinities ranged from 32.0 $^{o}/oo$ in the southern sector in December 1971 to 35.1 $^{o}/oo$ in the outside sector in March 1973. Salinities differed significantly between months ($W = 0.86$,

Table 2. Monthly rainfall expressed in millimeters from the U.S. Weather Bureau Station in Koror, Palau.

Month	Year												
	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	Mean	CV %
January	185	163	209	479	204	156	158	344	274	54	715	267	69.6
February	409	331	84	95	395	74	147	271	275	31	203	210	63.8
March	177	371	255	183	218	130	123	282	558	75	349	247	56.1
April	189	181	388	118	192	173	82	211	180	287	276	207	40.6
May	465	248	231	252	242	298	210	414	241	258	206	279	30.1
June	308	504	265	437	178	426	314	498	525	350	247	368	31.7
July	105	776	601	310	417	717	320	368	283	325	537	433	46.9
August	400	426	246	435	279	315	401	264	403	288	349	346	20.2
September	179	330	183	171	311	356	216	355	378	309	376	288	29.0
October	259	246	423	433	291	249	330	498	250	486	571	367	32.4
November	349	156	299	299	207	230	233	261	253	421	400	283	29.1
December	291	322	379	311	405	161	376	281	192	251	471	312	29.5
Total	3316	4054	3563	3523	3339	3285	2910	4047	3812	3135	4700	3607	14.2
Mean	276	338	297	294	278	274	243	337	318	261	392		
CV %	40.8	51.5	45.3	45.3	31.3	63.1	43.0	27.8	38.7	54.4	40.2		

Figure 5. Surface temperatures in the main baiting area of Palau by months and sectors. Each point represents a single measurement.

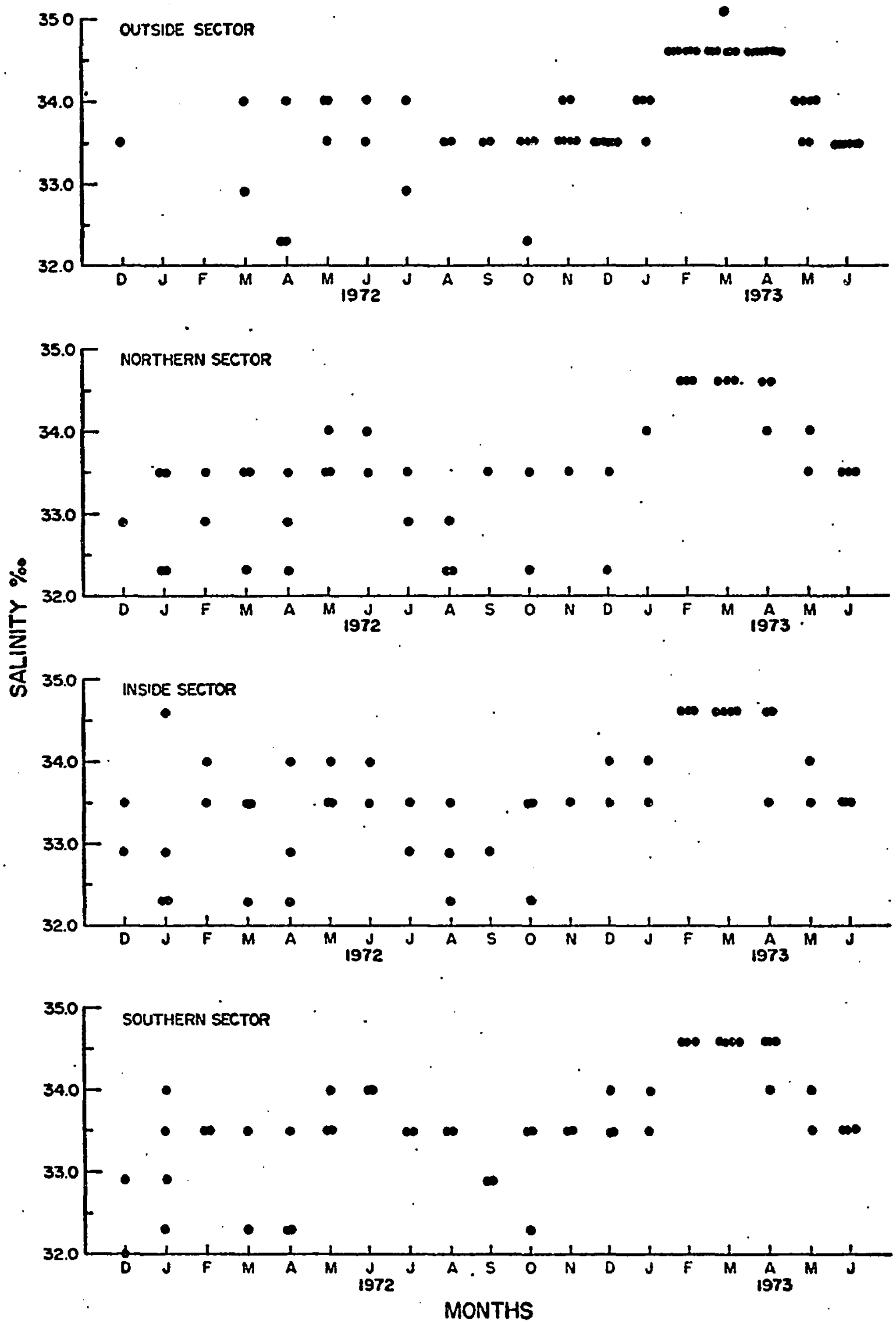

OUTSIDE SECTOR
NORTHERN SECTOR
INSIDE SECTOR
SOUTHERN SECTOR
32.0
30.0
28.0
26.0
SURFACE TEMPERATURE °C
D J F M A M J J A S O N D J F M A M J
1972
1973
MONTHS

$P < 0.01$) and to a lesser extent between sectors ($W = 0.20$, $P < 0.05$). As expected, salinity was higher during the drought in early 1973. The higher salinity and cooler temperatures observed in the outside sector most likely reflect a combination of more exchange with the oceanic water and the outside sector's greater exposure to wind and subsequent higher evaporation.

Only those months with secchi depth information in all sectors (Figure 7) were tested with the concordance test. Again, there were significant differences between months ($W = 0.68$, $P < 0.01$) and between sectors ($W = 0.61$, $P < 0.01$). The outside and northern sectors were more transparent. The range of secchi depths in the baiting area was from 8.8 m in the northern sector in January 1972 to 26.0 m in the outside sector in May 1973. This range is similar to that observed earlier in Palau, from 8 m in a semi-enclosed bay (Matsuya 1937) to 28 m in the anchorage of Malakal harbor (Motoda 1939). Fewer secchi observations were made in the outside and northern sectors because there were no receivers in these exposed sectors. With the skiff drifting, the line to the secchi disk was not vertical and so the results were not comparable.

Zooplankton abundance, as measured by settled volumes (Figure 8), varied significantly between months ($W = 0.73$, $P < 0.01$) but not between sectors ($W = 0.09$). The volumes for all four sectors were combined and the monthly means are shown in Table 3. After converting the monthly sector mean values to logarithms, regression coefficients were calculated by sector between zooplankton and secchi depth. The zooplankton abundance was negatively related to secchi depth in the

Figure 6. Salinity in the main baiting area of Palau by months and sectors. Each point represents a single measurement.



OUTSIDE SECTOR
NORTHERN SECTOR
INSIDE SECTOR
SOUTHERN SECTOR
SALINITY ‰
35.0
34.0
33.0
32.0
D J F M A M J J A S O N D J F M A M J
1972
1973
MONTHS

Figure 7. Secchi depths in the main baiting area of Palau by months and sectors. Each point represents a single measurement.

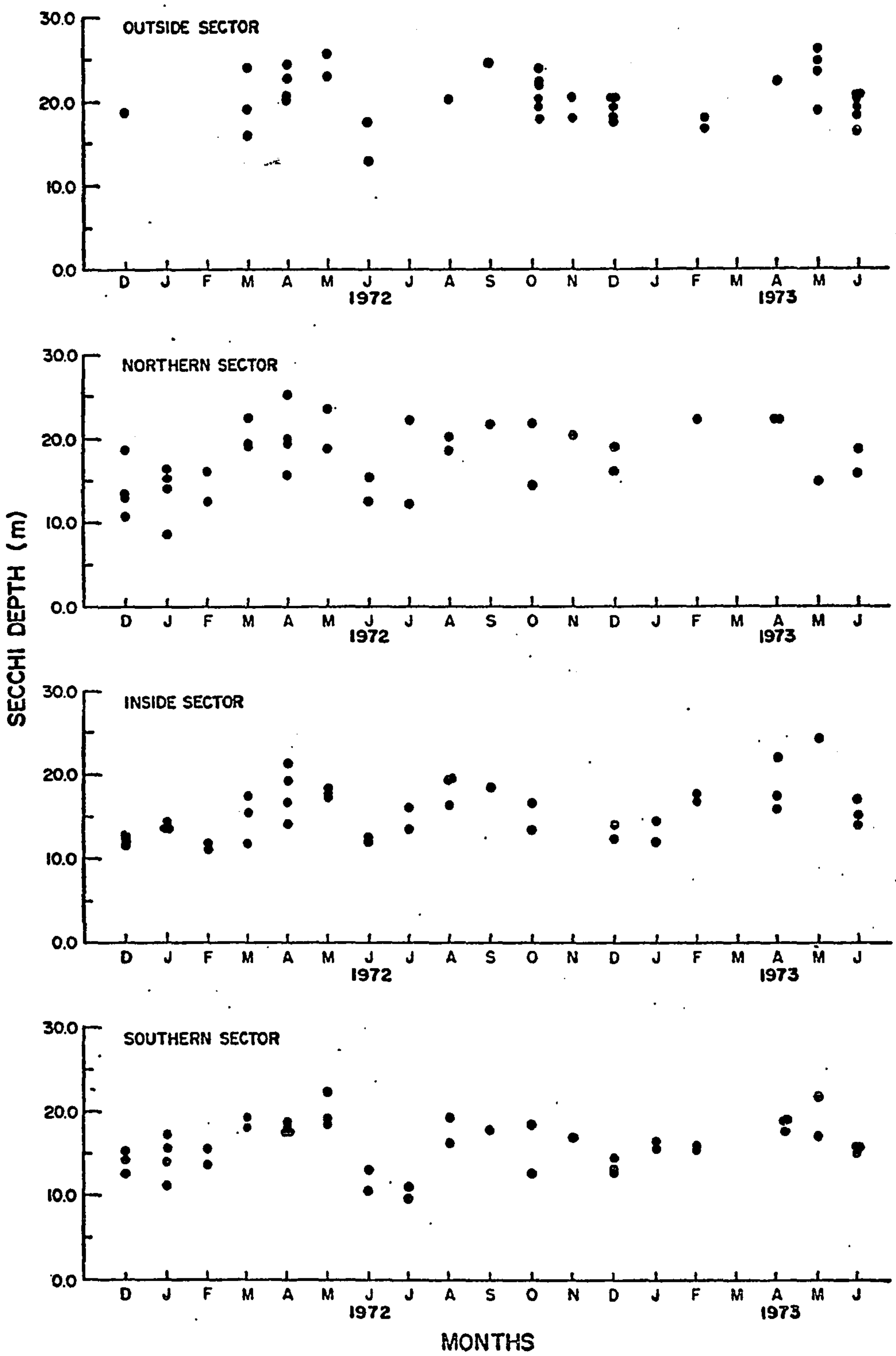
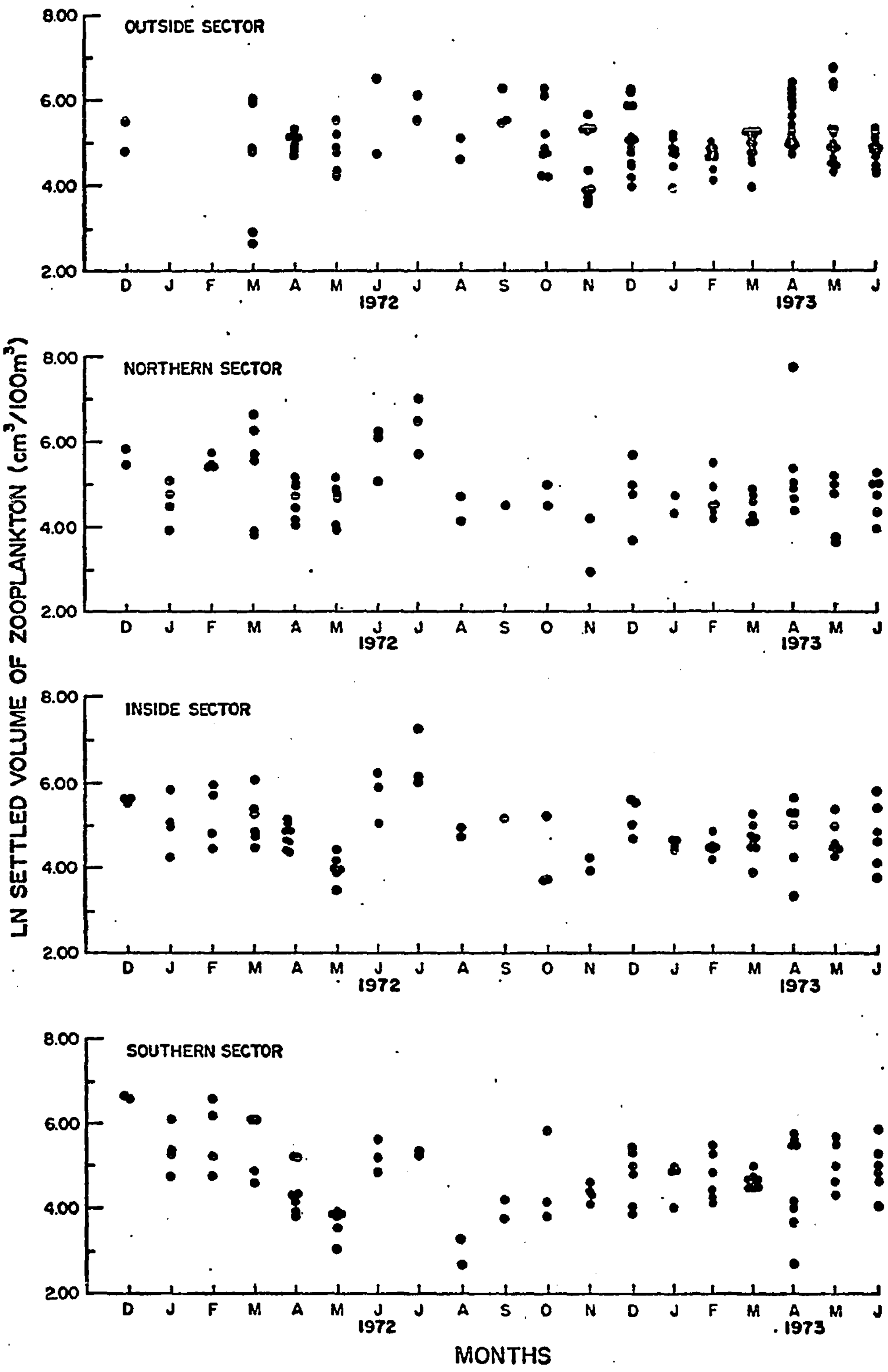

OUTSIDE SECTOR
NORTHERN SECTOR
INSIDE SECTOR
SOUTHERN SECTOR
SECCHI DEPTH (m)
30.0
20.0
10.0
0.0
D J F M A M J J A S O N D J F M A M J
1972
1973
MONTHS

Figure 8. Natural logarithms of the settled volume of zooplankton in the main baiting area of Palau by months and sectors. Each point represents a single measurement.



OUTSIDE SECTOR
NORTHERN SECTOR
INSIDE SECTOR
SOUTHERN SECTOR
8.00
6.00
4.00
2.00
D J F M A M J J A S O N D J F M A M J
1972
1973
LN SETTLED VOLUME OF ZOOPLANKTON (cm³/100m³)
MONTHS

inside and southern sectors ($t = -2.12$, $df = 15$, $P = 0.051$) and ($t = -2.32$, $df = 16$, $P = 0.034$ respectively). The negative relationship indicates that higher zooplankton volumes were caught in more turbid water. The grand mean of the settled volumes (Table 3) was 175 $cm^3/100\ m^3$ which corresponds to Tokioka's (1942) grand mean of 168 $cm^3/100\ m^3$ for the Malakal anchorage.

Zooplankton standing crop has often been expressed as displacement wet volumes. The displacement wet volume from 25 randomly selected tows were measured by filtering the contents of the tows through a 64 μ mesh net, 10 cm in diameter. Afterwards, the material on the filter was added to 10.0 ml of water in a 50 ml graduate and the new volume recorded. The zooplankton volumes, Z, were again standardized to $cm^3/100\ m^3$ sea water with the total volume of water sampled during the tow as measured by the flowmeter. The regression of the displacement wet volume, D, on settled volume for the 25 tows was

$$D = 0.0769\ Z + 2.61$$

$$r = 0.860,\ df = 23,\ P < 0.01 \qquad (5)$$

Interstitial water most likely accounts for the differences in magnitude between these two indices of zooplankton abundance. The grand mean of 175 $cm^3/100\ m^3$ settled volume is equivalent to 16.1 $cm^3/100\ m^3$ displacement volume.

The primary productivity estimates using labeled carbon were mostly unusable due to high dark bottle counts and the frequent lack of agreement between light bottles. Krasnick (1973) reported similar results in his C^{14} work on Fanning Island. He attributed the varia-

Table 3. Monthly mean settled volume of zooplankton in $cm^3/100\ m^3$ for all sectors combined

Month	No. Observations		Mean	S.D.	CV (%)
December 1971	9		264	63	23.9
January 1972 *	12		180	121	67.2
February *	12		293	188	64.2
March	22		247	201	81.4
April	32		121	46	38.0
May	24		88	57	64.8
June	11		323	179	55.4
July	10		555	401	72.3
August	8		99	48	48.5
September	7		202	176	87.1
October	16		165	150	90.9
November	19		102	77	75.5
December	28		180	121	67.2
January 1973	18		122	45	36.9
February	30		115	47	40.9
March	36		121	41	33.9
April	37		224	170	75.9
May	34		181	168	92.8
June	30		138	76	55.1
Total	395	Grand Mean	175	134**	76.6

* no data from Outside Sector

** square root of average variance

bility to the possible interactions between suspended $CaCO_3$ particles and the incubation medium. He also mentioned variability in the counts of the inoculating ampoules. In order to roughly estimate primary productivity, I have selected those measurements for which the dark bottle counts were low, i.e. under 200 counts per minute and the light bottle counts were within 10% of each other. The primary productivity as measured by C^{14} uptake, which yields a value intermediate between gross and net productivity, ranged from 11.7 mgC m^{-3} hr^{-1} in the outside sector to 26.9 mgC m^{-3} hr^{-1} for the inside sector during the spring of 1972 (Table 4). The other location listed in Table 4, Iwayama Bay, is an enclosed bay near Koror which serves as an additional baiting ground during times of bait scarcity. These productivity estimates indicate that Palau is fairly productive and comparable to other embayments with restricted access to the open ocean such as Kaneohe Bay, with a range of 5 to 39 mgC m^{-3} hr^{-1} (Caperon et al 1971), or Manila Bay, with a range of 3 to 64 mgC m^{-3} hr^{-1} (Doty and Capurro 1961). Motoda's (1969) estimate of 80 mgC m^{-2} d^{-1} is the only literature value for the lagoon in Palau. Since these units are not directly comparable to my estimates, I have converted his value to mgC m^{-3} hr^{-1} using his extinction coefficient and by assuming that primary productivity is proportional to light intensity but is inhibited in the surface waters (Ryther 1956, Figure 5, p. 66). An 11 hour day is used because of the low incident light angle during the first and last half hours of the day. Shade adaptation by phytoplankton has been ignored because of the mixing by the semi-daily, almost 2 m, tidal range. Integrating the water column

Table 4. Primary production in mgC m^{-3} hr^{-1} as measured by C^{14} uptake at various locations in Palau.

Location	Date	Primary Production mgC m^{-3} hr^{-1}
Outside Sector	May 17, 1972	11.7
Inside Sector	May 25, 1972	26.9
South Sector	May 17, 1972	25.9
Iwayama Bay	May 4, 1972	23.1
	May 15, 1972	12.5

and solving for the surface productivity, permits me to calculate the productivity at the productivity maximum, 0.22 mgC m^{-3} hr^{-1} at 12.6 m for an extinction coefficient of 0.106 m^{-1}. Following Ryther's figure, the inhibited surface productivity was 0.10 mgC m^{-3} hr^{-1} and linearly interpreting between these two values for 2 m yields 0.12 mgC m^{-3} hr^{-1}. Motoda's value is low because he was only using diatoms to estimate productivity and disregarded the contribution of the nannoplankton.

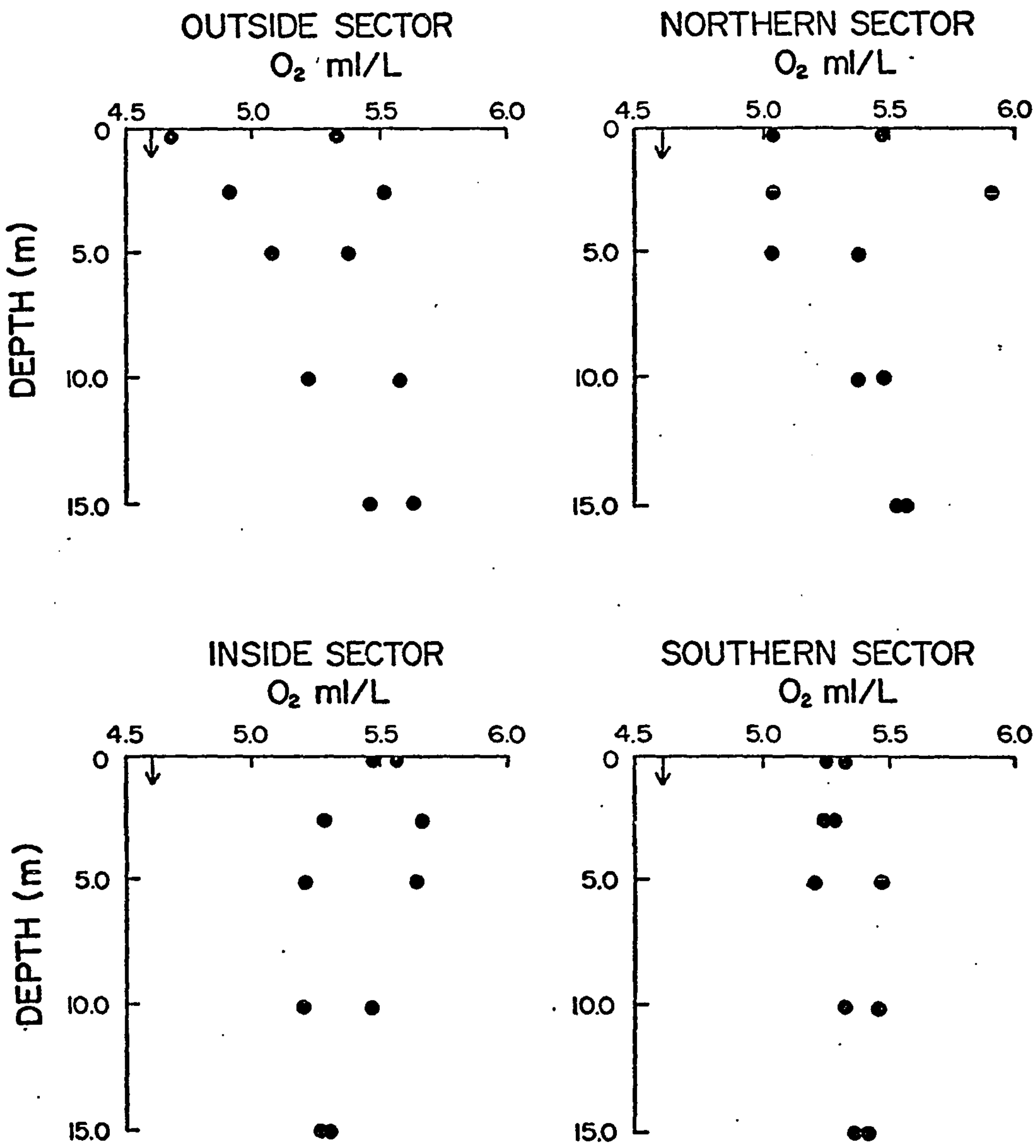
Figure 9 shows the results of two sets of oxygen determinations in May 1973 in each sector. The saturation value for sea water of 34 $^{o}/oo$ and 29^{o} was 4.62 ml/L (interpolated from Sverdrup et al 1942, Table 38, p. 188). All of the oxygen values were above the saturation value which supports the previous conclusion of high primary productivity. The maximum depth of 15 m was due to the 50 foot lead on the oxygen probe.

Habitat of *Stolephorus heterolobus*

S. heterolobus is not ubquitous in Indo-Pacific waters. It is found inshore from East Africa to Fiji and offshore in the shallow seas near Indonesia. This species has not been recorded from coral atolls nor from platform islands which lack extensive shallow water such as the Mariana Islands. It does occur in other "high" islands such as Ponape and Palau. Kearney et al (1972) reported higher catches of *S. heterolobus* and *S. devisi* in areas of New Guinea with extensive water, 12 to 25 m in depth. Lee (1973) reported higher bait catches in Fiji in areas with some freshwater flow.

The common denominator in the areas from which *S. heterolobus* has

Figure 9. Dissolved oxygen concentrations in the upper 15 meters in the main baiting area of Palau by sectors. The arrow indicates the saturation concentration.


OUTSIDE SECTOR
O2 ml/L
NORTHERN SECTOR
O2 ml/L
INSIDE SECTOR
O2 ml/L
SOUTHERN SECTOR
O2 ml/L
4.5
5.0
5.5
6.0
DEPTH (m)
0
5.0
10.0
15.0

been reported is high productivity, as defined here as over 2 mgC m^{-3} hr^{-1} as measured with the C^{14} uptake method. Streams and rivers were present in most of the areas except the Somali coast, the Gulf of Aden, and the Gulf of Oman (Anon. 1968). These three locales are influenced by upwelling during the SW monsoon season (Wyrtki 1971).

That S. heterolobus occurs inshore in regions with narrow continental shelves and offshore in the shallow seas of Indonesia is consistent with the productivity explanation. Kabonova (1961) estimated primary productivity of the coastal regions of the Arabian Sea as from 50 to 120 mgC^{-3} d^{-1} which, if we assume again an effective day length of 11 hours, is from 4 to 11 mgC m^{-3} hr^{-1}. Offshore in the Arabian Sea, the productivity was less, from 1 to 3 mgC m^{-3} hr^{-1}. Doty and Capurro (1961) measured primary productivity in the Java Sea, 4.8 mgC m^{-3} hr^{-1}, and in the Straits of Malacca, 6.2 mgC m^{-3} hr^{-1}. These offshore values are similar to the other inshore areas.

The productivity theory also explains why S. heterolobus is found in high islands with lagoons but not in either coral atolls nor platform islands without lagoons. Babelthuap in Palau District and Ponape in Ponape District have sufficient land area to form rivers which transport significant quantities of nutrients into the lagoons. Coral atolls, lacking sufficient land area to collect rainfall and form streams, must rely upon in situ recycling of nutrients. Doty and Capurro (1961) reported primary productivity values for Eniwetok lagoon, 0.75 mgC m^{-3} hr^{-1}, and for Rongelap lagoon, 0.44 mgC m^{-3} hr^{-1}. Gordon et al (1971) reported an exceptionally high value for Fanning's lagoon, 9.3 mgC m^{-3} hr^{-1}, but this value was discounted by Krasnick

(1973) because of a possible C^{14} exchange between suspended $CaCO_3$ particles and the incubation medium. Truk, although having high islands, has such an extensive lagoon that the terrestial contribution of nutrients to the lagoon is negligible except in specific localities. Fishing interests have sought unsuccessfully for the past fifty years to find populations of S. heterolobus in Truk's lagoon (Wilson 1971). Platform islands or pinnacles, such as Guam or Sonsorol, lack lagoons or shallow embayments and their streams, if present, carry nutrients from the land to the sea where the nutrients are quickly diluted and carried away down-current.

Life History Parameters

Growth

Figure 10 contains the monthly length frequencies and the fitted normal distributions for S. heterolobus. All of the samples obtained during each month were combined after the larger samples were down-weighted to minimize their potential for biasing the length frequencies (Howard and Landa 1958).

Successive months were compared for modal progressions, for example the mode at 35 mm in January 1972 was linked to the mode at 42 mm in February 1972. Figure 11 is a composite growth curve derived from the pairs of successive modes and scaled on the smallest observed modes. The scaling procedure utilized the time lag of two months which was observed between the pulse of eggs in the sector tows and the appearance of larvae, 25 to 33 mm SL, in the bait catches. Modes in this smallest size range were placed on the graph at two months and their linked modes were placed at three months. Similarly, additional modes in the size range of three month old fish were added and their linked modes were placed at four months. This process was repeated until all the links of modes were positioned. Differences in feeding, reproduction, individual variations, and low numbers of larger fish tended to merge the cohorts in later ages, and so the pair of points over a year old were arbitrarily located.

These data were summarized by fitting a von Bertanlanffy growth model whose general form is

$$l_t = L\infty(1 - \exp\ (K\ (t - t_o))) \tag{6}$$

where $L\infty$ is the asymptotic standard length, l_t is the standard length at age t, K is the intrinsic growth rate, and t_o is the intercept with the abscissa or that age with length zero. By using a mean hatching size of 2.0 mm to tie the curve to a time scale, the equation for S. heterobus in Palau is

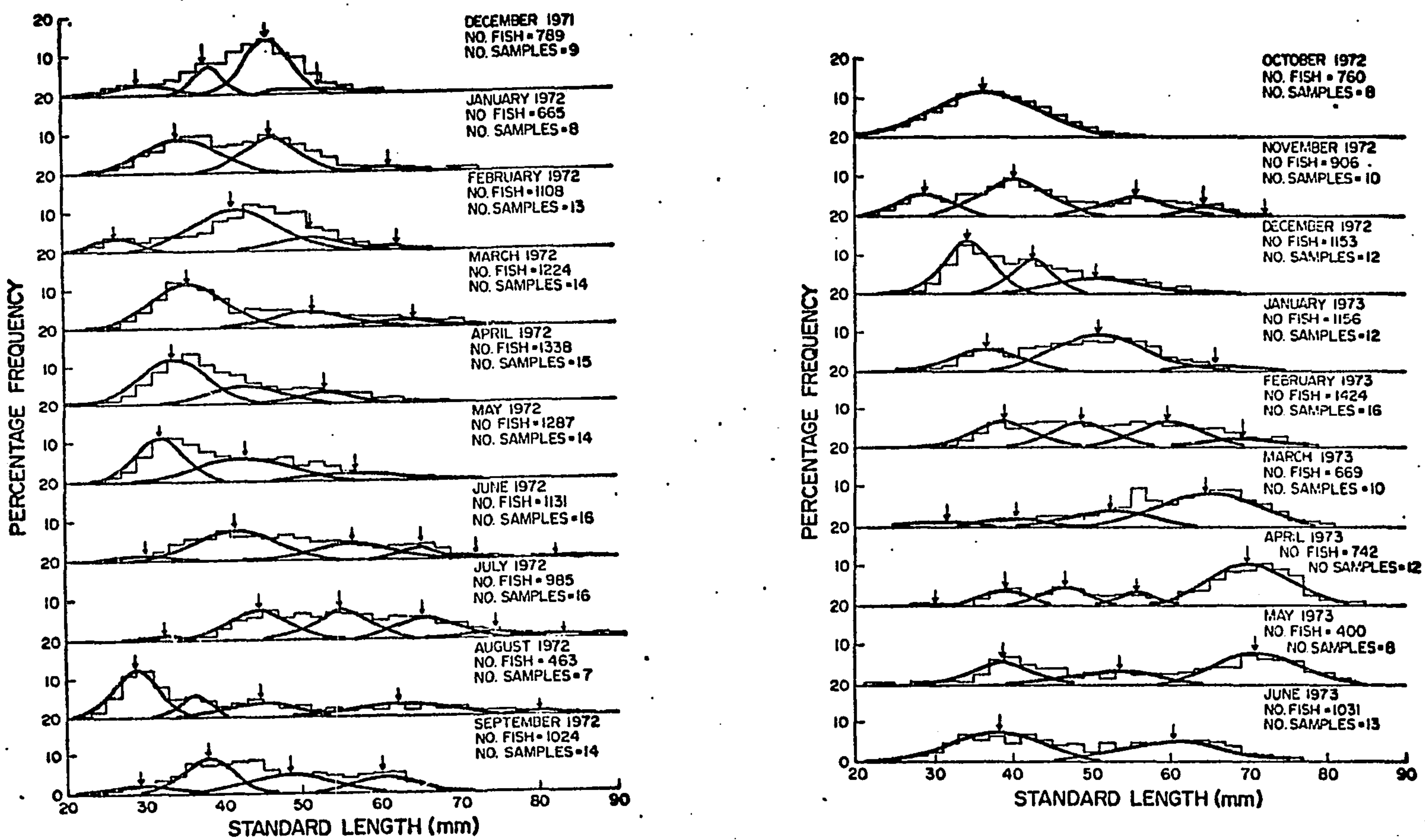
$$l_t = 91.1(1 - \exp(-0.174(t + 0.150))) \tag{7}$$

The curve is included in Figure 11.

As an independent check on the growth estimates derived from length frequencies, direct estimates of age were determined by counts of the daily rings on the otoliths. These estimates are indicated in Figure 11 as triangles. The agreement between these two methods for the smaller sizes is satisfactory but the otolith data suggest that the $L\infty$ value of 91 mm SL is perhaps a little high. However, one specimen of S. heterolobus collected during the study was 93 mm SL and six others were over 90 mm SL; 40,000 fish were examined.

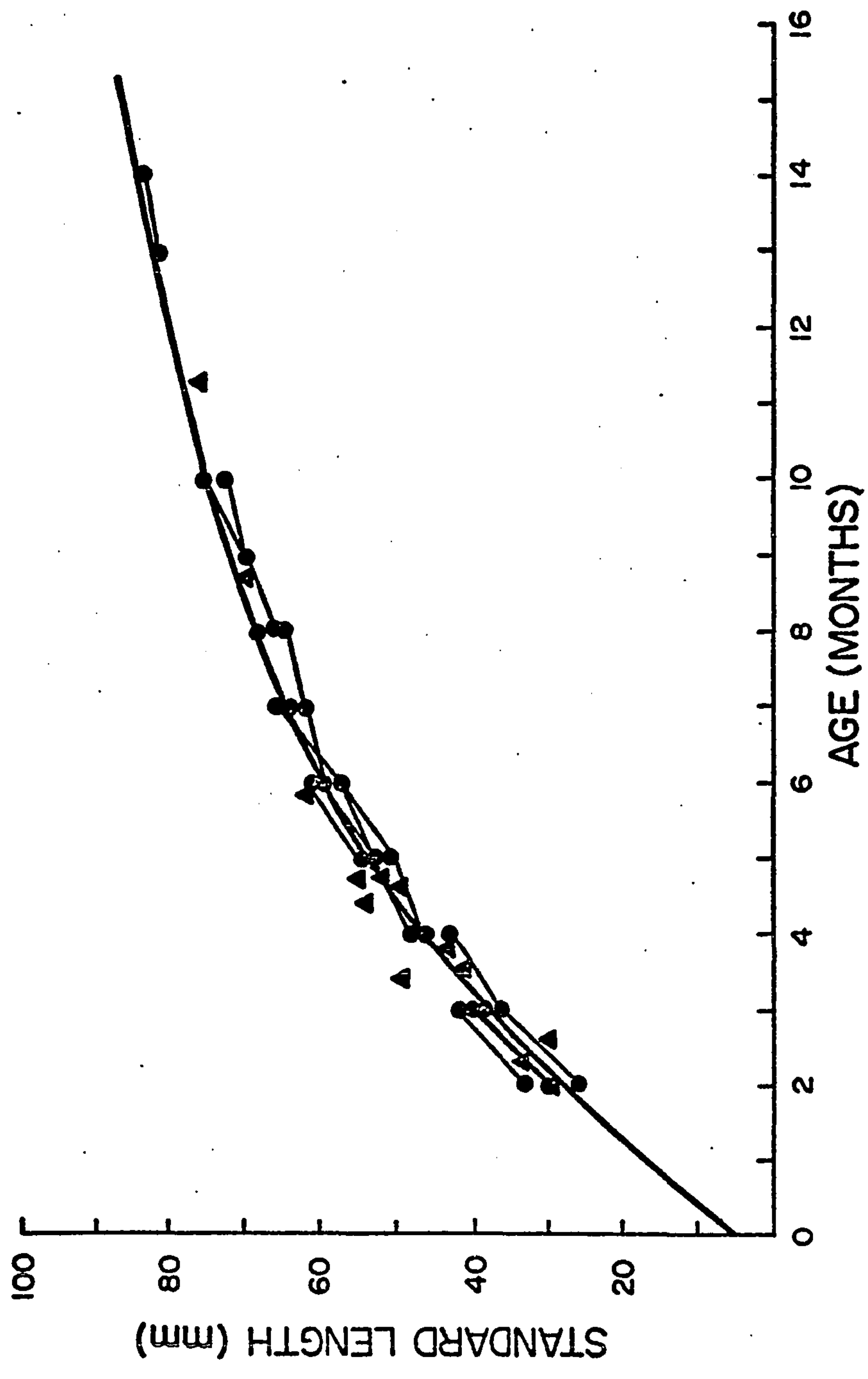
Tham (1966, 1969) determined a similar von Bertanlanffy equation

Figure 10. Histograms of monthly length frequencies of _S. heterolobus_ in 2 mm increments. Superimposed on the histograms are the normal curves for the modes identified by NORMSEP. The total number of fish and the number of samples are also included.



DECEMBER 1971
NO. FISH = 789
NO. SAMPLES = 9
JANUARY 1972
NO FISH = 665
NO. SAMPLES = 8
FEBRUARY 1972
NO. FISH = 1108
NO. SAMPLES = 13
MARCH 1972
NO. FISH = 1224
NO. SAMPLES = 14
APRIL 1972
NO. FISH = 1338
NO. SAMPLES = 15
MAY 1972
NO FISH = 1287
NO. SAMPLES = 14
JUNE 1972
NO. FISH = 1131
NO. SAMPLES = 16
JULY 1972
NO. FISH = 985
NO. SAMPLES = 16
AUGUST 1972
NO. FISH = 463
NO. SAMPLES = 7
SEPTEMBER 1972
NO. FISH = 1024
NO. SAMPLES = 14
PERCENTAGE FREQUENCY
STANDARD LENGTH (mm)
OCTOBER 1972
NO. FISH = 760
NO. SAMPLES = 8
NOVEMBER 1972
NO FISH = 906
NO. SAMPLES = 10
DECEMBER 1972
NO FISH = 1153
NO. SAMPLES = 12
JANUARY 1973
NO FISH = 1156
NO. SAMPLES = 12
FEBRUARY 1973
NO FISH = 1424
NO SAMPLES = 16
MARCH 1973
NO. FISH = 669
NO. SAMPLES = 10
APRIL 1973
NO FISH = 742
NO SAMPLES = 12
MAY 1973
NO. FISH = 400
NO SAMPLES = 8
JUNE 1973
NO. FISH = 1031
NO. SAMPLES = 13
PERCENTAGE FREQUENCY
STANDARD LENGTH (mm)

Figure 11. A composite plot of the linked pairs of modes, ●—●, scaled on the smallest mode and of otolith counts, ▲ . The fitted von Bertalanffy growth curve is also included in the figure.



STANDARD LENGTH (mm)
100
80
60
40
20
0
2
4
6
8
10
12
14
16
AGE (MONTHS)

for the growth of S. heterolobus in the Singapore Straits

$$l_t = 89\ (1 - \exp(-0.17(t + 0.53))) \qquad (8)$$

as before l_t is the length of a fish at age t in months. The only other estimate of the growth of S. heterolobus was Tiews et al's (1970) linear growth model with a growth rate of 30 mm per year TL. These authors recognized that their estimate was only a rough approximation.

Length and Weight Relationship

In later analyses, it will be necessary to calculate biomass for different sized or aged fish. Log-log regressions of weight on length were calculated for adult males, adult females, and larvae (<39 mm SL). An analysis of covariance (Snedecor and Cochran 1967) of the log transformed data revealed no significant differences between the sexes in variance ($F = 1.31$, $df = 47,45$, $P = 0.184$), slopes ($F = -0.82$, $df = 1,92$, $P = 0.368$), nor in elevations ($F = -2.09$, $df = 1,93$, $P = 0.152$). Since there were no differences between the sexes, a new regression for adult S. heterolobus was calculated after pooling the data for both sexes plus 25 fish which were measured and weighed but not sexed. The equation for calculating weight from length was

$$W_a = 7.61 \times 10^{-6}\ L_a^{3.09} \qquad (9)$$

$$(r^2 = 0.987,\ df = 119)$$

where W_a is the mass of an adult fish in grams and L_a is the standard length in millimeters.

Larval Stolephorus are elongate and do not resemble the adult fish. The regression for larvae was

$$W_1 = 9.54 \times 10^{-8} L_1^{4.27} \tag{10}$$

$$(r^2 = 0.982, \ df = 61)$$

where W_1 is the mass of a larval fish in grams and L_1 is the standard length in millimeters.

Tham (1966) published a length-weight equation for S. heterolobus in the Singapore Straits of

$$W = 3.717 \times 10^{-3} L^{3.594} \tag{11}$$

where W is, as before, the mass in grams but L is measured in centimeters. Tham did not specify if larval fish were included in his equation.

Sex Ratio

The sex ratio for S. heterolobus was determined by randomly selecting 10 to 15 fish from each of 21 samples. All together, 322 fish were sexed. The numbers of male and female fish in each sample were not significantly different (paired $t = 1.38$, $df = 20$, $P = 0.183$). Consequently, subsequent analyses will use a 1:1 ratio.

Fecundity

Table 5 contains the ovarian observations on S. heterolobus in Palau. The gonad development index, I, was the percentage of gonad weight to body weight (Vladykov 1956). This index ranged from 0.40 in an immature fish to 11.13 in a ripe fish. The size distribution of ovarian eggs was from unimodal to trimodal depending upon the state of gonadal development. Fish with low values of I, <1.4, were either immature or spent. Immature fish had a single mode of maturing eggs and spent fish had either a single mode of maturing eggs, e.g. the 87.5 mm specimen, or two modes with only a few mature eggs in the larger sized mode which were believed to be eggs which failed to hydrate, e.g. the 57.2 and 66.9 mm specimens. Fish gonad indices between 1.4 and 9.9 were designated as mature fish. These fish contained two modal sizes of elliptical ovarian eggs with the number of mature eggs being significantly less than the number of immature eggs (paired $t = 2.30$, $df = 12$, $P = 0.040$). The difference averaged 11.3%. Ripe fish, $I > 9.9$, contained three sizes of eggs with the third mode comprised of hydrated eggs. The observed hydrated eggs still were covered by the thick granulosa which is shed just prior to extrusion. One specimen, $I = 7.06$, was apparently captured in the process of hydration such that its eggs were intermediate in size between mature and hydrated egg sizes.

Fecundity can be expressed as either the absolute fecundity which is the number of mature eggs prior to spawning or as the relative fecundity which is the number of mature eggs per gram of body weight (Bagenal 1973). Table 6 contains a summary of the 10 fish whose eggs were enumerated. The 87.5 specimen had only a single mode of maturing eggs and was, therefore, not included in the regressions. The absolute fecundity was determined with a regression on mature egg number, F, on body weight, W, (Figure 12).

$$F = 457\ W + 2.70 \qquad (12)$$

$$r^2 = 0.918,\ df = 7$$

The absolute fecundity was also determined with a log-log regression on standard length in millimeters, L

Table 5. Standard length; body weight; gonad weight; percent gonad weight to body weight, I; and ovarian egg measurements from the left ovary of randomly selected S. heterolobus larger than 50 mm. A - Mean major axis length of immature eggs; B - Mean major axis length of mature eggs; and C - Mean major axis length of hydrated eggs.

Fish length mm	Body weight g	Gonad weight g	I %	Subsample No. eggs	A Mean length mm	S.D. mm	Subsample No. eggs	B Mean length mm	S.D. mm	Subsample No. eggs	C Mean length mm	S.D. mm
55.2	1.543	0.008	0.49	122	0.227	0.060						
57.4	2.084	0.008	0.40	115	0.221	0.045						
64.4	2.835	0.019	0.68	94	0.259	0.038						
87.5	7.495	0.097	1.29	153	0.313	0.066						
54.6	1.696	0.050	2.95	118	0.319	0.043	108	0.543	0.063			
56.4	1.849	0.033	1.78	60	0.310	0.058	54	0.542	0.032			
56.4	2.075	0.094	4.53	157	0.319	0.053	110	0.605	0.037			
57.2	1.999	0.012	0.60	92	0.289	0.060	7	0.503	0.026			
58.5	2.087	0.096	4.60	96	0.274	0.045	76	0.489	0.026			
59.9	2.281	0.036	1.58	92	0.316	0.062	68	0.557	0.042			
61.3	2.524	0.080	3.16	114	0.321	0.060	92	0.578	0.054			
62.1	2.224	0.055	2.46	178	0.278	0.059	167	0.561	0.044			
66.9	2.969	0.036	1.21	257	0.294	0.058	50	0.529	0.040			
69.0	3.780	0.165	4.37	87	0.265	0.044	105	0.504	0.033			
69.1	3.485	0.246	7.06	85	0.441	0.077	67	0.859	0.054			
69.3	3.092	0.066	2.13	107	0.299	0.059	83	0.518	0.042			
75.1	4.824	0.181	3.75	124	0.320	0.045	149	0.589	0.052			
77.9	4.843	0.066	1.36	219	0.317	0.064	61	0.499	0.038			
83.1	6.665	0.191	2.87	117	0.323	0.055	93	0.535	0.045			
84.0	6.496	0.160	2.46	75	0.358	0.049	79	0.528	0.037			
62.2	2.578	0.287	11.13	142	0.276	0.054	92	0.485	0.044	154	1.099	0.087
72.8	4.514	0.448	9.92	129	0.296	0.064	66	0.501	0.048	59	1.059	0.054
				2733	0.300	0.057	1527	0.555	0.045	213	1.088	0.079

$$F = 9.10 \times 10^{-4} L^{3.39} \tag{13}$$

$$r^2 = 0.856, \ df = 7$$

Thus, a 60 mm SL fish, weighing about 2.4 grams, would have approximately 1000 mature eggs.

The average relative fecundity of S. heterolobus was 450 eggs per gram body weight (Table 6). Table 7 lists the relative fecundity of some other species of engraulids. Tham's (1970) single estimate of fecundity is within one standard deviation of my estimate. The mean for S. heterolobus does not differ significantly from Leary et al's (1975) estimate for the relative fecundity of S. purpureus in Hawaii but the variance associated with their estimate was significantly greater ($F = 3.50$, $df = 40,8$, $P = 0.033$).

Evidence that an individual S. heterolobus in Palau possibly spawns more than once a year came from a variety of sources. First, the ovaries of S. heterolobus contained eggs in several stages of development: spherical eggs which were not included in the counts because of the difficulty in distinguishing these cells from the follicular cells; small, elliptical eggs which were transparent; larger elliptical eggs which were translucent; and hydrated eggs which were almost opaque. The differences in transparency resulted from the increasing thickness of the granulosa layer surrounding the ripening eggs (Polder 1961). Because of the difference in transparency, a small, mature egg can be distinguished from a large, immature egg. The underlying assumption is that each mode constitutes a single spawn. The 57.2 mm SL fish with just seven mature eggs in her left ovary and no mature eggs in her right ovary supports this assumption.

The second source of evidence for multiple spawning by an indivi-

Table 6. Standard length, body weight, number of mature eggs in both ovaries, and the number of mature eggs per gram of body weight of 10 randomly selected S. heterolobus.

Length mm	Weight g	Mature eggs	Mature eggs/gram
54.6	1.696	569	335
56.4	2.075	975	470
58.5	2.087	903	433
69.0	3.780	2014	533
69.1	3.485	1834	526
69.3	3.092	1083	350
75.1	4.824	2660	551
83.1	6.665	3020	453
84.0	6.496	2587	398
87.5	7.495	--	-
			450 $\pm$ 156

Figure 12. Number of mature eggs in both ovaries, F, of S. heterolobus on body weight, W: $F = 457\ W + 2.70$.

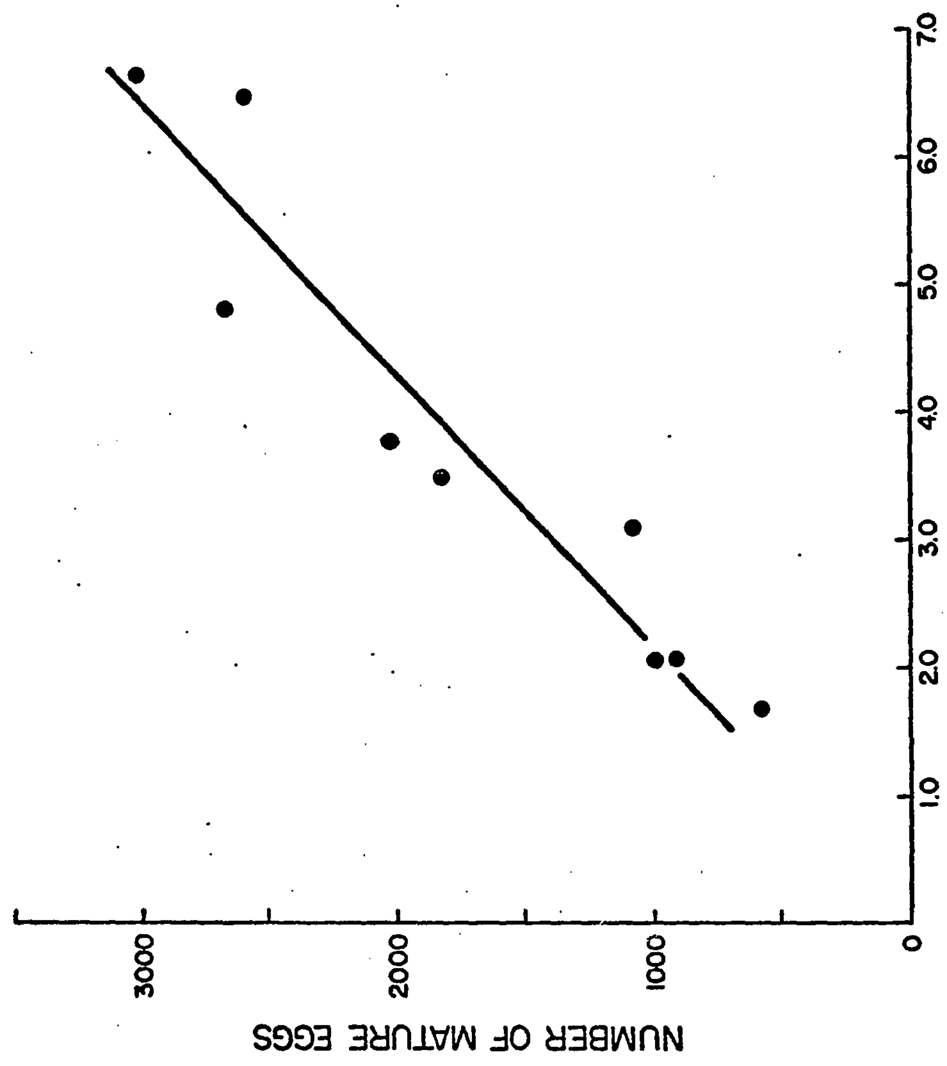

NUMBER OF MATURE EGGS
3000
2000
1000
0
BODY WEIGHT (G)
1.0
2.0
3.0
4.0
5.0
6.0
7.0

Table 7. Comparison of mean relative fecundity in eggs per gram body weight for various Pacific anchovies. The source, number and standard deviations are included in the table.

Species	Relative fecundity Mean No. eggs/gram	S.D.*	No. Fish	Source
Anchoa naso	860	327	12	Joseph 1963
Centengraulis mysticetus	836	251	86	Peterson 1961
Engraulis mordax	574	131	19	MacGregor 1968
Engraulis ringens	651	203	82	Minano 1968
Stolephorus heterolobus	570	-	1	Tham 1970
	450	156	9	Muller this study
Stolephorus purpureus	538	292	41	Leary et al 1975

* Standard deviations were calculated from the authors' data.

dual was the lack of correlation between body size and gonadal development in fish longer than 50 mm SL ($r = 0.059$, $df = 64$). Additional fish to those included in Table 5 (p.58) were measured and weighed and their gonads excised and weighed. There was an increase in gonadal development as the fish grows after metamorphosing at about 40 mm until they reach the size of first reproduction at about 50 mm. This lack of correlation in fish above 50 mm suggests that the presence of mature eggs in the ovaries of larger fish depends less upon size than upon other factors such as when they last spawned. The smallest fish observed during the study having mature eggs was 51.7 mm SL. Four fish, ranging in size from 55.2 to 87.5 mm SL, contained only maturing eggs (Table 5) which suggests either that these fish had never matured or that they had recently spawned. Leary et al (1975) concluded that large S. purpureus in Hawaii, which contained a single mode of maturing eggs, had continued to grow but that they had failed to reproduce due to some unidentified environmental factor. For S. heterolobus in Palau, I think a simpler interpretation for those fish which are above the size of first reproduction yet contain only a single mode of maturing eggs is that they have spawned recently and were captured when they were between spawnings. Evidence of this was given earlier with the 57.2 mm fish which contained only seven mature eggs which were most likely left over from an earlier spawn and have not yet resorbed. Raja (1966) noticed that spent Sardinella longiceps usually contained only a single mode of small eggs but frequently he found a few larger eggs, about 0.47 mm, which apparently did not hydrate.

The third line of evidence for multiple spawning was the greater number of maturing eggs than mature eggs. This finding is consistent with the assumption that S. heterolobus continues to grow throughout its life and since fecundity is linearly related to biomass, more eggs should be released later when the fish is larger. Spent fish or fish with hydrated eggs were not included in this analysis because the number of mature eggs present may not necessarily represent the number of mature eggs prior to spawning due to the possibility of an unknown portion of the eggs having been extruded.

The last line of evidence for multiple spawning was the slope of a regression of the mean size of the maturing eggs on the mean size of the mature eggs (Table 5) being significant and positive ($b = 0.402$, $t = 6.66$, $df = 17$, $P = 0.000$). The positive slope implies that the mean egg size in both groups is progressing as the eggs ripen. The one fish with intermediate sized eggs contributed heavily to this relationship such that the omission of this fish reduced the significance ($t = 2.11$, $df = 16$, $P = 0.051$). Since there was some doubt, the information from the right ovaries which had been examined was included and with this additional information, the slope was again significantly positive ($b = 0.406$, $t = 4.22$, $df = 22$, $P = 0.000$).

Clark (1934) used the first and last lines of evidence plus the presence of a few larger eggs together with the secondary mode to support her conclusion that Sardinops caerula spawns more than once. Naumov (1954) cited polymodality of egg sized as evidence of multiple spawning in Clupea harengula. Leary et al (1975) rejected multiple spawning in Stolephorus purpureus because the mean egg size of the immature eggs did not increase as the mature eggs developed. Tham

(1970) reported that, based upon length frequency data and Delsman's (1931) spawning data, S. heterolobus spawns throughout the year at intervals of from one to two months. Figure 13 illustrates a possible pattern of gonadal development in S. heterolobus.

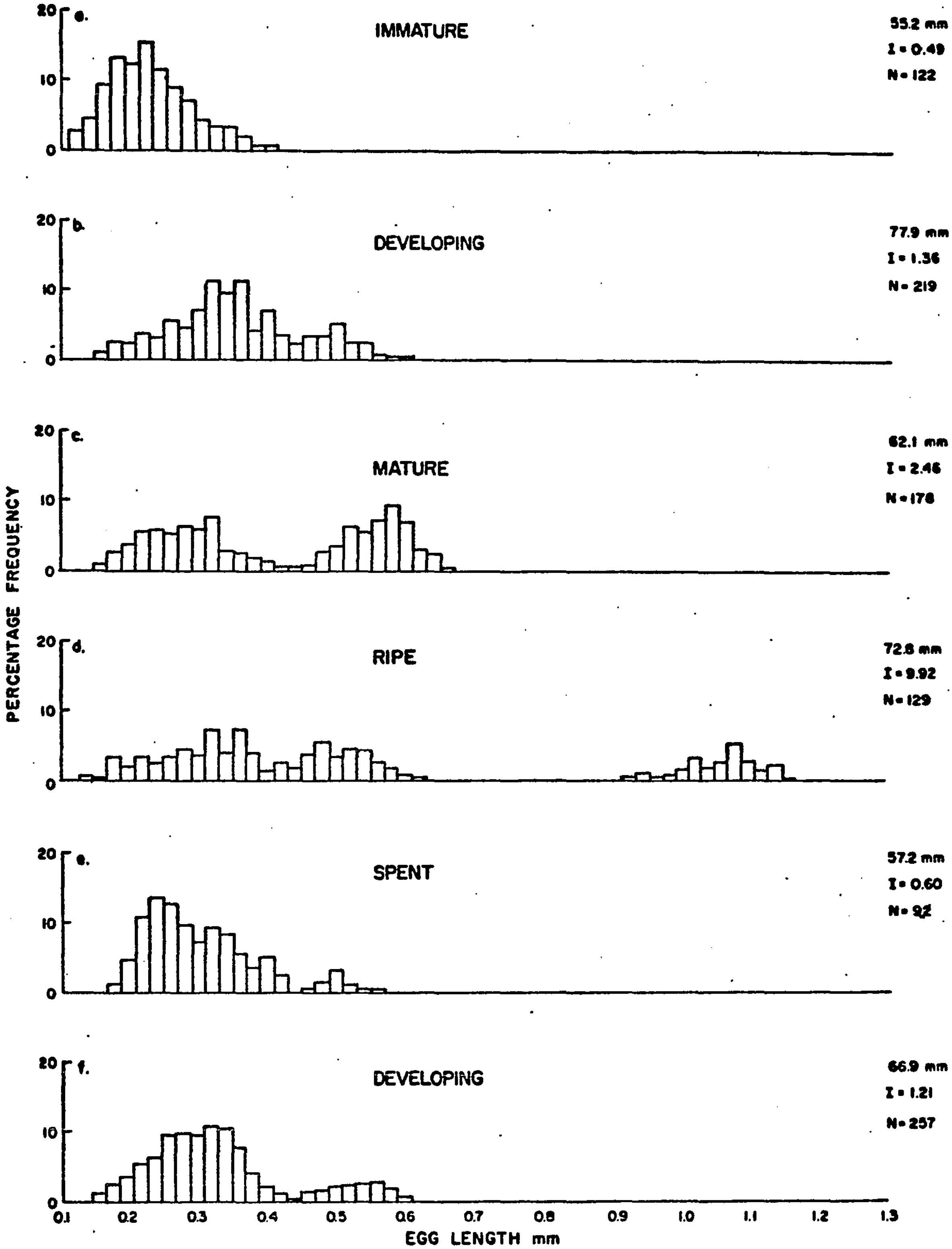
Spawning

The eggs of S. heterolobus in Palau were pelagic,ellipsoidal, and lacked an oil droplet. The mean major axis length for 550 eggs from the tows was 1.17 ± 0.020 mm for the minor axis. The precision term is one standard deviation. Thus, the hydrated eggs in the previous section had not yet attained their full size in the ovary. Figure 14 is a frequency histogram in ocular micrometer units, one division equals 0.0256 mm.

The counts of S. heterolobus eggs in the paired surface tows were highly variable. On July 14, 1972, no eggs were collected from any of the sectors and on June 13, 1973, the mean egg count for all sectors was 1816 eggs/100 m^3. The standard errors of the monthly means were strongly correlated to their means ($r = 0.91$, $df = 17$, $P < 0.01$). After transforming the egg counts to logarithms, the correlation was no longer significant ($r = 0.41$, $df = 17$). The actual transform was $\ln (x + 1)$ where x was the standardized egg count and the one accounted for the tows with no eggs (Barnes 1952, Tester 1955). All of the subsequent analyses of spawning used transformed counts.

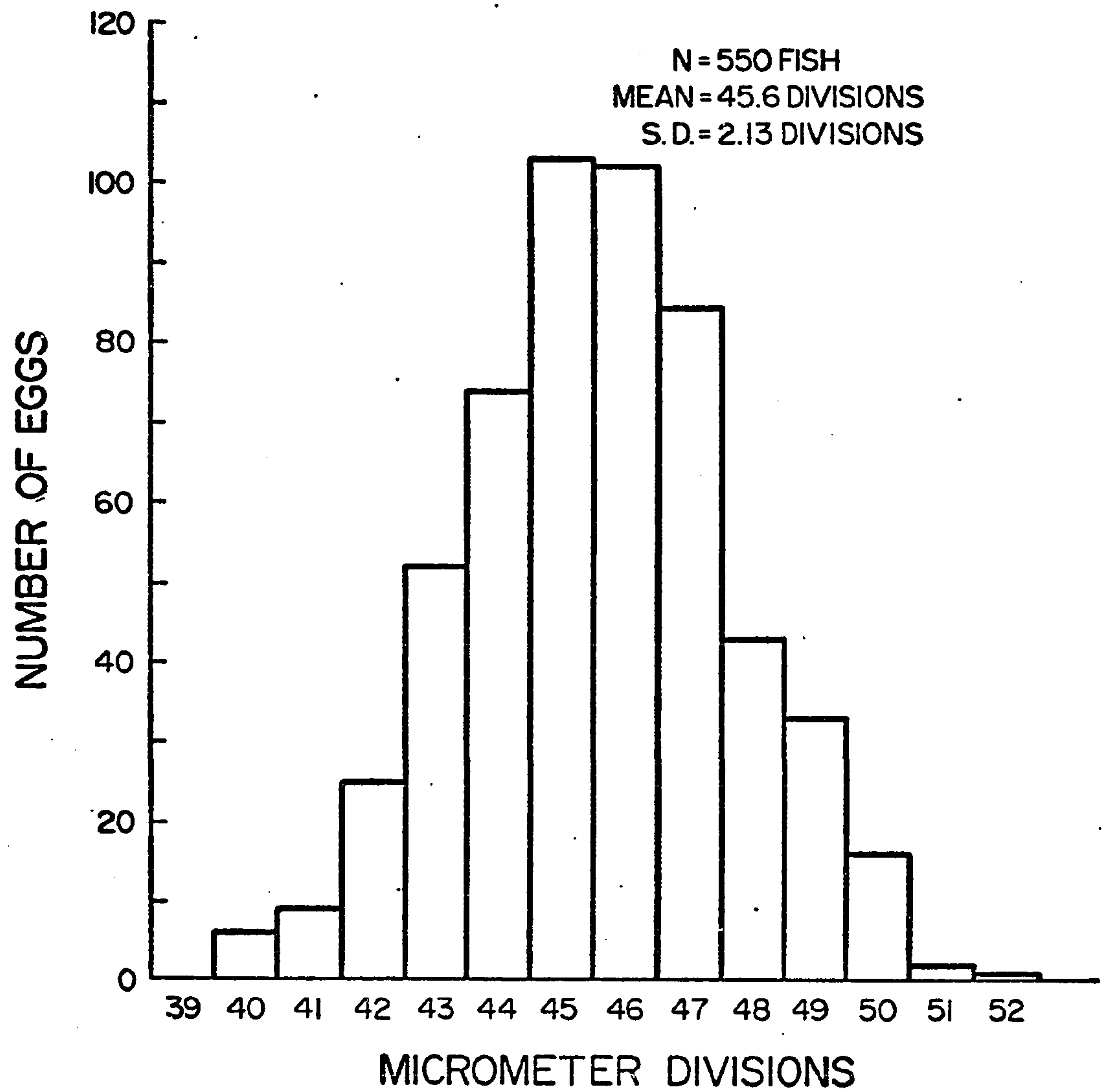
Tables 8 and 9 contain the egg counts by sector and date for the 34 dates on which all four sectors were sampled the same day. These dates were selected to facilitate inter-sector comparisons. The egg

Figure 13. Size distribution of ovarian eggs from six specimens of *Stolephorus heterolobus* selected over a range of I values to demonstrate a possible sequence of development. N is the number of eggs in the left ovary.



a.
IMMATURE
55.2 mm
I = 0.49
N = 122
b.
DEVELOPING
77.9 mm
I = 1.36
N = 219
c.
MATURE
62.1 mm
I = 2.46
N = 178
d.
RIPE
72.8 mm
I = 9.92
N = 129
e.
SPENT
57.2 mm
I = 0.60
N = 92
f.
DEVELOPING
66.9 mm
I = 1.21
N = 257
PERCENTAGE FREQUENCY
EGG LENGTH mm

Figure 14. Frequency histogram of the major axis length, in micrometer divisions, of S. heterolobus eggs which were caught in surface tows. One micrometer division equals 0.0256 mm.



N = 550 FISH
MEAN = 45.6 DIVISIONS
S. D. = 2.13 DIVISIONS
NUMBER OF EGGS
120
100
80
60
40
20
0
39
40
41
42
43
44
45
46
47
48
49
50
51
52
MICROMETER DIVISIONS

Table 8. Standardized egg counts per 100 m^3 for the 18 dates in 1972 on which all four sectors were sampled the same day.

Date	Outside	North	Inside	South
16 Mar	17.8	1.4	2.1	20.9
	19.8	0.0	8.3	32.3
23 Mar	158	1.9	62.7	0.0
	170	9.8	40.6	0.0
10 Apr	0.0	0.0	0.0	2.3
	0.0	0.0	0.0	0.0
18 Apr	3.4	0.0	11.0	0.0
	0.0	0.0	21.2	0.0
28 Apr	33.2	0.0	0.0	1.8
	25.8	0.0	0.0	4.2
9 May	0.0	3.6	0.0	0.0
	0.0	15.6	0.0	0.0
17 May	0.0	0.0	3.9	0.0
	0.0	0.0	0.0	0.0
25 May	1.8	0.0	7.5	0.0
	9.2	0.0	4.0	0.0
21 Jun	91.0	923	8.3	7.8
	91.4	809	0.0	11.8
7 Jul	0.0	88.2	0.0	0.0
	0.0	107	10.0	6.1
14 Jul	0.0	0.0	0.0	0.0
	0.0	0.0	0.0	0.0
10 Aug	137	0.0	0.0	5.7
	63.5	8.2	0.0	5.4
25 Sep	449	30.0	16.2	0.0
	425	43.8	0.0	0.0

Table 8 (continued). Standardized egg counts per 100 m^3 for the 18 dates in 1972 on which all four sectors were sampled the same day.

Date	Outside	North	Inside	South
23 Oct	0.9	0.0	0.0	0.0
	0.0	0.0	0.0	0.0
30 Oct	0.0	0.0	0.0	16.3
	0.0	0.0	0.0	10.2
7 Nov	6.6	0.0	0.0	1.9
	6.5	0.0	0.0	0.0
5 Dec	0.0	0.0	0.0	65.8
	107	0.0	0.0	34.9
14 Dec	10.9	5.2	0.0	0.0
	0.0	0.0	1.8	0.0
Geometric mean	6.0	2.3	1.3	1.6
Coefficient of variation (logs)	105%	165%	134%	133%

Table 9. Standardized egg counts per 100 m^3 for the 16 dates in 1973 on which all four sectors were sampled the same day.

Date	Outside	North	Inside	South
9 Jan	3.1	0.0	0.0	0.0
	43.8	0.0	0.0	0.0
5 Feb	201	8.3	114	20.9
	82.2	147	117	24.2
15 Feb	397	0.0	380	0.0
	40.9	0.0	117	0.0
22 Feb	536	36.7	882	163
	437	12.6	1280	173
1 Mar	935	9.9	446	2.3
	599	4.6	262	0.0
16 Mar	183	0.0	6.8	282
	10.5	0.0	0.0	287
23 Mar	176	213	34.4	1150
	208	498	53.9	368
12 Apr	11.3	0.0	34.8	3.5
	586	0.0	22.0	0.0
19 Apr	678	82.0	1400	17.7
	2240	82.2	1490	9.7
26 Apr	37.8	0.0	43.5	43.1
	253	0.0	68.1	11.3
4 May	2.2	2.9	71.6	98.8
	1.2	2.5	134	156
14 May	4.0	946	2.4	0.0
	676	688	5.1	0.0
24 May	9.2	0.0	184	0.0
	165	2.4	111	3.0

Table 9 (continued). Standardized egg counts per 100 m^3 for the 16 dates in 1973 on which all four sectors were sampled the same day.

Date	Outside	North	Inside	South
7 Jun	34.6	22.6	592	0.0
	0.0	7.7	724	2.6
13 Jun	3760	1530	4030	8.1
	191	1500	3480	31.0
29 Jun	14.6	0.0	0.0	0.0
	40.2	2.5	0.0	0.0
Geometric mean	83.0	9.9	69.9	8.8
Coefficient of variation (logs)	39.6%	106%	59.7%	99.0%

counts in 1972 were heterogenous with many zero counts. In 1973, many eggs were caught in all sectors. The significance of the spacial and temporal variation in the 34 sets of egg counts was tested with a two way analysis of variance (Table 10). The interpretation of the significant difference for sectors and dates is clouded by the significant non-additive component of the interaction term (Poole 1974). A second analysis of variance was calculated for the 16 dates in 1973 (Table 11). Again, there were significant differences between sectors and dates and while the interactive term was significant, the non-additive component was very small. The outside sector had the highest log average catch, 83 eggs/100 m^3, and the most consistency, CV = 39.6%. The inside sector had the second highest average, 70 eggs/100 m^3. In contrast to the 1973 value, the inside sector in 1972 had the lowest average catch. The low coefficient of variation for the outside sector indicates that this sector is a prime spawning area, but on 10 of the 16 dates in 1973, another sector had the highest egg count for the day. I conclude from this that the spawning stock is mobile throughout the baiting area.

Temporal variation was explored using multiple regression analysis. The dependent variable was the log mean egg count for the date and the independent variables were wind velocity, average tidal range of the three days preceeding the sampling date, the settled volume of zooplankton, average rainfall during the three days preceeding the sampling date, the spawning stock derived from a seven day period of three days before the sampling date to three days after, and the lunar phase expressed as days since the new moon.

Table 10. Two way analysis of variance for 34 dates, four sectors, and two surface tows per sector per date. The standardized egg counts per 100 m^3 have been converted to logarithms. Tukey's method was used to assess the non-additive component of the interaction. The table values were rounded off after calculation.

Source	df	S.S.	M.S.	F ratio	P
Sectors	3	100.1	33.4	44.1	<0.001
Dates	33	757.1	22.9	30.3	<0.001
Interaction	99	604.9	6.11	8.08	<0.001
Non-additive	1	35.3	35.3	6.08	0.015
Remainder	98	569.6	5.81		
Within	136	102.8	0.76		

Table 11. Two way analysis of variance for the 16 dates in 1973, four sectors, and two surface tows per sector per date. The standardized egg counts per 100 m^3 have been converted to logarithms. Tukey's method was used to assess the non-additive component of the interaction.

Source	df	S.S.	M.S.	F ratio	P
Sectors	3	129.8	43.3	43.3	<0.001
Dates	15	306.3	20.4	20.4	<0.001
Interaction	45	327.4	7.28	7.28	<0.001
Non-additive	1	0.027	0.027	0.0037	0.952
Remainder	44	327.4	7.44		
Within	64	64.0	1.00		

Salinity and settled volume of zooplankton accounted for 31% (r^2 = 0.314, df = 31) of the variation in egg counts. The importance of salinity is consonant with the consistent egg catches in the outside sector and with the higher egg catches in the inside sector in 1973 during the drought when the salinity in the inside sector was the same as for the outside sector. Delsman (1931) reported that _S. heterolobus_ spawns offshore in the Java Sea and Tham (1970) reported that _S. heterolobus_ goes offshore from Singapore during exceptionally heavy rainfall. A speculative explanation for the possible link with salinity is that unlike the eggs of its congener, _S. Species A_, the eggs of _S. heterolobus_ lack the buoyant oil droplet and hence slightly higher salinities would retard egg sinking.

The numerical value for spawning stock in the multiple regression (Table 12) was derived from the raised length frequencies, i.e., the number of fish per boat night, the length-weight relationship (Eq. 9, p. 55) and the absolute fecundity (Eq. 12, p. 57). The algorithm for this calculation was

$$S = \sum_{L=52}^{94} N_L \, (457 \, (7.61 \times 10^{-6} \, L^{3.09}) + 2.70) \qquad (14)$$

where S is the spawning stock expressed in eggs per boat night, N_L is the number of fish of standard length, L, in millimeters. The spawning stock is expressed in eggs because eggs give a numerical measure which is linear with biomass. The sum starts at the approximate size of reproduction, 52 mm, and continues to the largest fish observed during the study, 93 mm.

Spawning stock in the multiple regression did not account for a

Table 12. Monthly spawning stock expressed in eggs per boat night as calculated from monthly length frequencies, length-weight relationship, and the absolute fecundity.

Month	Spawning stock million eggs/boat night
December 1971	3.8
January 1972	12.6
February	8.8
March	11.0
April	9.1
May	13.1
June	23.1
July	26.6
August	15.5
September	7.8
October	2.3
November	10.8
December	11.1
January 1973	25.3
February	16.0
March	26.8
April	25.2
May	5.1
June	12.9

significant portion of the variability of the egg counts. As was pointed out in the growth section, the number of samples making up the length frequencies is important and for an analysis on a weekly scale, at most four samples comprised the raised length frequencies. When all of the samples from each month were used, a significant correlation ($r = 0.58$, $df = 14$, $P < 0.05$) was obtained between the log monthly mean egg count and the spawning stock for those months with more than two sets of samples. All of the sectors were grouped together because earlier it was shown that most likely the spawning stock moves throughout the baiting area.

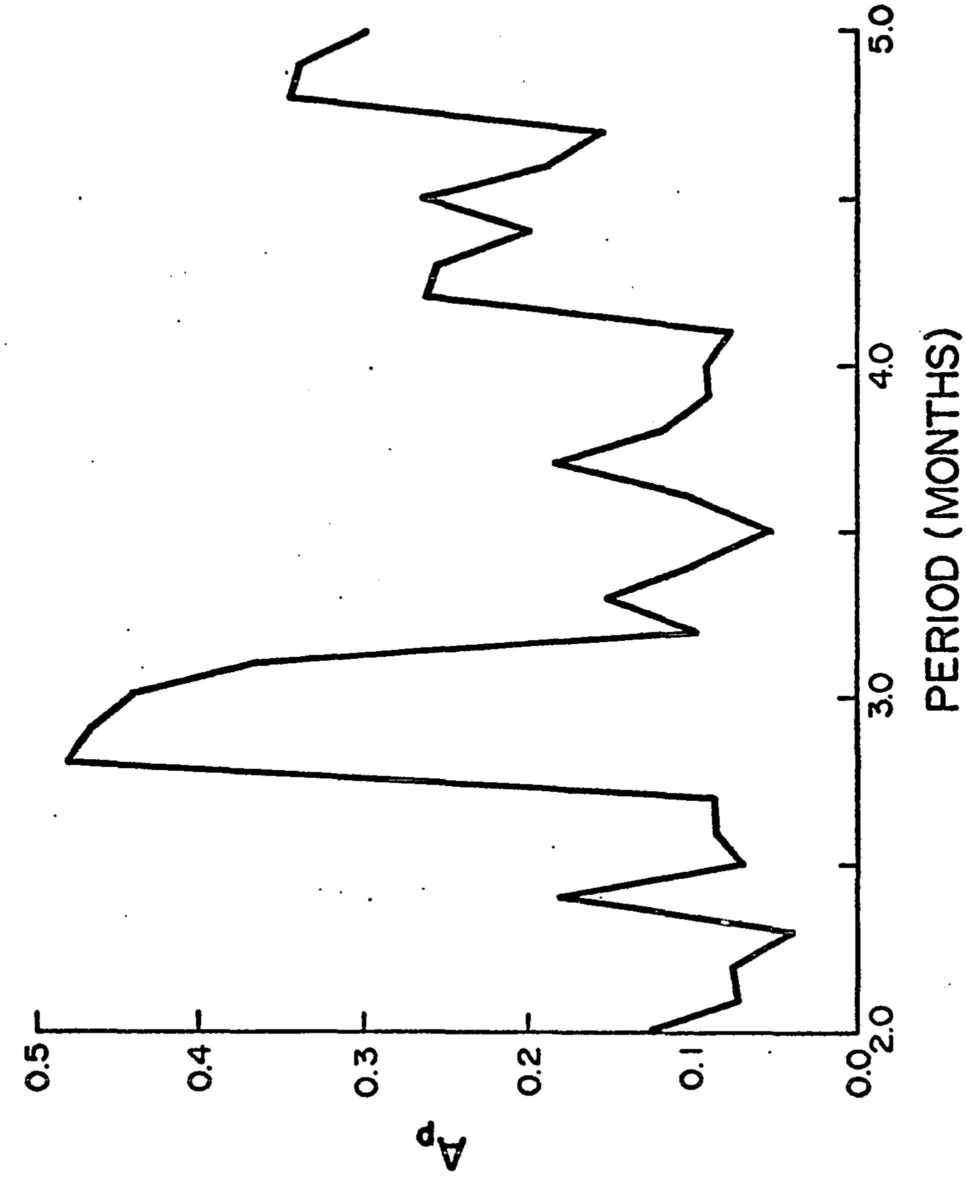
The perodicity of spawning was determined from a periodogram of the monthly log means. The peak in Figure 15 at an interpolated value of 2.9 months implies a quarterly spawning regime.

Spawning appears to be a function of salinity, food abundance, and spawning stock, but over half of its variation is unaccounted for and is due to complex factors. From these limited data, I am led to conclude that differential abundance of spawners in the baiting area is a more likely explanation for differences in spawning activity than a comparatively stable spawning stock which reproduces in synchrony. I will use a spawning interval of three months in subsequent analyses realizing that if this value is too long, then the productivity will be higher.

Stock and Recruitment

The capability of predicting the number of progeny surviving to recruit into the fishery from a given parent stock size would permit

Figure 15. Periodogram of the combined spawning data with a peak at 2.9 months.



0.5
0.4
0.3
0.2
0.1
0.0
2.0
3.0
4.0
5.0
PERIOD (MONTHS)
A_p

the making of long range managerial decisions in fisheries. Unfortunately, recruitment from a given parent stock can be quite variable. Mortality during the larval stages of development can obliterate the underlying relationship between the number of eggs released by the parent stock and the number of fish which actually enter the fishery some time later. We can divide the larval mortality into two components: one density dependent and the other density independent.

Ricker (1954) developed a density dependent stock and recruitment model

$$R = S \exp ((S_r - S)/S_m) \qquad (15)$$

where R is a numerical measure of recruitment; S is a comparable measure of the spawning stock giving rise to the recruitment; S_r is the replacement spawning stock size, i.e., when S = R; and S_m is the spawning stock size giving rise to the maximum number of recruits. This model stems from interpreting the lack of a relationship between stock and recruitment as implying a compensatory mechanism such that the number of recruits per unit spawner is higher at low spawning stocks and reduced at higher spawning stocks. The linear transform of this model, as suggested by Rounsefel (1958), is

$$\ln (R/S) = S_r/S_m - S/S_m \qquad (16)$$

Thus, the slope of the linear fit is the negative reciprocal of the parent stock size giving rise to the maximum number of recruits, S_m, and the product of the intercept times S_m yields the replacement parent stock size, S_r.

This model was developed for the fish with discrete generations, and to be applicable to fish which spawn continuously, such as

S. heterolobus, it is necessary to redefine what is meant by spawning stock and recruitment. In the spawning section, evidence was presented suggesting that these fish do not spawn in synchrony and that these fish could have a three month spawning interval. For the data presented in Table 12 (p. 79), assuming a three month spawning interval, the probability that a given fish would be ripe is assumed to be one third. With a 1:1 sex ratio (p. 56) and considering only females, by convention, the probability is further reduced. The values for spawning stock in Table 13 are one-sixth those entered in Table 12.

Redefining recruitment is not as straightforward as redefining the spawning stock. The ideal index of recruitment would be expressed in the same terms as the spawning stock and measure the contribution to the next generation by these fish entering the fishery. The measure of recruitment that Murphy (1966) proposed was the potential number of eggs that a cohort could produce throughout its lifetime if it reproduced at set intervals and if its numbers were decreasing only from natural causes. An advantage of this index is that by being expressed in eggs, it is directly comparable to the spawning stock. A second advantage is that the potential number of eggs per recruit is a scalar. Being a scalar implies that any errors stemming from assessing the natural mortality or from the determination of the spawning interval will deflect the conclusions by a constant amount and the relationships or the shape of the curve will not be affected. The amount of deflection can be assessed by performing the analysis for different combinations of natural mortality and spawning intervals.

Determining the recruitment involves two procedures: first,

Table 13. Spawning stock expressed in eggs per boat night from December 1971 to March 1973 and the resulting recruitment expressed in eggs per boat night potential production.

Month	Spawning Stock millions of eggs/boat night	Month	Recruitment millions of eggs/boat night
December 1971	0.63	March 1972	10.16
January 1972	2.10	April	11.51
February	1.47	May	13.62
March	1.84	June	4.46
April	1.52	July	1.21
May	2.18	August	5.19
June	3.85	September	5.74
July	4.43	October	22.97
August	2.58	November	9.64
September	1.30	December	24.86
October	0.39	January 1973	5.33
November	1.79	February	3.77
December	1.84	March	0.59
January 1973	4.21	April	0.87
February	2.66	May	0.46
March	4.47	June	4.15

calculating how many fish entered the fishery during a given month; and second, how many eggs would each recruit produce if there were no fishing? To determine how many new fish enter the fishery during each month, we must know their entry age. The length frequencies were regrouped using the von Bertalanffy growth equation (Eq. 7 p. 50) into age frequencies. The age group with the maximum number of fish was three months and this age is then taken to be the age by which S. heterolobus is fully available to the lift nets. Since there is a three month difference between when the spawning stock release their eggs and when the new fish enter the fishery, there are only 16 sets of points out of the 19 months of length data.

To determine the potential egg production by a cohort, I have assumed an exponential decrease with time using a natural mortality coefficient of M = 0.37 per month. The details for estimating the natural mortality will be given later when discussing the interactions of the bait population and the bait fishery. Because S. heterolobus continues to grow throughout its life, the number of eggs produced during each spawning cycle increases. Its effective lifespan, assuming only natural mortality, is $0.001 = \exp(-0.37\ (t-3))$ or 22 months. The algorithm for calculating the potential egg production per a cohort, Rt, of 1000 fish is

$$R^* = 1000/6 \sum_{t=3}^{22} \exp(M(t-3))\ f(t) \qquad (17)$$

where 1000 is the number of fish in the cohort, 1/6 is the probability of a ripe female, M is the natural mortality coefficient of 0.37 per month, t is age in months, the (t-3) term is necessary because by the time the fish recruit, they are already three months old, and f(t) is the absolute fecundity of _S. heterolobus_ at a mean age of t months. The actual values of f(t) depends upon the von Bertalanffy equation (Eq. 7), the length-weight relationship (Eq. 9), and the absolute fecundity (Eq. 12). The fecundity was zero for fish aged three or four months because the onset of reproduction occurs near 52 mm SL or about five months. With these assumptions and dividing by 1000, we obtain the potential egg production per recruit of 358 eggs per boat night. Multiplying the number of recruits by this potential production yields the values for recruitment entered in Table 13.

The fit of these stock and recruitment data to the Ricker equation was significant ($r = -0.51$, $df = 14$, $P < 0.05$) but the lack of recruits during the spring of 1973 suggested that the density independent factors such as rainfall also might be important in determining the numbers of fish which survive to recruit. To assess the effects of rainfall and also of zooplankton abundance, the Ricker model was expanded to include terms for rainfall and zooplankton. A stepwise multiple linear regression (Dixon 1975), (Table 14) gave a substantially improved fit ($r^2 = 0.56$, $df = 13$, $P < 0.01$) with the inclusion of a rainfall term. The further addition of a zooplankton term only slightly improved the fit ($r^2 = 0.61$, $df = 12$, $P < 0.05$). Therefore, the recruitment model for Palau is

$$\ln (R/S) = -4.26 - 3.50 \times 10^{-7} S + 1.10 \ln (P) \qquad (18)$$

or

$$R = 1.41 \times 10^{-2} S P^{1.10} \exp (-3.50 \times 10^{-7} S) \qquad (19)$$

where R and S are the recruits and spawners as before and P is precipitation in millimeters per month (Table 2, p. 31).

In the tranform of Ricker's model (Eq. 16), the parent stock size giving rise to the maximum number of recruits, S_m, was the negative reciprocal of the spawning stock coefficient. In the expanded model (Eq. 19), S_m is still the negative reciprocal of the spawning stock coefficient. This relationship can be verified by setting dR/dS from Eq. 19 equal to zero and solving for S. The parent stock for S. heterolobus in Palau which gives rise to the maximum number of recruits is $-1/(-3.50 \times 10^{-7})$ or 2.86 million eggs per boat night. The actual number of recruits resulting from this spawn will depend also upon the rainfall.

The replacement stock size, S_r, in the expanded model now depends upon rainfall and can be calculated from an empirical function of rainfall derived from setting R and S equal to S_r in Eq. 19 and rearranging

$$S_r = 3.14 \times 10^6 \ln(P) - 1.22 \times 10^7 \quad (20)$$

The average rainfall during the study was 266 mm a month and inserting this value into Eq. 20 yields a replacement stock of 5.33 million eggs per boat night. The replacement stock size can also be expressed as a spawning biomass, using the relative fecundity of 450 eggs per gram of spawner per boat night, of 11,800 grams per boat night. The replacement equation has positive values only for rainfall levels above 49 mm per month thus reflecting the scarcity of recruits during the drought months.

Rainfall in Palau is important to the survival of larval fish because heavy rains can wash potential nutrients for primary producers, in the form of decaying vegetation, guano, and leached phosphate, into

Table 14. Stepwise multiple regression and partial correlation coefficients of the monthly recruitment per spawning stock, ln (R/S); on spawning stock in eggs per boat night three months earlier, S; on precipitation in millimeters during the first month of life, ln (P); and on settled volume of zooplankton in $cm^3/100\ m^3$ also during the first month of life, ln (Z).

1. Ln (R/S) on S

$$\ln (R/S) = 2.20 - 5.89 \times 10^{-7} S$$

Correlation coefficient	df = 14	$r^2 = 0.257$	
ln (R/S) and S	= −0.507		P <0.05

2. Ln (R/S) on S and ln (P)

$$\ln (R/S) = -4.26 - 3.50 \times 10^{-7} S + 1.10 \ln (P)$$

Partial correlation coefficients	df = 13	$r^2 = 0.560$	
ln (R/S) and S	= −0.393		
ln (R/S) and ln (P)	= 0.639		P <0.01
S and ln (P)	= 0.005		

3. Ln (R/S) on S, ln (P), and ln (Z)

$$\ln (R/S) = -6.45 - 4.34 \times 10^{-7} S + 0.845 \ln (P) + 0.730 \ln (Z)$$

Partial correlation coefficients	df = 12	$r^2 = 0.606$	
ln (R/S) and S	= −0.470		
ln (R/S) and ln (P)	= 0.500		P <0.05
ln (R/S) and ln (Z)	= 0.323		
S and ln (P)	= −0.099		
S and ln (Z)	= 0.400		
ln (P) and ln (Z)	= 0.259		

the lagoon. This enrichment ultimately is reflected in the zooplankton standing crop, albeit damped somewhat by grazing. Several workers have demonstrated that larval survival is directly related to food density (see May 1975). Recruitment at age three months was significantly correlated with the settled zooplankton volumes during the month of hatching ($r = 0.59$, $df = 14$, $P < 0.05$). At lower food concentrations, the mean distance between prey items increases and consequently the larval fish must expend more energy to capture the same food as before (Braum 1967, Burdick 1969). O'Connell and Raymond (1970) have shown that at very low food densities, i.e., less than 0.1 nauplius/ml, no larval anchovies, *Engraulis mordax*, survived. In addition to this increased expenditure of energy tending to reduce larval survival, Cushing (1969) has also argued that predation is a function of food supply because with less food available, the larval fish grows more slowly which prolongs the duration of larval vulnerability.

Total Mortality

Catch curves (Figure 16) were constructed from both the earlier NMFS raised length frequencies and the recent raised length frequencies. The monthly length frequencies were converted to age frequencies using the von Bertalanffy growth equation (Eq. 7, p. 50). The NMFS data were included to determine if there had been detectable changes in total mortality during the intervening five years. Only an average mortality could be expected because all 34 months of data were grouped together to approximate the assumptions of constant survival and constant recruitment. Similarly, the estimate for the recent data represents an average of 19 months.

The maxima in both curves occurred at three months which indicates that by three months, S. heterolobus are fully recruited into the bait fishery. The recent curve flattens out for ages above 15 months because a few large fish appeared in the catches in June and July 1972.

Chapman and Robson (1960) and later Robson and Chapman (1961) demonstrated that for a fish population which was approximately in equilibrium, the age frequency distribution for randomly selected fish could be described by a geometric distribution. The age frequency with a geometric distribution can be determined from

$$f(x) = as^{x} \tag{21}$$

where x is the coded age of the fish, s is the annual survival rate, and a is (1 - s) or the annual mortality rate. The ages have been coded by setting the age at recruitment equal to zero.

The unbiased estimate of survival, $\hat{s}$, for the geometric age distribution is

$$\hat{s} = \overline{X}/(1 + \overline{X} - 1/N) \tag{22}$$

where $\overline{X}$ is the mean coded age and N is the number of fish being considered. If N is large, the Equation 22 reduces to

$$s = \overline{X}/(1 + \overline{X}) \tag{23}$$

and its variance is given by

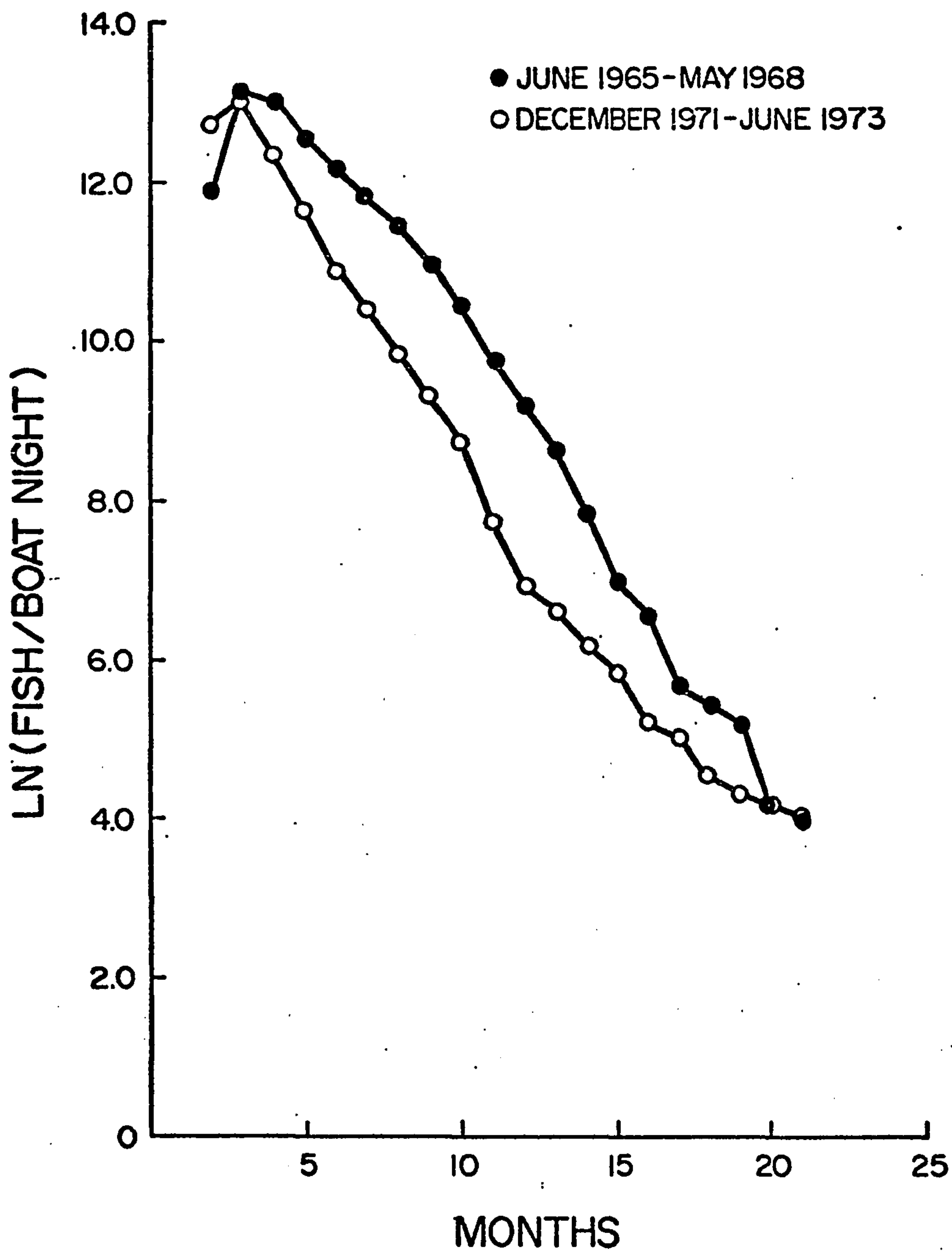
$$v = \hat{s}\ (1 - \hat{s})/N \tag{24}$$

The estimate of annual survival can be converted to an instantaneous mortality rate, Z, by

$$Z = -\ln\ (\hat{s}) \tag{25}$$

The length frequencies comprising the age frequencies were raised

Figure 16. Catch curves of logarithm of number of fish of age x on age x for two periods in the history of the fishery: June 1965 to May 1968 and December 1971 to June 1973.



JUNE 1965-MAY 1968
DECEMBER 1971-JUNE 1973
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0
5
10
15
20
25
LN (FISH/BOAT NIGHT)
MONTHS

from the number of fish in a sample to the number of fish caught during the night's baiting operation. A consequence of this raising is that the total number of fish used in testing the goodness of fit is inflated. Therefore, cumulative percentage frequencies of the raised data were multiplied by the actual number of fish measured. The age distribution of the recent data was satisfactorily described by the geometric model (Kolmogorov-Smirnov $d_{max} = 0.9\%$, $D_{0.05} = 1.0\%$, $N = 18255$). The large number of 4 month old fish in the earlier NMFS data resulted in a poor fit ($d_{max} = 5.0\%$, $D_{0.05} = 1.0\%$, $N = 17251$). The average total mortality coefficient for the recent data was 0.658 ± 0.007 per month, the precision term being two standard deviations.

Total mortality was also estimated for both time periods as minus the slope of a semi-logarithmic regression of log-number of fish per boat night on age. An analysis of covariance, after testing for significant differences in variance ($F = 0.355$, $df = 17,17$, $P = 0.500$), showed that the mortality coefficients (NMFS - 0.550 per month, recent - 0.527 per month) were not significantly different ($F = 0.735$, $df = 1,34$, $P = 0.397$). Reexamination of the catch curve shows a few large fish in the recent data flattening out the curve. If we use an effective lifespan of 15 months, when only 0.1% of the recruits remain, then the variances are different ($F = 5.61$, $df = 11,11$, $P = 0.004$) and the total mortality coefficients are different ($F = 28.8$, $df = 1,22$, $P = 0.000$). The total mortality coefficient for the recent data is 0.649 ± 0.020 per month which is quite similar to the previous estimate of 0.658 per month from the geometric model; the precision term in the regression estimate is two standard errors. The total mortality coefficient for the earlier NMFS data is 0.511 $\pm$ 0.048 per month. The recent total mortality is from 12 to 44% greater than that during the early stages of the bait fishery.

The agreement between the recent total mortality estimates is good but it must be remembered that these estimates are based upon age data that were calculated from the von Bertalanffy growth equation. Keeping this note of caution in mind, future analyses involving total mortality will use a coefficient of 0.65 per month. With this mortality and recruitment at age three months, the average age in the population is 4.5 months.

Life Table

A life table (Table 15) concisely summarizes the life history parameters of growth, reproduction, and mortality. The age specific fecundity, m_x, was taken from the derivation of the reproductive potential of a recruit. As before, the number of mature eggs have been reduced to account for the three month spawning interval and for the 1:1 sex ratio. The number of fish in each age category, l_x, has been assumed to decrease exponentially with a total mortality coefficient of 0.65 per month beginning with recruitment at age three months. There are no data on larval survival and so the table contains no entries for ages one and two months. In lieu of fractional survival values, the number of recruits, l_3, was linearly adjusted until the sum of the product, $l_x m_x$, equalled a million eggs.

Table 15 is a relative life table depicting the equilibrium state for these life history parameters. If the million scalar is ignored,

Table 15. Relative life table depicting equilibrium state of *Stolephorus heterolobus* in Palau.

Age Months x	Number of fish surviving l_x	Mean fecundity m_x	Egg production $l_x m_x$	%	Cumulative %
0	1.0×10^6	0	0	0	0
3	9550	0	0	0	0
4	4990	0	0	0	0
5	2600	131	340000	34.0	34.0
6	1360	180	245000	24.5	58.5
7	709	231	164000	16.4	74.9
8	370	280	104000	10.4	85.3
9	193	326	63000	6.3	91.6
10	101	369	37200	3.7	95.3
11	53	408	21500	2.1	97.4
12	28	442	12200	1.2	98.6
13	14	473	6790	0.7	99.3
14	7	500	3750	0.4	99.7
15	4	523	2050	0.2	99.9
16	2	543	1110	0.1	100.0
17	1	561	598	0.1	100.1 *
			1.0×10^6	100.1 *	

* total exceeds 100.0% because of rounding errors

then one egg ultimately gives rise to one egg. At equilibrium, the intrinsic rate of increase, r, is equal to zero, and, accordingly, the net reproductive rate is 1.0.

There were two reasons for constructing this table. First, a crude estimate of larval mortality is possible from the survivorship from egg to recruitment in order to maintain the equilibrium. Comparable values from the literature are non-existant, but Smith (1973) estimated that larval mortality decreases from 0.3 per day to 0.1 per day during the first few weeks of a Pacific sardine, Sardinops caerulea. This information tends to support Murphy's (1967) estimate that only about 0.0014% of Sardinops caerulea eggs produced recruits two and a half years later. Application of Smith's pattern to S. heterolobus in Palau reveals that the duration of the high mortality, 0.3 to 0.1 per day, would be one week followed by a decrease from 0.1 per day to 0.37 per month during the remainder of the three month pre-recruit period. This scheme yields 9950 recruits as compared to the table value of 9550 recruits. This calculation is more qualitative than quantitative because there is no reason to believe that S. heterolobus will have the exact degree of predation as the sardine; but it is logical to assume that as the larval fish grow, the mortality rate decreases until it reaches some equilibrium value which I have taken to be the natural mortality coefficient of an adult.

The second reason for constructing the life table was to assess the contribution by each age class to the total egg production. The last two columns in Table 15 contain the breakdown of the expected egg production by percent and cumulative percent for the different ages.

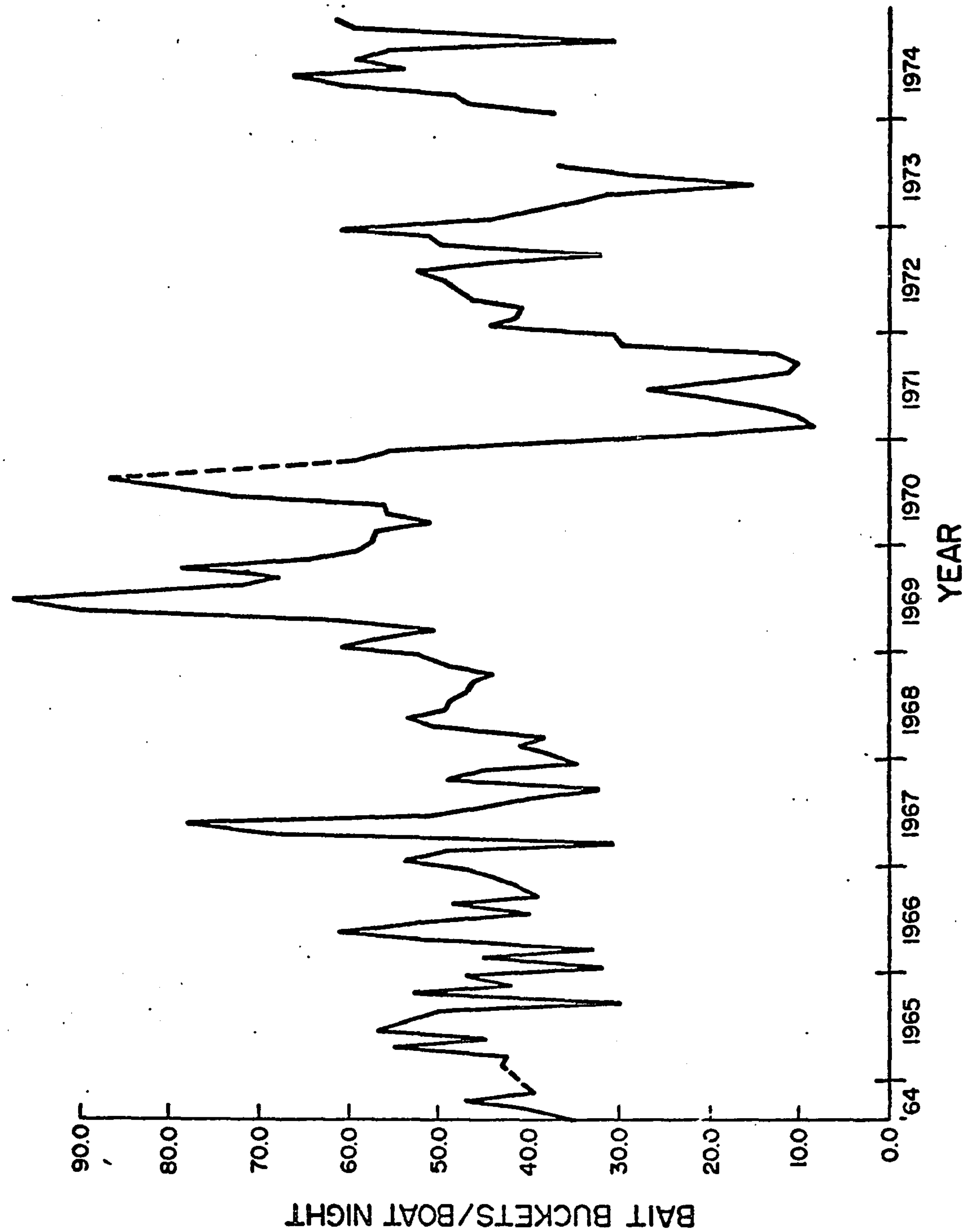
If we assume that fish aged five, six, and most of seven months are spawning for the first time, then only about 30% of the total eggs are produced by repeat spawners. If the number of fish per age, l_x, are recalculated using only the natural mortality coefficient, M = 0.37 per month, (Table 16) instead of the total mortality coefficient of Z = 0.65 per month, the number of eggs produced by repeat spawners increases to 52%. Murphy (1967, 1968) has pointed out that an iteoparous mode of reproduction has a selective advantage in situations with variable environments. Earlier in the stock and recruitment section, it was shown that the variable recruitment in S. heterolobus was significantly correlated with zooplankton abundance. What this exercise suggests is that one of the possible effects of fishing has been to remove the older age categories and, consequently, to remove the environmental buffer. Thus, the bait population, by being more susceptible to the vagaries of the environment, would be expected to fluctuate more now than before. Figure 17 is the monthly bait catch per boat night, an index of abundance (Gulland 1963), from 1964 to 1974. The fluctuations up to 1969 were considerably less than during the recent years (F = 4.97, df = 66,50, P = 0.000). The cutoff point as the beginning of 1969 is arbitrarily chosen as a point when there is little likelihood that the fish being caught were still remnants of the virgin population. Continuing with this line of reasoning, the mean bait catch per boat night during the early years is not significantly different from the recent years (46.3 vs. 47.2 buckets per boat night, t = 0.303, df = 116, P = 0.762), but the coefficient of variation rose from 20% in the early years to 44% recently. Using

Table 16. Relative life table for <u>Stolephorus</u> <u>heterolobus</u> calculated using only the natural mortality M = 0.37 per month.

Age Months x	Number of fish surviving l_x	Mean fecundity m_x	Egg production $l_x m_x$	%	Cumulative %
0	1.0×10^6	0	0	0	0
3	2780	0	0	0	0
4	1920	0	0	0	0
5	1330	131	173000	17.3	17.3
6	916	180	165000	16.5	33.8
7	633	231	146000	14.6	48.4
8	437	280	122000	12.2	60.6
9	302	326	98500	9.8	70.4
10	209	369	76900	7.7	78.1
11	144	408	58700	5.9	84.0
12	100	442	44000	4.4	88.4
13	69	473	32500	3.3	91.7
14	47	500	23700	2.4	94.1
15	33	523	17200	1.7	95.8
16	23	543	12300	1.2	97.0
17	16	561	8770	0.9	97.9
18	11	576	6220	0.6	98.5
19	7	588	4390	0.4	98.9
20	5	599	3090	0.3	99.2
21	4	608	2170	0.2	99.4
22	2	616	1520	0.2	99.6
23	2	623	1060	0.1	99.7
24	1	628	737	0.1	99.8
25	1	633	513	0.1	99.9 *
			1.0×10^6	99.9 *	

* total does not equal 100.0% because of rounding errors

Figure 17. Monthly bait catch per boat night in buckets per boat night from August 1964 to December 1974. Data from all areas of Palau.


BAIT BUCKETS/BOAT NIGHT
0.0
10.0
20.0
30.0
40.0
50.0
60.0
70.0
80.0
90.0
'64
1965
1966
1967
1968
1969
1970
1971
1972
1973
1974
YEAR

rainfall as an index of environmental influences, for the same two time periods, there were no significant differences in the mean rainfall ($t = 0.208$, $df = 116$, $P = 0.836$) nor in variability ($F = 1.16$, $df = 66, 50$, $P = 0.294$). The coefficient of variation for rainfall was 44% initially and now 46% and the 2% difference is insignificant. Thus, the recent variability of the bait catch per effort is quite similar to that of the rainfall which tends to support the hypothesis that the bait population is less buffered than before.

Bait Fishery

Catch Statistics

The overall goal of this study is to obtain insights into the dynamics of S. heterolobus in Palau. The results present thus far have been concerned with the determination of estimates for the biological parameters - reproduction, growth, and mortality. In the last section, one effect of the bait fishery was discussed, now I would like to examine the bait fishery itself.

The annual catch statistics (Table 17) were compiled from the daily catch reports (see Figure 3, p. 23 for an example) submitted to Marine Resources Division Headquarters of the Trust Territory Government. The catch data for the period of August 1973 to December 1973 were unavailable from either Marine Resources or Van Camp Seafood Company. For comparisons, the missing data were estimated as the monthly mean catches or effort for the given months from the other years' data.

Figure 17 (p. 101) was a plot of the monthly bait catch in buckets per boat night from August 1964 to December 1974. Time series analysis of these data had a peak in the periodogram (Figure 18) at six months. Examination of the length frequencies from 1965 to 1968 and from 1971 to 1973 showed increases in the bait catches in May - July and November - December resulting from the influx of recruits.

In addition to the total catch statistics which include catches from throughout the island chain, the monthly catch statistics from July 1970 to December 1974 have been tallied for the main baiting area alone (Table 18).

Table 18 contains both measures of effort available in the Palauan bait fishery: the lift and the boat night. These data were used to develop a functional relationship (Ricker 1973) between the measures so as to be able to convert from lifts to boat nights and from boat nights to lifts. The functional regression is a symmetric fit not a least squares fit because it determines the best compromise for minimizing the residuals of both the dependent variable and the independent variable. Thus, the functional relationships are

$$BN = 13.1 + 0.586\ L \tag{26}$$

and

$$L = -22.3 + 1.71\ BN \tag{27}$$

$$r^2 = 0.850,\ df = 47,\ P < 0.01$$

where BN is the number of boat nights during the month and L is the number of lifts. The high correlation ($r = 0.93$, $df = 47$) between lifts and boat nights indicates that the fishermen are relatively consistent with respect to the number of lifts they make per boat per night. On a time scale of a month, the fishermen average about 1.7 lifts per boat night. A consequence of this consistency is that the boat night,

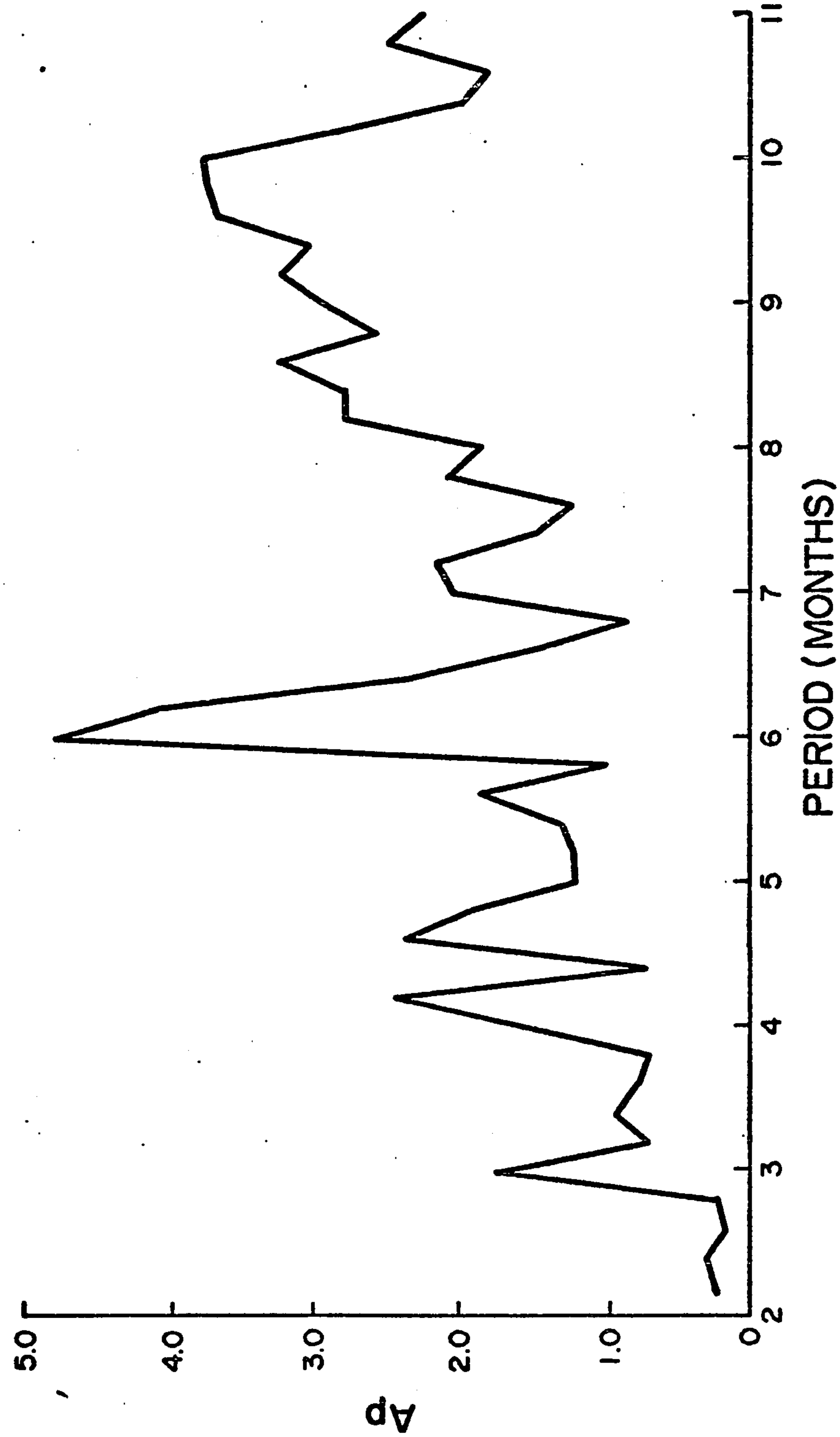
Table 17. Annual bait catch in buckets, effort in boat nights and catch per effort.

Year	Buckets	Boat nights	Buckets/boat night
1964	10888 **	270 **	40.3
1965	53358	1073	49.7
1966	62780	1406	44.7
1967	73620	1616	45.6
1968	82082	1784	46.0
1969	111103	1590	69.9
1970	96462	1565	61.6
1971	48674	2860	17.0
1972	80630	1755	45.9
1973	67811*	1827*	37.1
1974	106368	1928	55.2

* Catch data for the months of August through December were estimated as their monthly means.

** Fishing began in August.

Figure 18. Periodogram of the monthly bait catch per unit of effort in buckets per boat night from August 1964 to December 1974.



Ap
5.0
4.0
3.0
2.0
1.0
0
2
3
4
5
6
7
8
9
10
11
PERIOD (MONTHS)

Table 18. Monthly bait catch statistics compiled for only the main baiting area.

Month	Catch Buckets	Boat nights	Lifts	Catch/boat night	Catch/lift	F mo^{-1}
July 1970	8394	104	136	80.7	61.7	0.16
August	8724	99	130	88.1	67.1	0.16
September	-	-	-	-	-	-
October	2423	41	61	59.1	39.7	0.07
November	4900	94	182	52.1	26.9	0.22
December	1748	51	102	34.3	17.1	0.12
January 1971	1214	121	236	10.0	5.1	0.28
February	662	72	144	9.2	4.6	0.17
March	1529	82	164	18.6	9.3	0.20
April	2270	168	259	13.5	8.8	0.31
May	3642	189	338	19.3	10.8	0.41
June	3474	167	228	20.8	15.2	0.27
July	2334	163	274	14.3	8.5	0.33
August	3200	330	474	9.7	6.8	0.57
September	1805	244	277	7.4	6.5	0.33
October	1387	110	118	12.6	11.8	0.14
November	4580	154	165	29.7	27.8	0.20
December	3078	101	106	30.5	27.7	0.13
January 1972	4576	103	106	44.4	43.2	0.13
February	5381	130	144	41.4	37.4	0.17
March	5332	130	201	41.0	26.5	0.24
April	7376	160	265	46.1	27.8	0.32
May	10473	219	333	47.6	31.3	0.40
June	7867	160	243	49.2	32.4	0.29
July	8684	166	251	52.3	34.6	0.30
August	8901	197	359	45.4	25.1	0.43
September	6353	196	375	32.4	16.9	0.45
October	5380	108	185	49.8	29.1	0.22
November	5041	100	156	50.4	32.3	0.19
December	5166	85	111	60.8	46.5	0.13

Table 18. (Continued) Monthly bait catch statistics compiled for only the main baiting area.

Month	Catch Buckets	Boat nights	Lifts	Catch/boat night	Catch/lift	F mo^{-1}
January 1973	5532	125	184	44.3	30.1	0.22
February	4538	113	174	40.2	26.1	0.21
March	3357	96	149	35.0	22.5	0.18
April	4653	133	220	35.0	21.2	0.26
May	3673	241	465	15.2	7.9	0.56
June	6620	227	373	29.2	17.7	0.45
July	8508	232	383	36.7	22.2	0.46
January 1974	2574	58	105	44.4	24.5	0.13
February	6816	129	235	52.8	29.0	0.28
March	8200	167	323	49.1	25.4	0.39
April	10862	173	299	62.8	36.3	0.36
May	15565	226	374	68.9	41.6	0.45
June	12339	215	320	57.4	38.6	0.38
July	12560	196	280	64.1	44.9	0.34
August	9217	150	181	61.4	50.9	0.22
September	274	9	16	30.4	17.1	0.02
October	12069	190	265	63.5	45.5	0.32
November	6445	100	129	64.5	50.0	0.15
December	7303	147	171	49.7	42.7	0.20

at least since July 1970, does provide a satisfactory measure of effort in practice if not theory.

The number of lifts in the baiting area can be used to partition the total mortality into that portion explained by the bait fishery and the remaining unexplained or natural mortality.

Partitioning the total mortality

Tagging methods were not possible with this bait fishery because individual fish are not handled except during the actual chumming operation. Hence, tag recoveries would be minimal, Also, considering the high total mortality, $Z = 0.65$ per month, and the rapid turnover, the age at first spawning is only five months, it would be difficult to mark a significant portion of the population. Therefore, fishing mortality was estimated indirectly using the swept area concept (Beverton and Holt 1956, Hirayama 1972).

In Palau, bait fish are attracted with a 1000 W underwater light and then captured with a lift net. The probability of a fish being captured should be the ratio of the volume of water being sampled by the gear to the volume of suitable habitat times the probability of catching a fish in the illuminated water. The volume of water being sampled is the volume of water illuminated before the net is hauled. The appendix gives the details of the calculation of this volume. For a 1000 W underwater light, a mean extinction coefficient of 0.106 m^{-1}, a light threshold of 9.1×10^{-5} $\mu W\ cm^{-2}$ for a positive photo response, and a duration of four hours, the volume of water illuminated is 0.11 km^3. The volume of the lagoon excluding the barrier reef and patch reefs is

9.2 km^3. Therefore, the probability of being caught, if all fish are captured after being attracted to the light, is 0.011/9.2 or 0.0012. And, the instantaneous mortality associated with one lift of the net is 0.0012 per lift.

Inherent in this method of assessing the fishing mortality is the assumption that the fish are equally available throughout the lagoon. This hypothesis was tested by examining the number of lifts and their catch rates in the main baiting area and those from elsewhere in the lagoon for those 18 months during which some of the boats reported lifts from outside the main baiting area (Table 19). The main baiting area averaged 269 lifts per month with an average catch rate of 20.0 buckets per lift. Fishing outside of the main baiting area averaged only 30 lifts per month with an average catch rate of 28.4 buckets per lift. The difference between these catch rates was not significant (paired $t = 1.59$, $df = 17$, $P = 0.130$) which supports the assumption of equal availability throughout the lagoon.

The assumption that a fish which perceives the light is eventually caught systematically overestimates the fishing mortality. Dimming the light just prior to hauling the net causes the bait to form into a dense school circling the light such that most if not all of the fish present are captured. The bias stems from that percentage of the fish which perceive the light and either do not approach or they come near the light and then leave prior to the hauling of the net. The usual pattern was for the quantity of bait to increase with time but occasionally carangids or other predators would scatter the bait. I have no data for assessing this portion of the bait and so the fishing

Table 19. Bait catch statistics from the main baiting area and from outside the main baiting area for the 18 months during which outside fishing was reported.

Month	Main Baiting Area Lifts	Main Baiting Area Buckets/lift	Remainder of Lagoon Lifts	Remainder of Lagoon Buckets/lift
October 1970	61	39.7	2	30.0
November	182	26.9	61	25.7
December	102	17.1	114	21.1
January 1971	236	5.1	80	10.5
February	144	4.6	62	3.8
March	163	9.3	62	4.3
June	228	15.2	12	13.9
July	274	8.5	35	7.9
August	474	6.8	32	22.4
September	277	6.5	38	25.1
May 1972	333	31.3	2	0.0
April 1973	220	21.2	3	19.7
May	465	7.9	5	16.0
June	373	17.7	4	15.8
March 1974	323	25.4	20	32.6
April	200	36.3	1	100.0
May	374	41.6	3	100.7
June	320	38.6	10	62.4
Mean	269	20.0	30	28.4
S.D.	115	13.1	33	29.7
CV (%)	42.8	65.5	110	105

mortality is a maximal coefficient and the actual value is less.

If $p = 0.0012$ is the probability of being caught, then $1 - p$ is the probability of surviving one lift of the net. The survival, S, of all the lifts during a month, E, is

$$S = (1 - p)^E \tag{28}$$

The corresponding monthly instantaneous fishing mortality, F, is

$$F = - \ln (S) \tag{29}$$

The calculated monthly fishing mortality coefficients are included in Table 18. The average fishing mortality for the 19 months from December 1971 to June 1973, weighted by the number of lifts in each month, was 0.28 per month.

If E is a measure of effort, we would like to develop a relationship which gives us the fishing mortalities as a function of effort. The catchability coefficient was determined by combining equations (28) and (29)

$$F = - E \ln (1 - p) \tag{30}$$

For $-1 < p \leq 1$, $\ln (1 - p)$ can be expanded by a Taylor series

$$\ln (1 - p) = -p + \frac{p^2}{2} - \frac{p^3}{3} + \frac{p^4}{4} - \ldots \tag{31}$$

but for small values of p, such as 1.2×10^{-3}, the higher terms are negligible. This simplifies equation (31) to $\ln (1 - p) = -p$ and substitution of this expression into equation (29) gives

$$F = p E \tag{32}$$

Since the instantaneous fishing mortality is a linear function of effort or in this case the number of lifts, p is equivalent to the catchability coefficient, q (k_2 in Schaefer's original derivation (1954)). The average catchability was determined also following the computational scheme set forth in Schaefer and Beverton (1963) using the monthly bait catch in buckets and the number of lifts from July 1970, when the number of lifts began to be recorded, to July 1973. The catchability determined from just catch and effort statistics was 8.4 x 10^{-4} per lift which supports the previous maximal estimate of 1.2 x 10^{-3} but the precision of neither estimate is known.

Assuming that the mortality estimates have some basis in reality, then the natural mortality not due to fishing can be estimated as the difference between the average total mortality, Z = 0.65 per month, and the average fishing mortality, F = 0.28 per month, which gives a natural mortality of 0.37 per month.

Positive evidence of predation on S. heterolobus came from a mackerel, Grammatorcynus bilineatus, whose gut contained 6 specimens of S. heterolobus the largest of which was 70 mm SL. An artificial source of predation occurred when birds fed on the excess bait which were confined in floating nets in the baiting area. The main species of birds involved were three types of terns: Anous tenirostris, Sterna lunata, and S. sumatrana; also involved was the reef heron, Demigretta sacra. Nests of all these species were located and observed extensively. The main fish prey species, identified from samples regurgitated by chicks in the nests, were Spratelloides delicatulus and Pranesus pinguis. Both species are found at the surface during the day. Common noddy terns, Anous stolidus, follow the tuna boats as they leave the baiting area and lagoon to retrieve the dead and dying Stolephorus heterolobus which wash out the holes in the bottom of the baitwells.

Yield Models for the Bait Fishery

The primary tool in the management of a fishery is the regulation of fishing effort. Therefore, a relationship between the expected catch for a level of effort or at least an approximation of this relationship is essential. Several models have been proposed all of which assume the existance of a steady state for a given level of fishing on the population biomass and a certain yield associated with that exploitation. Somewhere along the resulting curve of yield and fishing intensity, there is a maximum which is called the maximum sustainable yield.

The simplest and most widely used model is Schaefer's logistic model (Schaefer 1954, Schaefer and Beverton 1963). As the name implies, the logistic model assumes that the increase in population biomass can be approximated by a Verhulst-Pearl growth curve of the form

$$dB/dt = R\ B\ (K - B) \tag{33}$$

where B is the population biomass, R is the intrinsic growth rate of the population biomass, and K is the carrying capacity of the environment.

In the Schaefer logistic fishery model, changes in the biomass are described by

$$1/B\ dB/dt = R\ (K - B) - F(x) \tag{34}$$

where F(x) is the effect of the fishery upon the population. Assuming that the fishery and the exploited population reach an equilibrium, then, $dB/dt = 0$ and equation (34) reduces to

$$F(x) = R\ (K - B) \tag{35}$$

The rationale is that the fishery is capturing the incremental growth of the population such that there is no net change in the population. The instantaneous fishing mortality was shown earlier to be linear with effort, $F(x) = p\ E$. In the absence of direct estimates of population biomass, the catch per unit of effort is used to approximate the biomass, $B = a\ C/E$, where a is the constant which relates catch per effort to bait density. Constant catchability is implied in using this approximation. With these substitutions, Equation (35) becomes

$$p\ E = R\ (K - a\ C/E) \tag{36}$$

and rearranging the terms in Equation (36) gives a linear relationship for catch per effort on effort

$$C/E = K/a - (p/(a\ R))\ E \tag{37}$$

and by letting $b = p/(a\ R)$ and $K' = K/a$

$$C/E = K' - b\ E \tag{38}$$

This model was originally developed for the yellowfin tuna in the eastern tropical Pacific when the only available data were catch statistics. The main difficulty with this model stems from trying to justify it from the theoretical considerations of the logistic growth model. This model assumes that the carrying capacity is constant which is quite unlikely since the carrying capacity is a function of the environment. The model assumes that a unit of the population exerts the same influence exactly regardless of the population density. More importantly, this model hinges on the existence of an equilibrium but the time lags in fish populations; resulting from the myriad processes of growth, maturation, and reproduction; induce oscillations in the population (May 1974, MacDonald 1976). Therefore, I think that it is more practical just to utilize the empirical relationship between catch per effort and effort. Depending upon the fit of the catch statistics, future catch rates can be predicted from fishing effort.

The catch and effort record for the bait fishery (see Figure 17, p. 101) has many months during which, for a variety of reasons such as labor strikes, there was no fishing; but from 1965 to 1974, for the months of February through July, the record is complete. The average monthly bait catch and the average number of boat nights per month were determined from these months for each year (Table 20). The second list of effort is the corrected effort considering the reduced attracting power of the 350 W underwater lights which were used through 1968. The corrected efforts were determined by dividing the listed number of boat nights by the ratio of the capture radii for the 350 W light and the 1000 W light, 0.89. The details of calculating the capture radius for a given intensity of light is given in the appendix.

The "logistic" fishery model for S. heterolobus was

$$C/E = 81.8 - 0.196\ E \tag{39}$$

$$r = 0.732,\ df = 8,\ 0.05<P<0.01$$

The parabolic yield relationship is found by multiplying by E

$$C = E\ (81.8 - 0.196\ E) \tag{40}$$

where C is the bait catch in buckets per month and E is the corrected number of boat nights during a month. Figure 19 is a linear plot of the average monthly catch and corrected effort data and Figure 20 is the corresponding yield curve. This model, being parabolic, is symmetrical with a maximum yield of 8530 buckets per month occurring with an effort of 209 boat nights per month.

Table 20. Average monthly bait catch in buckets per boat night, average effort in boat nights per month, and the corrected average effort on a 1000 W underwater light basis. The monthly averages were calculated using the months of February through July in each year.

Year	Catch Buckets	Effort Boat nights	Corrected Effort Boat nights	Catch/Corrected Effort Buckets/boat nights
1965	5172	99	88	58.6
1966	5723	123	109	52.1
1967	5211	100	89	58.7
1968	8508	182	162	52.5
1969	7941	105	105	75.8
1970	11040	173	173	63.7
1971	5094	292	292	17.4
1972	7518	161	161	46.7
1973	5284	178	178	29.6
1974	11440	202	202	56.7
Mean	7293	162	156	51.2
S.D.	2435	59.5	62.6	16.8
CV	33.3	36.8	40.1	32.7

Few fish populations have been observed to have their maximal yields at precisely half of the carrying capacity, usually the maxima have been attained at lower levels of effort (Schaefer and Beverton 1963). Fox (1970) developed an exponential model without the constraint of symmetry which is analogous to Ricker's density dependent stock and recruitment model. Effort is assumed to have a negative exponential effect on the catch per effort, that is, a rapid decrease in catch per effort initially with the onset of fishing and a more gradual decrease later at higher levels of fishing. The North Sea herring exhibited this pattern after the fishery resumed after World War II (Cushing 1968, Figure 46). A possible biological interpretation of this pattern is that the fish population compensates for the increased mortality with an increase in the reproductive rate. The reproductive rate can increase either through an increase in fecundity or, more likely, through earlier maturation albeit at a smaller size. This later alternative would explain the common complaint by fishermen that the fish get smaller (Cushing 1968, p. 99). Fox (1970) found that his exponential model fit the yellowfin tuna catch statistics better than the earlier Schaefer model. Silliman (1971) compared three simple fishery models, fishery models which only require catch statistics, with his experimental fishery on guppies where the exploitation rates were known and found the exponential model satisfactory.

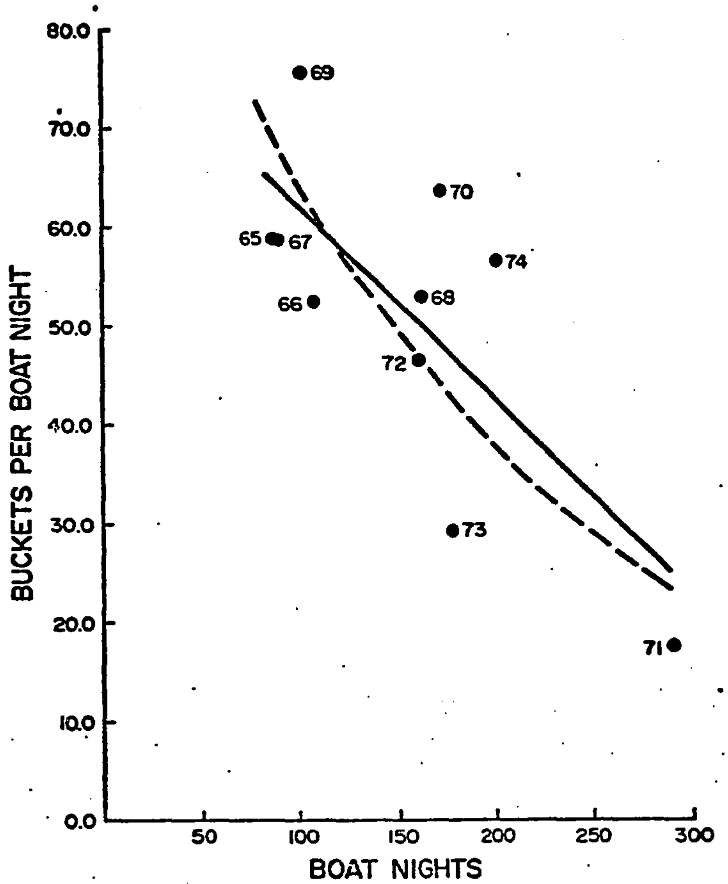
The exponential model is easily fit to catch data with the linear transform

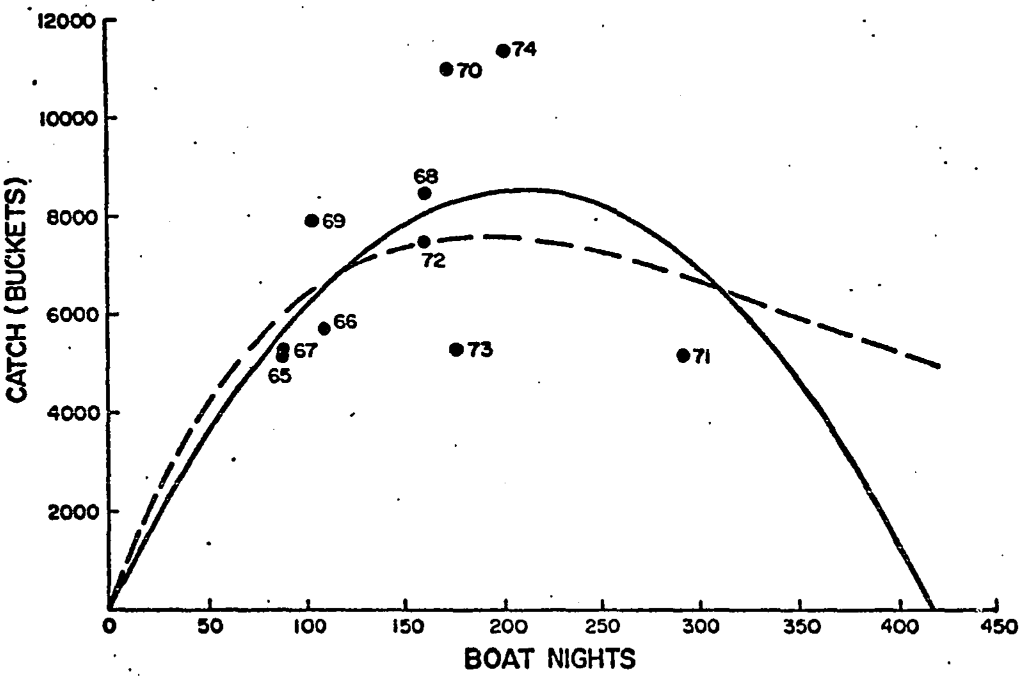
$$\ln (C/E) = a - b\,E \tag{41}$$

where a and b are fitted constants. The exponential model for *S.*

Figure 19. Mean monthly bait catch per effort on effort where the catch is in buckets and the effort is in boat nights which have been corrected for underwater light source. The monthly means were calculated using the months of February through July from each year. Solid line - logistic model; broken line - exponential model.

Figure 20. Sustainable yields at various fishing intensities as predicted by the logistic model (solid line) and the exponential model (broken line).


80.0
70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
BUCKETS PER BOAT NIGHT
50
100
150
200
250
300
BOAT NIGHTS
69
70
65
67
74
66
68
72
73
71


12000
10000
8000
6000
4000
2000
CATCH (BUCKETS)
0
50
100
150
200
250
300
350
400
450
BOAT NIGHTS
74
70
68
69
72
66
67
65
73
71

heterolobus, using the catch results in Table 20, was

$$\ln (C/E) = 4.71 - 5.37 \times 10^{-3} E \qquad (42)$$

$$r^2 = 0.611,\ df = 8,\ 0.05 < P < 0.01$$

and the corresponding yield relationship was

$$C = 111\, E \exp (-5.37 \times 10^{-3} E) \qquad (43)$$

The maximum yield was obtained by first finding the necessary level of effort and then calculating the yield in Equation (43). Since the level of effort necessary to produce the maximum yield is analogous to S_m, the parent stock necessary to produce the maximum number of recruits, the necessary effort to produce the maximum yield is the negative reciprocal of the slope of the linearized fit (Equation 42) - 186 boat nights per month. The maximum yield of the exponential model was 7600 buckets per month.

Since this study is a pre-management study, a primary objective was to evaluate the catch data in order to relate different fishing levels with their associated yields. Figures 19 and 20 compare these two models with the data. Both models fit the data about the same. The main differences are apparent at fishing levels above the maximum yields. The logistic model is premised upon a linear decrease in the catch per effort with increasing effort. The extreme result of this premise is to have no catch for fishing levels above 417 boat nights per month. The model actually predicts negative catches for fishing levels above 417 boat nights whereas the exponential model asymptotically approaches no catch at infinitely high fishing levels. As was mentioned earlier, the asymptotic approach could result from a substitution of fishing mortality for part of the natural mortality. Also, a fishery which is acting long enough can exert selective pressures on the population to reproduce at an earlier age - the fish which is caught and has not reproduced does not pass on the genes for delayed reproduction.

Fishery evidence to support the advocacy of the exponential model comes from a period of high fishing intensity, April through August of 1971. The average effort during this period, considering all of Palau, was 345 boat nights per month with an average catch per boat night of 17.9 buckets per boat night (Table 21). The exponential model predicts a catch rate of 17.4 buckets per boat night at 345 boat nights and the logistic model predicts 14.2 buckets per boat night. The highest monthly level on record for Palau occurred in May 1971 with 389 boat nights with an average catch rate of 19.4 buckets per boat night. May is a prime month for young fish entering the fishery which swell the catch rate. The exponential model predicted 13.7 buckets per boat night while the logistic predicted only 5.6 buckets per boat night. As expected the exponential model had closer agreement than the logistic model.

A difficulty in fitting simple models to the bait fishery is the narrow range of effort levels, CV = 40.1% (Table 20). The only year with high fishing intensity was 1971. Bait samples from 1971 contained mostly recruits suggesting that entry into the fishery was normal or above and perhaps that the low catch rate did, indeed, reflect the scarcity of large fish. Earlier, it was mentioned that catch rates from all over Palau showed this same scarcity which implies that the larger fish did not just emigrate to another part of the lagoon. Thus, I think that 1971 was not unduly emphasized in these analyses.

Table 21. Bait catch statistics from all of Palau for the five months with the highest fishing intensity, April through August 1971.

Month	Buckets	Boat nights	Buckets/boat night
April	3975	298	13.3
May	7534	389	19.4
June	9019	338	26.7
July	6400	349	18.3
August	3917	351	11.2
Mean	6169	345	17.9

Constant recruitment is implied in these simple models but recruitment of S. heterolobus in Palau is not constant. Again using the data in Table 18 (p. 107), the mean catch in 1973, a year with poor recruitment, was less than 70% of the value predicted by the exponential model and conversely the mean catch in 1974, a year with good recruitment, was over 51% above the predicted values. The simple models provide coarse overviews which may be satisfactory for general planning; however, finer resolution requires the incorporation of recruitment, growth, and mortalities. The dynamic pool model (Beverton and Holt 1957) uses the biological parameters of the population to determine the mean size of capture on a per recruit basis. The recruit is assumed to follow a particular pattern of growth, in this case described by the von Bertalanffy growth equation (Eq. 7), and is subject to both fishing and natural mortalities. Since the number of recruits is usually not known, the meaningful statistic is the yield per recruit which can then be determined for different levels of exploitation.

The yield per recruit in grams per fish was calculated from

$$Y/R = F\ W \sum_{n=0}^{3} U_n \exp\ (-nK(t_c - t_o))/(F + M + nK) \qquad (44)$$

where $U_o = 1$, $U_1 = -3$, $U_2 = 3$, $U_3 = -1$; F is the instantaneous fishing mortality; M is the instantaneous natural mortality; W is the asymptotic weight; K is the growth rate in the von Bertalanffy equation; t_c is the age at recruitment; and t_o is the age at which the weight would be zero (Gulland 1969). A computer program, YIELD, was developed to calculate the yield per recruit in grams per fish given a natural mortality coefficient of 0.37 per month, and asymptotic length of 91.1 mm SL, K = 0.174 per month, and recruitment at age three months with a mean length of 39 mm SL.

Equation (44) determined the proportion of the population biomass, on a per recruit basis, which is caught by the fishery operating at a level of F. The summation term stems from the assumption that weight can be thought of as a function of the length cubed. This assumption was verified for S. heterolobus with a least squares fit of the weight on the length cubed. The resulting equation was

$$W = 1.10 \times 10^{-5} L^3 \qquad (45)$$

$$r^2 = 0.981, \ df = 119, \ P<0.001$$

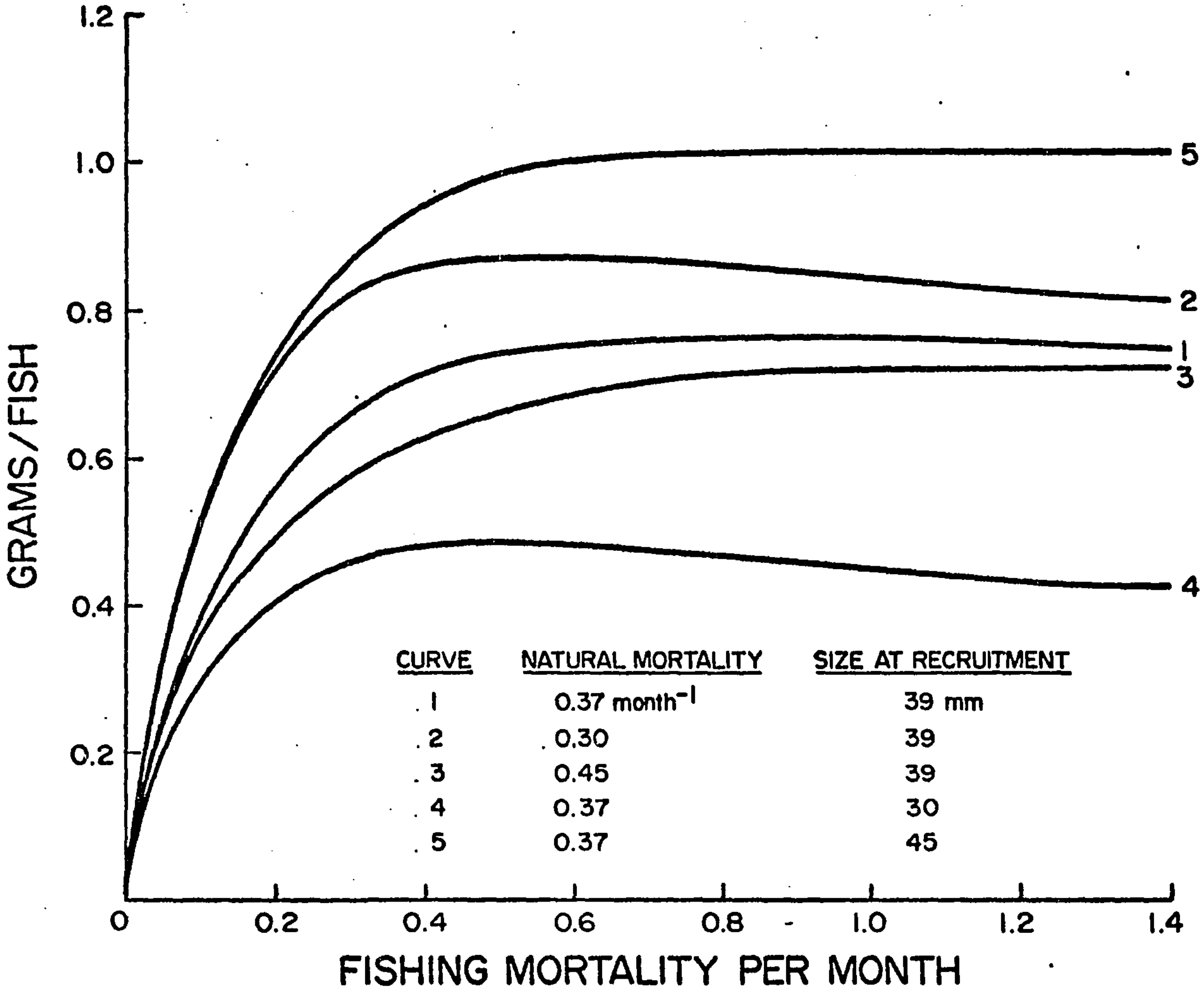
The yield per recruit as a function of fishing intensity is shown in Figure 21. For the parameters given earlier, the maximum yield per recruit was 0.76 grams per fish with a fishing intensity of 0.84 per month. In the process of estimating the natural mortality, the average fishing mortality from December 1971 to June 1973 was calculated as 0.28 per month. The yield per recruit for a fishing intensity of 0.28 per month is 0.65 grams per fish. Thus, to attain the maximum yield per recruit, only 16% above the present level, the fishing intensity would have to be increased 300%. Another way of looking at this is that to catch the maximum yield per recruit, the catch per effort would decrease 61% from the current levels.

The yield per recruit statistic can be used also as an index to assess the effects of changes in natural mortality or changes in the size at recruitment. Earlier, it was noted that the indirect method of determining fishing mortality tended to overestimate the fishing mortality which then underestimates the natural mortality. Natural mortality coefficients greater than 0.37 per month will lower the yield per recruit only slightly. For example in Figure 21, the maximum yield per recruit for M = 0.45 per month is only 3.7% less than that for M = 0.37 per month, but the necessary level of fishing to capture that maximum is up 64.3%. The main implication of underestimating the natural mortality coefficient is that while the bait population can probably accomodate more fishing than is presently exerted, the total catch will probably not increase significantly except through increased recruitment with favorable environmental conditions.

The size at recruitment strongly influences both the maximum yield per recruit and the level of effort necessary to attain the maximum. If the length of recruitment were to decrease to 30 mm SL, essentially having the fish enter the fishery one month earlier, the maximum yield would decline 38% at 52% less effort. Conversely, if the size of recruitment were 45 mm SL, the maximum would increase 38% and the amount of effort necessary to capture the maximum yield would be up 81%. Curve 4 in Figure 21 illustrates the folly of intense fishing during those months when the bait catches are comprised mostly of recruits and metamorphosing larvae.

A logical extension of the dynamic pool concept is the yield derived from a population projection matrix. The population projection matrix or Leslie matrix (Leslie 1945, Pielou 1969) integrates the number of females, l_x, their age specific fecundity, m_x, and their age specific mortality so as to predict the number of females in the next time period. The monthly bait catches were calculated by determining

Figure 21. Yield per recruit as a function of fishing intensity for five combinations of natural mortality and size at recruitment. Curve 1 illustrates the present situation in the bait fishery.


GRAMS / FISH
FISHING MORTALITY PER MONTH
1.2
1.0
0.8
0.6
0.4
0.2
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
5
2
1
3
4
CURVE
NATURAL MORTALITY
SIZE AT RECRUITMENT
1 0.37 month^{-1} 39 mm
2 0.30 39
3 0.45 39
4 0.37 30
5 0.37 45

how many females were caught in each age category, using the sex ratio to determine how many fish of both sexes were caught, and finally multiplying the number of caught fish in each category by their mean weight.

$$Y = \int_{t_c}^{t_L} 2(F/(F + M))\ N_t\ (1 - \exp(-F-M))\ W_t\ dt \qquad (46)$$

where Y is the yield in grams per boat night, t_c is the age of recruitment, t_L is the maximum age, the 2 accounts for the 1:1 sex ratio, F and M are the instantaneous fishing and natural mortalities respectively, N_t is the number of female fish aged t months, and W_t is the mean weight of t month old fish. This equation has its origins in Ricker (1944) and Gulland (1969). In the simulations, the fishing mortality was the product of the monthly mean number of lifts from Table 18 (p. 107) times the average catchability coefficient, p = 0.0012 per lift. The natural mortality coefficient was the previously estimated value of M = 0.37 per month. To account for the three month time lag between spawning and subsequent recruitment, the number of three month old fish was determined from the stock and recruitment model (Eq. 19, p. 87) using the monthly mean rainfall values at the time of hatching. The spawning stock was determined as before except the numbers of fish were generated by the projection matrix. The mean weight was determined from the von Bertalanffy equation (Eq. 7, p. 50) which yielded the mean length at age t months and this mean length was then used in the length-weight equation (Eq. 9, p. 55). To compare the different simulations, the population was allowed to achieve a steady state. In actual practice, the bait population most likely will not achieve a steady state because of the time lags in the response of the bait population to changes in mortality. If secchi disk readings were routinely taken in the Palau fishery, individual catchabilities could be calculated for each month, but in the absence of this information, I have used the average catchability coefficient of 0.0012 per lift.

This projection model still has the maximum number of recruits entering the fishery from a spawning stock of 2.86 million eggs per boat night. And for any spawning stock, the yield, Y, increases slightly more than linearly with the rainfall during the first month after hatching: $Y = aP^{1.10}$ where a represents the combined effects of the spawning stock and the mortalities and P is the rainfall in millimeters (see Eq. 19, p. 87).

A standard run was calculated and the results of the other simulations were expressed as the percent change in the catch per effort from the standard run. The first simulation used the effort and rainfall from 1974 which predicted an increase in the monthly mean catch per effort of 34%. The actual increase in catch per effort for 1974 was 38% as compared with the monthly mean in Table 18 (p. 107). The second simulation used the effort and rainfall from 1973 which predicted a decline in the catch per effort of 28% and the actual decline was 29%. Since 1973 only had catch values for the first seven months of the year, the comparisons were only for the first seven months but because of the three month time lag between spawning and recruitment and because of the time necessary for the model to come to steady state, I completed the year with the monthly mean effort values for August through December. The third simulation consisted of a series of runs to explore the behavior of the yield and the catch per effort as a function of fishing intensity. The monthly mean efforts were multiplied by a factor which assumed values from 0.25x to 4.00x in 0.25x increments. The maximum yield was only 11.6% more than the yield of the standard run but since it occurred at 2.75x the mean effort, the catch per effort associated with the maximum yield was down 57.2%. This conclusion is the same as before: increases in effort at the higher intensities will primarily decrease the catch per effort, not increase the catch. The population projection model will be used later to quantify the effects of different management schemes.

Management Considerations

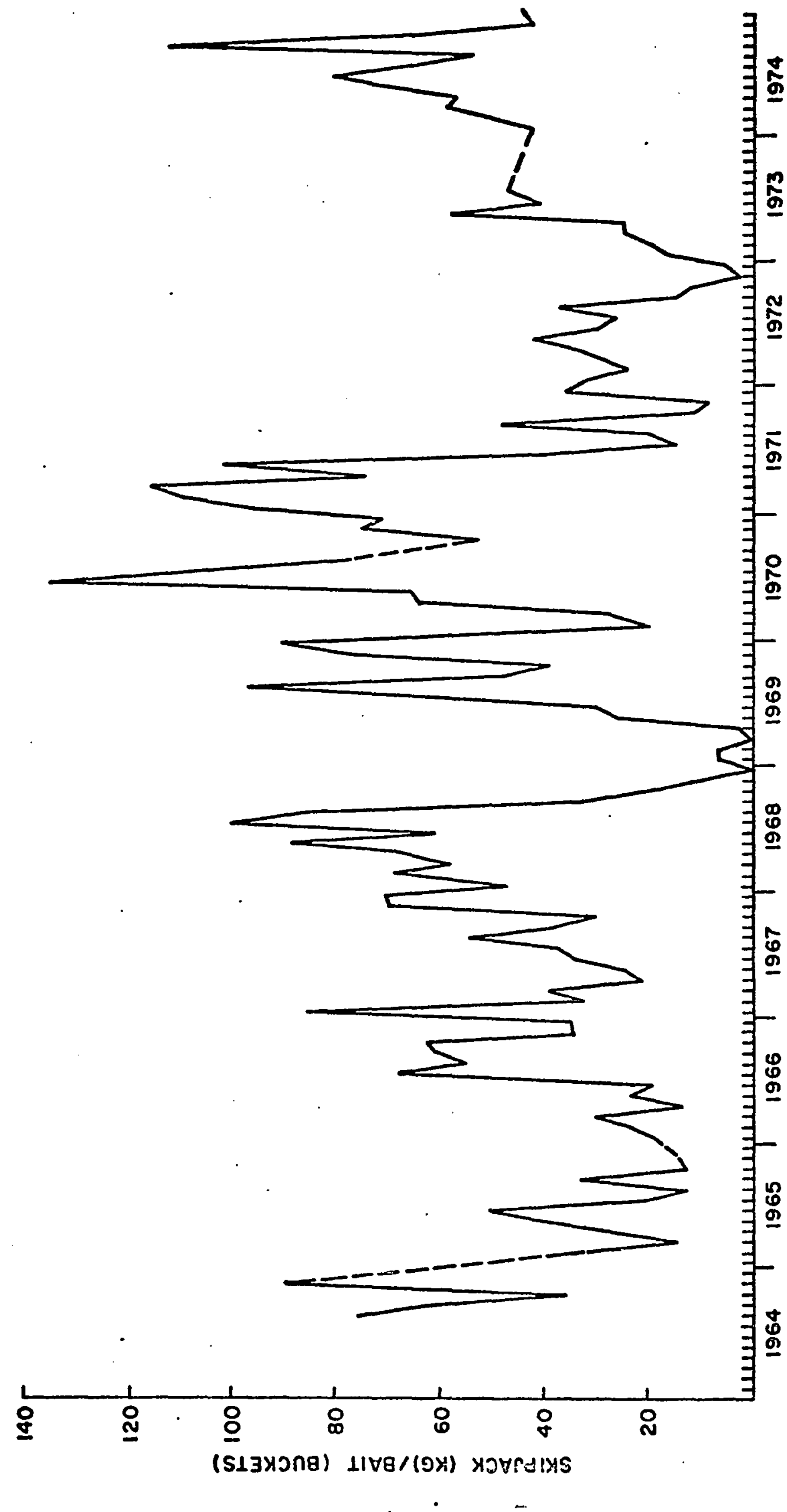
The successful management of the Palauan bait fishery depends upon the successful integration of the natural history of *S. heterolobus* and the goals of the fishery. A fundamental difference between this fishery and most others is that the bait fishery is a supportive fishery. The primary goal of the fishermen is to maximize the skipjack tuna catch not the catch of *S. heterolobus*. This means that an effective bait management program will have to be compatible with the tuna fishery.

Yuen (1959) described the characteristics of a good bait fish species for skipjack tuna fishing. One of his observations was that, within limits, size is not critical. Since the tuna react to the number of bait targets instead of to the size of the bait fish, the ideal bait fishery should supply a maximal number of bait fish to the fishing fleet. To maximize the number of fish in a cohort, bait should be caught as young as possible because the maximal number was at spawning and the numbers have rapidly decreased during the larval stages. However, there are other considerations besides quantity in choosing a good bait fish. The fish must be able to survive in the bait wells on board the tuna boats because the tuna fishing grounds are up to 100 km away from the baiting grounds. During interviews, the tuna fishermen in Palau said that the larvae die quickly in the bait wells and that the hardiest anchovies are the adult fish up to a length of about 65 mm SL. More importantly, a good bait fish must attract tuna; the larvae of Stolephorus are nearly transparent and only attain the silver lateral stripe after metamorphosing into juveniles at a length of about 39 mm SL. Thus, a compromise must be made between the number of bait fish and the fewer but more effective bait fish.

A second consideration in bait management is an awareness that the tuna fishery is not always limited by bait. Figure 22 shows the catch of tuna in kilograms per bucket of bait which gives a relative measure of tuna availability. Tuna are not equally available to the fishery throughout the year. Catches during the spring and early summer months are usually higher than those during the other months, although there may be a secondary increase in December and January.

In addition to the seasonal pattern of tuna availability, longer term fluctuations in tuna availability occurred. Three times during the history of the recent tuna fishery, tuna have been scarce. The most recent period of tuna scarcity began in the middle of 1971 and continued until the beginning of 1974 (Figure 22). When tuna were scarce, increasing the bait supply probably would not have increased

Figure 22. Monthly ratio of skipjack catch in kilograms to bait catch in buckets from August 1964 to December 1974.


SKIPJACK (KG)/BAIT (BUCKETS)
140
120
100
80
60
40
20
MONTHS
1964
1965
1966
1967
1968
1969
1970
1971
1972
1973
1974

the tuna catches significantly. A regression of daily tuna catch on daily bait catch was calculated for the fleet as a whole during November 1972, a time when tuna were exceptionally scarce, and the bait catch accounted for only 2% ($r^2 = 0.020$, df = 28) of the variation in the tuna catch. Similar regressions were calculated for two boats using the daily catch information from February to July 1974, a period when bait and tuna were both readily available. Bait supply explained only 19% ($r^2 = 0.190$, df = 100) of the variation in tuna catch for one boat and 50% ($r^2 = 0.497$, df = 110) of the tuna catch variation in the other boat. Thus, even during times of abundant bait and tuna, other components of the fishery such as labor, maintenance, breakdowns, etc., account for 50% to 81% of the variations in tuna yield.

Fishing strategy is important in utilizing the bait effectively. Kearney (1974) noted a curvilinear relationship between the skipjack catch and the bait catch in the Papua New Guinea skipjack fishery. The curve flattened out at higher catches which suggests a saturation condition. He raised the possibility of sharing high bait catches between boats because if the saturation condition is real, then two boats, each with 50 buckets of bait on board, should catch more tuna than one boat with 100 buckets of bait.

Kearney's saturation condition was tested against the situation in Palau. Again, the catch data from the first six months of 1974 were used in the analysis because it was believed that if both bait and tuna were abundant, then the saturation condition should be obvious if present. However, the relationship between tuna catch and bait load for these months was linear not asymptotic

$$T = 8.43 \times 10^{-2} B - 1.39 \tag{47}$$

$$r = 0.744,\ df = 197,\ P<0.001$$

where T is the skipjack catch in metric tons and B is the bait load in buckets of bait per boat night. Of interest to us is the negative Y intercept which suggests that there is a minimum bait load which is necessary for a successful trip. Since not every school of tuna encountered can be successfully fished, the concept of a minimum bait load seems reasonable because if a boat departs with only a few buckets of bait on board, there is the possibility that the chummer will expend the bait before a good school is located. An example of this variable response in tuna schools occurred in January 1972 when I accompanied one boat which left the baiting grounds with 30 buckets of bait and, although three skipjack schools were approached and bait broadcasted, only 28 skipjack were caught during the entire day.

The linear relationship between tuna catch and bait load also could be the result of the two different sized tuna boats used in Palau. The 22 m boats are faster and carry more bait than the 15 m boats. Vessel speed is a factor in catching tuna because for the same density of tuna schools, the faster boats would have less time between schools. Hence, the larger, faster boats have the potential for using more bait and catching more tuna.

Although tuna catches are not solely explained by variations in the bait supply, an understanding of the sources of variations in the bait supply, i.e., *S. heterolobus* catches, will be fruitful. The main considerations are: the effectiveness of the fishing gear, the expenditure of fishing effort, and the density of bait in the baiting area.

First, the effectiveness of attracting bait with an underwater light depends upon the wattage of the underwater light, the ambient light intensity, and the water clarity. To compare the relative importance of these factors, radii were calculated from Appendix Equation 1 (p. 153) for the maximum, minimum, and mean secchi depth measurements (Figure 7, p. 38) using light sources of 1000 W and 100 W with threshold light intensities of 6×10^{-4} $\mu W\ cm^{-2}$, full moonlight at 2 m, and of 9.1×10^{-5} $\mu W\ cm^{-2}$, the threshold for new moon nights. Table 22 lists the radii.

All of the boats currently use 1000 W underwater lights; however, until 1968, 350 W lights were used. The catchability of the 350 W light is about 0.9 that of the 1000 W light. The radius for the 100 W light on a new moon night is about the same as the radius for the 1000 W light on a full moon night.

Ambient light levels changed with the lunar cycle. The phases of the moon were determined from the American Ephemeris and Nautical Almanac for the appropriate year. The daily catch of bait, skipjack, and the number of lifts were tallied for the new moon and for the full moon. The time of the respective phase was calculated for Palau, then the statistics from three days prior to three days after that time were summed. No significant difference was observed between the number of lifts made during each lunar phase (paired $t = 0.217$, $df = 42$, $P = 0.829$). Furthermore, again using the tuna catch per bucket of bait as an index of tuna availability, tuna was apparently more available during full moon days (paired $t = 2.49$, $df = 39$, $P = 0.017$). The increase could reflect, as will be shown next, the lower bait load

Table 22. Radii in meters of volumes of illuminated water as calculated with a range of transparencies, two wattages of light sources, and the lunar phases.

		Maximum	Mean	Minimum
Secchi depth m		24.5	16.0	10.4
K	m^{-1}	0.069	0.106	0.163
Wattage	Moon		Radius m	
1000	New	125	88	62
	Full	103	74	52
100	New	99	71	50
	Full	78	57	41

during full moon nights. Thus, while effort and motivation, as judged by tuna availability, were similar or higher for full moon versus new moon, the lifts during the full moon contained, on the average, 40% less bait than those made during the new moon (paired $t = 6.24$, $df = 42$, $P = 0.000$). I attributed the difference in catch rates to the higher ambient light intensities which reduced the attracting power of the underwater light. This difference was used earlier in determining the threshold light intensity for a positive photo-response in _S. heterolobus_.

Water clarity appeared to exert the greatest influence on the catchability. Depending upon the transparency, the radius of the illuminated water could vary twofold and the corresponding instantaneous fishing mortality would vary from 7.0×10^{-4} per lift to 1.6×10^{-3} per lift. The effect of this variation in catchability when using the catch per lift as an index of abundance is to underestimate the bait density during the rainy season when the water is more turbid and to overestimate the bait density during the dry season when the water is more transparent. This information can be used to refine the catch and effort models. For example, if the exponential fishery model is recalculated for the months with secchi data, we can determine the yield as a function of effort using just the catch and lift data and then determine the yield using the catch and fishing mortality estimates for each month. By calculating separate catchability coefficients for each month (Table 23) using the average secchi depth for the month, the fit of these data to the exponential model improves from $r^2 = 0.590$ for catch and lifts to $r^2 = 0.785$ ($df = 16$). The yield expression

Table 23. Monthly catch, effort, catchability coefficients, and instantaneous fishing mortality from December 1971 to June 1973. Also included in this table are the mean secchi depths; extinction coefficients; capture radii, based upon the secchi depths; the volume of water illuminated at one instant, V'; and the volume of water flowing through the lighted cross section, V". The entries in the table have been rounded after final calculation.

Month	Catch Buckets	Effort Lifts	Secchi Depth m	K m^{-1}	R m	V' $10^5 m^3$	V" $10^6 m^3$	Total Volume 10^{-3} km^3	q 10^{-3} lift	F $month^{-1}$
December 71	3078	111	12.3	0.138	70.8	4.56	8.41	8.87	0.9	0.107
January 72	4576	106	13.8	0.123	77.9	5.57	9.30	9.86	1.1	0.114
February	5381	144	11.7	0.145	67.9	4.18	8.05	8.45	0.9	0.133
March	5332	201	15.0	0.113	83.5	6.44	10.00	10.64	1.2	0.232
April	7376	265	17.9	0.095	96.3	8.65	11.59	12.45	1.4	0.359
May	10473	335	17.9	0.095	96.3	8.65	11.59	12.45	1.4	0.453
June	7867	243	12.4	0.137	71.2	4.62	8.46	8.93	1.0	0.236
July	8684	251	15.0	0.113	83.5	6.44	10.00	10.64	1.2	0.290
August	8901	355	18.7	0.091	99.8	9.30	12.02	12.95	1.4	0.500
September	6353	375	18.4	0.092	98.9	9.13	11.91	12.82	1.4	0.523
October	5420	185	15.2	0.112	84.1	6.54	10.07	10.73	1.2	0.216
November	5091	156	18.5	0.092	98.9	9.13	11.91	12.82	1.4	0.217
December	5176	111	13.4	0.127	75.8	5.27	9.04	9.57	1.0	0.115
January 73	5532	184	13.4	0.127	75.8	5.27	9.04	9.57	1.0	0.191
February	4538	174	17.5	0.097	94.7	8.35	11.39	12.22	1.3	0.231
March	3407	150	16.0*	0.106	88.0	7.18	10.56	11.28	1.2	0.184
April	4702	251	18.5	0.092	98.9	9.13	11.91	12.82	1.4	0.350
May	3798	479	24.5	0.069	125.0	14.74	15.13	16.60	1.8	0.864
June	6692	378	15.5	0.110	85.4	6.74	10.23	10.91	1.2	0.448

* estimated as overall mean secchi depth

for fishing mortalities is

$$C = 4.65 \times 10^4 F \exp(-2.49 F) \qquad (48)$$

where C is the catch in buckets and F is the fishing mortality per month. The maximum yield of the equation is 6850 buckets per month taken at $F = 0.40$ per month. For a constant catchability coefficient of 0.0012 per lift, the fishing mortality is attained with 333 lifts per month which by equation (26) (p. 103) is equivalent to 208 boat nights. These results are similar to the earlier estimates based upon a six month period from each of 10 years of 7600 buckets at 186 boat nights.

The second source of variation in bait catches is the expenditure of effort. The number of lifts during a month depends upon the number of boats fishing and upon the number of boats in the Palauan skipjack tuna fleet has varied from four boats in 1967 to over 20 boats in 1971. The maximum fleet size is inexact because in 1971 several mother ships and their accompanying catcher boats fished intermittently without submitting adequate catch reports. The modal fleet size has been eight boats with the maximal number of 12 boats allowed since 1972. The 12 boat limit was set by the Trust Territory Government and is subject to revision by Marine Resources Division.

The number of fishing trips that a boat makes during a month depends upon the crews and breakdowns as well as upon the probability of successful fishing. The efficiency of the shore management was quantified as the ratio of the actual number of boat nights to the maximal number of boat nights, i.e., if every boat fished every night during the month. The ratio varied from 50% to 70%. The fishermen fish more if tuna is available. The number of lifts during a month and the tuna abundance, as measured by the catch of skipjack per bucket of bait, were significantly correlated ($r = 0.59$, $df = 124$, $P<0.01$). Effort is seasonal with more lifts from May to September (Table 18, p. 107).

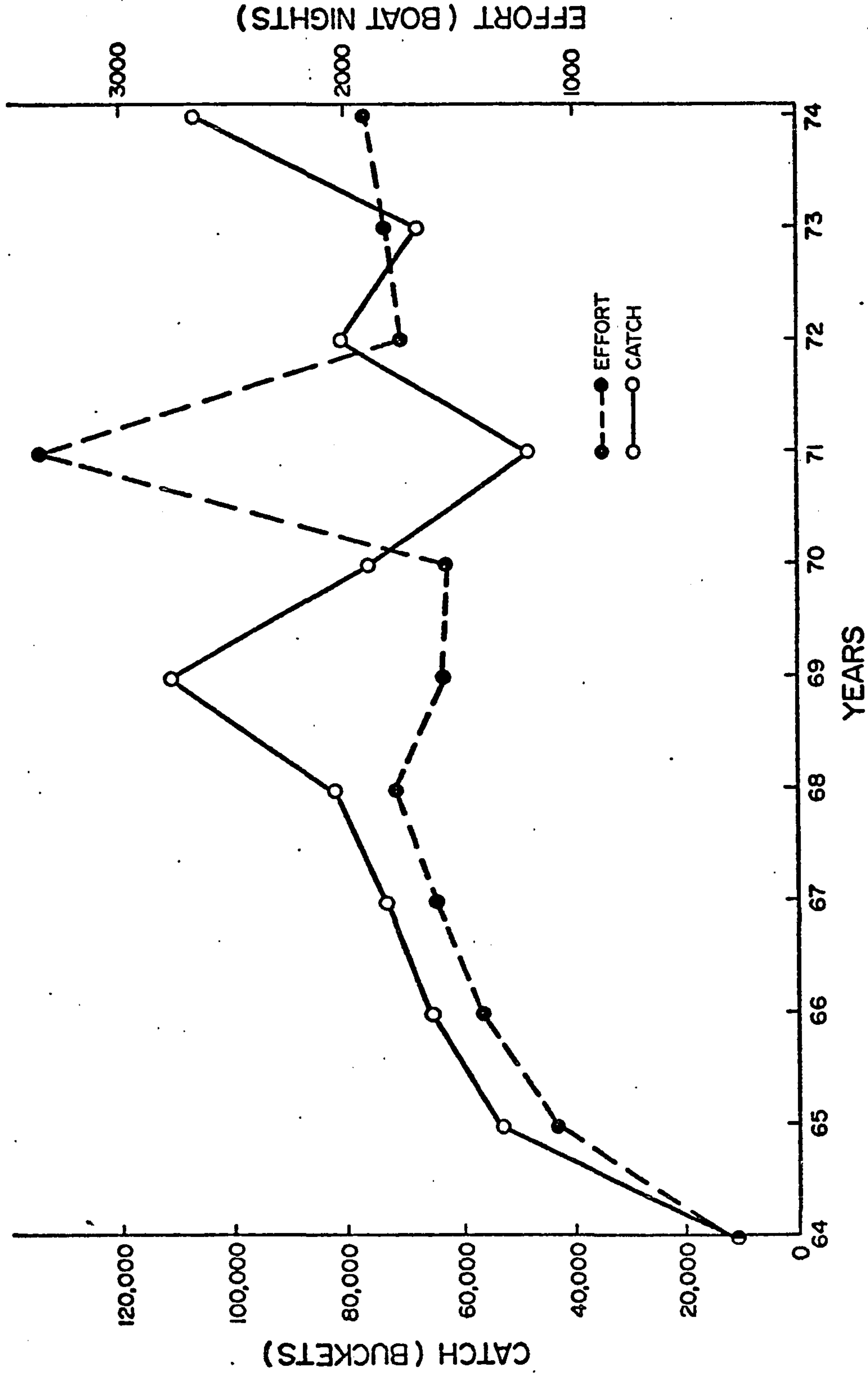
The last source of variation in the bait catches stems from the actual differences in the bait density in the baiting area. The bait density depends upon migration, mortality, and recruitment. Mortality and recruitment have already been discussed: environmental factors become very important at high fishing mortalities when the actual number of fish are important as compared to effort being very important at low fishing mortalities when the catches increase with more effort. Migration was not addressed in the design of this study, but no physical barriers prevent S. heterolobus from migrating throughout Palau. Yamaguchi (1972) reported anchovy eggs believed to be S. heterolobus in all of the passages in the barrier reef surrounding the main island chain. Further, in Figure 10 (p. 52) there are two modes, one in June and the other in July 1972, of fish larger than 80 mm which suddenly appeared in the bait samples. Another example from the length frequencies was the appearance of many sizes of fish in the November 1972 bait samples when the October bait samples just before were unimodal. Also, I concluded earlier that the spawning stock moved throughout the lagoon. Thus, while the decreases in catch per effort can be the result of the bulk of the population migrating, the pattern outside of the baiting area seems to be that the first night catches are good but there is an almost immediate, within a week, decrease to the prevailing catch rates.

The similarity of the catch rates from elsewhere and from those in the main baiting area suggests that the decreases in catch per effort reflect an actual decrease in numbers of fish.

In light of these sources of variation in the bait catches, I would like to attempt a reconstruction of the history of the fishery. From 1964 to 1968 (Figure 23), the catch closely paralleled the increasing effort, as predicted in the fishery models. During these years, effort was moderate, about 1500 boat nights per year, and rainfall was also moderate, about 3.5 m per year. The record high bait catch per effort in 1969 resulted most likely from the combination of high rainfall in December 1968, 405 mm, which would enhance recruitment and the sharp decline in effort after a tropical storm in October 1968 reduced the fleet to five boats. Rainfall was below average in late 1969 and early 1970 suggesting reduced spring recruitment. Detailed bait information, which began in July 1970, revealed that much of the baiting in 1970 took place outside of the main baiting area. The decrease in catch per effort in the latter half of 1970 was quite evident: the December 1970 catch rate was only 17.1 buckets per lift as compared to the rate for the previous August which was 67.1 buckets per lift.

Probably the most informative year for understanding the bait fishery was 1971. The decrease in bait catch rates which began in 1970 continued into 1971 although rainfall was high suggesting good larval survival in the spring. The prediction of good recruitment from the rainfall was borne out as the bait samples collected by Marine Resources personnel in March through May 1971 were almost exclusively recruits (30 mm to 35 mm SL). Had these fish been allowed to grow,

Figure 23. Annual bait catch in buckets and the annual fishing effort in boat nights from 1964 to 1974. Solid line - catch; broken line - effort.



EFFORT (BOAT NIGHTS)
3000
2000
1000
CATCH (BUCKETS)
120,000
100,000
80,000
60,000
40,000
20,000
0
64
65
66
67
68
69
70
71
72
73
74
YEARS
EFFORT
CATCH

the bait shortage would probably not have been so severe, but at the same time as the larvae and the juveniles were supporting the fishery, the fleet size was doubled. Fishing companies in Palau brought in mother ships, each with one or more catcher boats. By summer, the average catch had declined to less than 8 buckets per lift. By November, only one mother ship with one catcher boat remained and by December, only the six local boats were operating. With the recruitment of the fall 1971 spawn, the December catch rate had increased to 27.7 buckets per lift.

Catch levels in 1972 resembled the earlier years of 1965 to 1968 with moderate fishing and moderate rainfall. Beginning in late 1972, rainfall was below average and by January 1973, Palau was experiencing a severe drought. Rainfall in February 1973 was only 31 mm, 164 mm below the February average. Few recruits were collected in the bait samples during the drought - the bait fishery was catching the survivors from 1972. By May, the catch rate was only 7.9 buckets per lift, a 75% decrease from the previous year's levels. Rain began to fall again in early April and recruits began entering the fishery in late June. Unfortunately, the catch data from mid-August to December 1973 are unavailable. Rainfall since April 1973 has been abundant and with the spring recruitment in 1974, the 1974 catch per effort levels have been average or above.

If this reconstruction of events in the history of the bait fishery has some basis in reality, then there are three main insights here into the bait population - fishery interactions: first, the bait supply is susceptible to environmental factors; second, fishing pressure can compound bait scarcities by removing the larvae and juveniles; and third, the bait resource is resilient. These three points are the foundation of an effective management policy for the bait fishery.

In the absence of physical barriers to migration, the bait population in Palau is assumed to represent a single stock (see Table 19, p. 111). If this assumption is valid, then the possibility of locating a virgin stock is remote and management will have to concentrate on maximizing the utilization of existing bait supplies.

Management techniques considered for S. heterolobus in Palau included gear restrictions, closed seasons, and limited entry. The population projection model developed earlier provides a vehicle for quantifying the effects of these different management schemes. These evaluations were also compared against the standard run which used the lift history data and estimates together with the mean monthly fishery statistics.

Regulating the minimum mesh size so as to allow for a larger size at recruitment at first seemed promising. For a recruitment size of 45 mm SL, or entry into the fishery at age four months instead of the present three months, the dynamic pool model predicted a yield per recruit of 0.85 grams per fish at the present fishing mortality of 0.28 per month. This yield is an increase of 31% over the present predicted yield per recruit of 0.65 grams per fish. Further, the higher age of recruitment should provide more repeat spawners to the bait stock which, in turn, can act as a buffer against environmentally induced fluctuations. The problem with postponing recruitment is that with the estimated high natural mortality of *S. heterolobus*, the gain in yield per recruit is offset by the reduced number of fish entering the fishery. The simulation indicated an overall decrease in catch per effort of 21.3%. A second reservation against changing the mesh size is R. Kearney's observation (personal communication) that few *S. heterolobus* survive passing through the net because of their deciduous scales and the resulting osmotic unbalance.

The second management technique which was considered was the institution of a closed season. Ideally, the tuna and bait fisheries would close down during a time when tuna were less available and when bait are just recruiting. The desired result is to let the small fish grow into more effective bait later in the summer when the tuna are more available. Figure 22 (p. 134) showed that tuna abundance was usually lower during March and April than during the summer, except for 1971. Therefore, simulations were run with closed seasons in February, March, April; February and March; and March and April. The greatest increase in the catch per effort, 25%, during the summer season, May through August, came from closing down during March and April; the second greatest increase, 14%, came from closing down just during April. In addition to the increased bait during the summer tuna season, the closed season provides a regular time for refurbishing the fleet prior to the onset of the "real" tuna season.

A more variable alternative to this method would be to monitor the bait catches during the spring with the proviso of being able to shut down the fishery if the proportion of recruits exceeds a specified level. The flexibility of this method is also its main drawback because it does not allow sufficient warning to permit the scheduling of crews, drydock facilities, parts or other materials.

Gear restrictions and closed seasons, while attempting to increase the bait supply, do not address the prime question: what is the optimal fleet size that the bait supply can support? Presently, the maximum number of boat operating in the Palauan skipjack fishery is restricted to 12 boats by the Trust Territory Government. However, there is interest in expanding the fleet which has been prompted by the high tuna and bait catches in 1974 and the first half of 1975.

Now I would like to examine the rationale behind the present 12 boat limit. The catch statistics in Table 18 (p. 107) give a mean number of lifts per month and a mean of 143 boat nights per month. During these 47 months, the mean fleet size was 8.9 boats. Thus, the average boat made 143/8.9 or 16 baiting trips a month. With everything else being equal, then 12 boats would make 193 boat nights a month. The average boat made 221/143 or 1.5 lifts per boat night. The 12 boat fleet would then made 290 lifts per month which, for average turbidity, is equivalent to a fishing mortality coefficient of 0.35 per month. If we use the dynamic pool model, increasing the instantaneous fishing mortality to 0.35 per month will decrease the catch per effort 18%. In pole and line tuna fishing, the most important bait statistic is the bait load or the number of buckets of bait caught during the nightly baiting session. The average catch of bait per boat night during these 47 months was 39.8 buckets per boat night and decreasing this amount by 18% gives 32.5 buckets per boat night for the 12 boat fleet. Earlier a relationship between tuna catch and bait load

(Eq. 47, p. 136) was determined for the daily catch data in the spring of 1974 with a positive X intercept which implies a minimum bait load for successful tuna fishing. A bait load of 32.5 buckets per boat night would expect a skipjack catch of 1.3 metric tons during a time of tuna abundance. The average bait load of 39.8 buckets would expect a skipjack catch of 2.0 metric tons and they actually yielded 2.1 metric tons. The economic break-even point for a boat in Palau is in between these two catch levels. The ultimate impact from 12 boats would be if every boat were to make two lifts every night or 720 lifts per month, $F = 0.86$ per month. The catch per effort corresponding to this fishing intensity is 15 buckets per boat night which is below the minimum necessary load of 16 buckets per boat night from Eq. (47).

This exercise has been based upon the average values from the 47 months of catch data presented in Table 18 (p. 107). Further, these results were determined with the dynamic pool model which was based upon the partitioning of the total mortality into that due to fishing and that due to natural causes. Because it would be difficult to state the precision of the natural mortality determined this way, a similar analysis to the above was calculated using a natural mortality coefficient equal to the average total mortality, $Z = 0.65$ per month. The catch per effort decreased more slowly with increasing fishing intensities but the conclusion is still the same: the yield per recruit per boat night will not increase with more boats. When this type of exercise was run using the exponential yield model instead of the dynamic pool model, the conclusions were the same.

From all the foregoing, I conclude that the present fishery is operating near its optimum level with respect to the bait supply.

If the fishery is near its optimum level, how can the fishery expand? The preceding conclusion has been derived from the fishery data from August 1964 to December 1974. During this period, the range of effort has been quite narrow except for the ill-timed increase in 1971. Since the 12 boat limit went into effect in 1972, the mean number of active boats has been only 8.2 boats - only two-thirds of the allowable limit. Furthermore, those 8.2 boats averaged only 19 trips a month, and so there is room for expansion within the existing regulation. The fishery should expand to the allowable limit in order to test the validity of these findings. The scarcity of data at fishing intensities around 250 to 300 boat nights per month has tended to generate conservative conclusions.

The main recommendation of this study is to actively monitor the catch levels and the size composition of the bait catches, and to annually review the conclusions of the fishery models in light of the increasing body of knowledge on bait dynamics.

SUMMARY

Life History

1. The distribution of S. heterolobus parallels the distribution of high primary productivity waters in the Indo-Pacific.

2. Length frequencies from twice weekly bait samples obtained from the commercial fleet were used to estimate growth, mortality, and recruitment in S. heterolobus.

3. Growth of S. heterolobus could be described by a von Bertalanffy equation

$$l_t = 91.1\ (1 - \exp\ (-0.174\ (t + 0.150)))$$

where l_t is the length at time t months, 91.1 is the asymptotic length in millimeters SL, and 0.174 per month is the growth rate. Counts of the daily rings on the otoliths from 13 fish corroborated the length frequency growth estimates.

4. Fecundity was determined from 10 female fish

$$F = 457\ W + 2.70$$

where F is the number of mature eggs and W is the body weight in grams. The relative fecundity was 450 eggs per gram of body weight.

5. Ovarian egg size distributions from 21 fish gave evidence that S. heterolobus spawns more than once with an interval between spawnings of approximately three months.

6. The average total mortality from December 1971 to June 1973 was 0.65 per month.

7. Rainfall was important in determining recruitment. The modified Ricker equation describing the relationship between the spawning

stock and the successive recruitment three months later is

$$R = 1.41 \times 10^{-2} \, S \, P^{1.10} \exp(-3.50 \times 10^{-7} \, S)$$

where R is the recruitment expressed in eggs per boat night, S is the spawning stock in eggs per boat night, and P is precipitation millimeters per month.

Bait Fishery

1. Bait catches during the full moon averaged 40% less bait than those lifts made during new moon nights.
2. Equilibrium yield models based upon catch and effort statistics suggest that the present fishery is near its optimum level.
3. The average catchability of one lift of the blanket net was estimated as 0.0012 per lift. For an average of 232 lifts per month, the equivalent instantaneous fishing mortality was 0.28 per month. Thus, the total mortality, Z = 0.65 per month, was partitioned into fishing mortality, F = 0.28 per month, and the unexplained or natural mortality, M = 0.37 per month.
4. Dynamic pool models with a natural mortality coefficient of 0.37 per month gave a maximum yield per recruit of 0.76 grams per fish at a fishing mortality of 0.84 per month, the equivalent of 700 lifts per month. The yield per recruit at the average fishing mortality of 0.28 per month was 0.65 grams per fish or within 16% of the maximum.
5. A population projection model combining the dynamic pool concept and the stock and recruitment relationship suggested that environmental factors are more important in determining the catch at

higher levels of exploitation and the fishing intensity is more important at lower levels of exploitation,

6. The yield models predict that the catch will not continue to increase with increased fishing. Expansion of the bait fishery will have to be at the expense of increased competition between the tuna boats.
7. A relationship between tuna catch per trip and bait load per trip was significant and it had a positive X-intercept which implies that there is a minimum number of buckets of bait necessary for a successful trip.
8. Limited entry is presently the main management technique currently used in Palau to regulate the bait fishery. This policy should be continued and could be augmented by closing the fishery during March and April.
9. A bait monitoring program should be established to collect bait samples and to analyze catch information for periodic revisions of the existing management regulations.

APPENDIX

Fishing mortality was assessed indirectly using the swept area concept - one unit of fishing affects a known segment of the population. In Palau, bait fish are attracted with an underwater light and then captured with a lift net. By assuming that once a fish perceives the light, it is eventually caught, the probability of being caught simplifies to the probability of being in the illuminated water. This probability is then the ratio of the volume of water illuminated to the volume of suitable habitat.

The volume of illuminated water can be calculated from the output of the underwater light, the threshold light intensity for a positive photo response in the bait fish, and the extinction coefficient for the water. The extinction coefficient was initially obtained from a K-meter and later with a secchi disk. Before the demise of the K-meter, four stations used both methods to estimate the extinction coefficient and the differences were insignificant (paired $t = 0.25$, $df = 3$, $P = 0.591$).

There are no data on light sensitivity for S. heterolobus in the literature other than the observation that S. heterolobus is attracted to light (Tham 1970). To quantify this attraction somewhat, I used the difference in bait catch per effort on full moon nights and on new moon nights as a means of approximating the threshold light intensity for S. heterolobus. The minimum light intensity for a positive photo response during full moon nights should be no lower than the ambient light intensity, 6×10^{-4} µW cm^{-2} at 2 m (interpolated from Clarke 1971). This ambient light value was used as the initial threshold intensity.

Light is attenuated in water by dilution which follows the inverse square law and by absorption which is measured by the extinction coefficient (Nicol 1958). Combining these two processes yields an expression for the light intensity at any distance from the source. This expression is similar to Nikonorov's (1959) equation for the nightlighting of the Caspian kilka, Clupeonells Sp.

$$I_R = I_o \text{ (exp } - (K\ R))/4\pi R^2) \qquad (1)$$

where I_R is the intensity at a distance R meters from the source, I_o is the output of the light source, K is the extinction coefficient, and the 4π term is necessary because the light can be considered a point source. Solving equation (1) iteratively for R gives a capture radius of 74 m for a 1000 W light, K = 0.106 per meter, and I_R = 6×10^{-4} μW cm^{-2}.

During this study, bait catches from nights near the full moon averaged 40% less bait than those catches during moonless nights ($t = 3.20$, $df = 60$). This decline was attributed to the higher ambient light levels reducing the effectiveness of the nightlight. Thus, a new radius of 88 m was calculated for moonless nights by increasing the volume of illuminated water 40% and solving for this radius. The resulting threshold for a positive photo response for S. heterolobus without the moon was 9.1×10^{-5} μW cm^{-2}.

The total volume of water illuminated during a baiting session, V, is the amount of water illuminated at any one instant, V', plus the tidal flow through the lighted cross section, V".

From the basic equation of a circle with its center at the origin

$$R^2 = X^2 + Z^2 \tag{2}$$

where R is the radius, X is the horizontal distance, and Z is depth, the amount of water illuminated at any one distance, V', can be easily calculated via the elementary technique of integrating solids of revolution. The horizontal distance can be considered as a radius about the ordinate; the area of this disk is πX^2 and its volume is $\pi X^2\,dz$. If the light is assumed to be positioned at the origin and increasing depth is positive, then the volume of water illuminated at any one instant is the sum of the disks each with a volume of $\pi X^2\,dz$, from the surface, -2.0 m, to the mean bottom depth, 28.5 m, or

$$V' = \pi \int_{-2.0}^{28.5} X^2\,dz \tag{3}$$

but from equation (2), $X^2 = R^2 - Z^2$ and so for R = 88 m

$$V' = \pi \int_{-2.0}^{28.5} (R^2 - Z^2)\,dz \tag{4}$$

$$= 7.2 \times 10^{-4}\ \mathrm{km}^3$$

Half of the illuminated, cross sectional area is obtained by a straightforward integration from the surface to the bottom. Again, Z is depth and X is horizontal distance. Each increment has an area of X dz. From equation (2), $X = (R^2 - Z^2)^{\frac{1}{2}}$, and with the assumption of symmetry, the cross sectional area is

$$A = 2 \int_{-2.0}^{28.5} (R^2 - Z^2)^{\frac{1}{2}}\,dz \tag{5}$$

Tidal currents in the baiting area ranged up to 0.3 m $\sec^{-1}$ or 1 km hr^{-1}, based upon timing floating objects and drogues. The average tidal velocity was 0.5 km hr^{-1} and the typical period between lifts was 4 hr. Thus, the volume of water flowing through the lighted cross section was

$$V'' = (0.5 \text{ km hr}^{-1}\ 4.0 \text{ hr})\ A \tag{6}$$
$$= 1.0 \times 10^{-2} \text{ km}^3$$

The total amount of water being sampled during an average lift is

$$V = V' + V'' \tag{7}$$
$$= 1.1 \times 10^{-2} \text{ km}^3$$

The volume of habitat, 9.2 km^3, was calculated as the product of the mean depth, 30.5 m as determined from echo soundings, and the area of the lagoon between the barrier reef and the islands of Babelthuap, Koror, Urukthapel, and Aulong, 300 km^2 as planimetered from U.S. Navy Hydrographic Chart No. 6073.

The lift net in Palau is about 13 m on a side and after the light is dimmed prior to hauling, the bait forms a ball approximately 7 m in diameter and most of the fish are caught. With the assumption that fish in the illuminated water are caught, the probability of a fish being caught is

$$P = 1.1 \times 10^{-2} \text{ km}^3 / 9.2 \text{ km}^3 \tag{8}$$
$$= 1.2 \times 10^{-3}$$

Thus, the instantaneous mortality associated with one unit of effort is 0.0012 per lift.

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