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Growth, mortality, parasitism, and potential yields of two *Priacanthus* species in the South China Sea

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In the northern part of the South China Sea the ' big-eye ', *Priacanthus tayenus*, spawned once a year in June, had von Bertalanffy growth parameters of $k=0{\cdot}8$ and $L_\infty=30$ cm, and a mean total annual instantaneous mortality of $Z=2{\cdot}0$, calculated from adjusted catch curves and a mean length equation. The natural mortality rate $M=1{\cdot}4$, fishing mortality rate $F=0{\cdot}6$, and the exploitation rate (E) was 0·27. The maximum potential yield, calculated using Marten's method, was 0·06 kg/recruit when $F=5{\cdot}4$. The fish were heavily parasitised by the protozoan *Pleistophora priacanthicola*.

A second big-eye, *P. macracanthus*, spawned twice a year in May–June and September, had growth parameters of $k=0{\cdot}7$ and $L_\infty=32$, and population parameters of $Z=2{\cdot}0$, $F=0{\cdot}7$, and $E=0{\cdot}34$. The maximum potential yield was 0·13 kg/recruit when $F=5{\cdot}8$.

A marked reduction in fishing mortality occurred for both species between 1965 and 1966, coinciding with the onset of the Chinese Cultural Revolution. Our estimates of maximum potential yield correspond to fishing mortalities eight times estimated levels, though such heavy exploitation could risk recruitment failure.

I. INTRODUCTION

Priacanthus species or big-eyes are a commercially valuable group in Southeast Asia. In Hong Kong over 10,000 t were landed in 1982. This accounted for 15% of the total fin-fish landings (Lee, pers. comm.). In 1966 they constituted 13% of the total weight of fish landed by pair trawlers, being 8% *P. tayenus* and the remaining 5% *P. macracanthus*. They were also taken by longliners. Williamson (1968) reported that 1400 t of *P. tayenus* were landed annually at the Hong Kong Fish Marketing Organization markets between 1963 and 1967.

The authors are unaware of papers on the population biology of *P. macracanthus*, or of work describing the population biology of priacanthids for the South China Sea, despite their importance to the fisheries in the region. Estimates of various growth parameters for *P. tayenus* were reported by Chomjurai & Bunnag (1970), and by Pauly (1980*a*) based on Boonyubol & Hongskul (1978) for the Gulf of Thailand. Tiews (1965) reported that a large increase in the fishing effort did not result in decreased catch per unit effort of *P. tayenus* in the Gulf of Thailand. Beddington & May (1982), however, reported a declining catch per unit effort of *Priacanthus* sp. in the Gulf of Thailand over a 15-year period from 1963. Lester (1968) described the diurnal variability in catch per unit effort for *P. tayenus* and *P. macracanthus* near Hong Kong.

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In this paper we present length frequency and other observations made in Hong Kong between 1964 and 1967, and use them to estimate potential yields.

II. MATERIALS AND METHODS

Length measurements (snout to caudal fork to nearest cm below) were obtained from market landings. Random samples of approximately 200 fish were measured twice monthly. Over 44 000 *P. tayenus* and 28 000 *P. macracanthus* were measured during 1965, 1966 and 1967. The locations where the fish were caught were provided by the captain of the fishing vessel when the fish were measured. The quarterly average catch rates for the different areas (P. J. Gaiger, unpubl. data) were then combined with the length frequency data to give the relative abundance of the various size classes by season for different parts of the South China continental shelf.

A gross examination of the body cavities of about 50 fish of each species each month was made for 1 year to determine the state of gonad maturation. These fish came from a ground 100 km south of Hong Kong in 90 m. Most were taken by the R.V. *Cape St. Mary* and examined at sea. At the same time information was collected on the prevalence of a parasite, the microsporan *Pleistophora priacanthicola* (He, 1982). Fecundity of females was estimated by opening a 'running ripe' gonad, suspending the eggs in a measured volume of saline, and counting the number of eggs in a small aliquot.

Relative ages based on the spawning period suggested by maturity data were assigned to the modal peaks of the length frequency plots. The numbers and average lengths were calculated for each relative age for each month by assuming a normal distribution about the modal peaks. *Priacanthus macracanthus* that resulted from spring and autumn spawnings, hereafter referred to as spring and autumn fish respectively, were separated using their growth pattern as criteria. It was assumed that spring *P. macracanthus* would grow at a similar rate to *P. tayenus* which was also a spring spawner. Although evidence presented later suggested that males and females had different growth rates, analyses were done on combined data as fish were not sexed during market measuring.

Computer programmes using the least squares method were used to fit both the regular von Bertalanffy growth curve (Dr G. Kirkwood, CSIRO Fisheries, Hobart, Australia; pers. comm.), and an expanded formula allowing for seasonal growth (Pauly & Gaschütz, 1979). For these and subsequent analyses the spring and autumn *P. macracanthus* were combined. Analysis of variance techniques were used to test if the addition of a seasonal component to the von Bertalanffy growth equation significantly improved the fit.

Catch curves were adjusted to allow for the slower growth of older fish by dividing the natural log of the numbers of fish at each relative age by the time needed to grow through the size class (Ricker, 1975). These adjusted numbers were plotted against the relative age estimates and the descending limbs of the resulting catch curves were used to estimate total mortality, Z. Beverton & Holt's (1956) equation which uses the length at full recruitment or critical length, l_c, the average size of fully recruited fish, L, and the asymptotic length, L_∞, was also used to estimate total mortalities.

The parameters of the weight–length relationship were calculated from 128 *P. tayenus* and 132 *P. macracanthus* measured and weighed at the Hong Kong Fish Market in 1982 and 1983. An empirical estimate of natural mortality, M, was calculated using the asymptotic weight W_∞, k, and the mean environmental water temperature in degrees centigrade (Pauly, 1980*b*). The mean temperature in the study area at 40–140 m depth was 23° C (Williamson, 1968). It was assumed that this did not change markedly during the study years.

Fishing mortality, F, was calculated by subtracting natural mortality from total mortality for each of the study years. Exploitation rates, E, were calculated as F/Z.

Optimum yields were calculated using a formula derived by Marten (1978) which uses fishing mortality, natural mortality, and the critical time of recruitment, t_c. The last approaches 1·0 as the asymptotic length is reached. Values for t_c were calculated from the critical length of recruitment, l_c, assuming linear growth. Marten's (1978) yield formula assumes linear growth after t_c. This condition was satisfied ($P<0·05$) as both *P. tayenus*

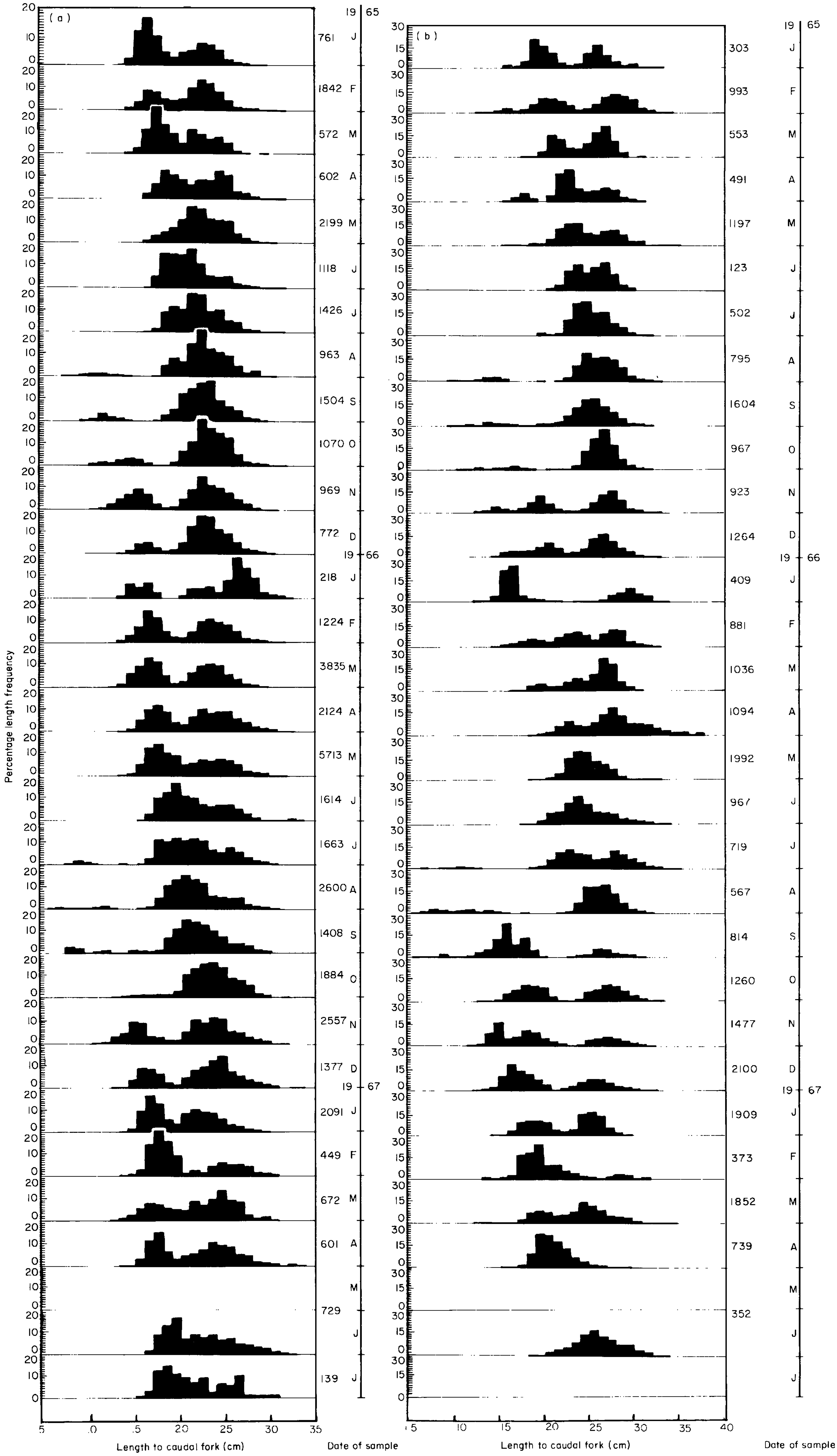


FIG. 1. Monthly length-frequencies of (a) *Priacanthus tayenus* and (b) *P. macracanthus* for 1965, 1966 and 1967. Percentage length frequency plotted against length to caudal fork (cm), monthly sample size on right. The total sample size for *P. tayenus* was 44 696 and for *P. macracanthus* was 28 256.

and *P. macracanthus* grew to more than two-thirds of their asymptotic length before they were fully recruited. Using the calculated asymptotic weights, W_∞, the potential yields in grams per individual recruited (R) could be estimated.

III. RESULTS

(a) PRIACANTHUS TAYENUS

Reproduction

Priacanthus tayenus apparently spawned over a short period once a year in June. Female gonads were pinkish, translucent, and less than 0·25 of the body cavity length, from September to March. From March to June they contained white flecks, were opaque, and had grown to 0·3–0·6 of the body cavity. In May, June and July, clear eggs were visible through the ovary wall and the gonad length was up to 0·75 of the body cavity length. In June and occasionally in July, ripe eggs were easily extruded. In July and August, most gonads were red to pink and had shrunk to 0·2–0·3 of the body cavity length.

In males, the changes were less marked. In May and June, and to some extent in July, the white gonad had increased in size from a thin strap about 0·2 of the body cavity length, to a thickened triangular shape about 0·3 of the body cavity length, and milt was present in a swollen vas deferens. In July and August most testes were greyish, shrunken, and covered in fine red blood vessels.

Females first spawned at the end of their second year. A 22 cm female produced about 50 000 eggs per spawning.

Length frequency

Graphs of monthly length frequencies for the years 1965, 1966 and 1967 indicated a simple progression of clear modes (Fig. 1). There was no evidence from this, or from the maturity data, that *P. tayenus* had more than one spawning period per year. The smallest fish, 5–7 cm, were caught in July and August. These fish were assumed to have hatched from the June spawning of the previous year, and were assigned ages of 13 and 14 months. The growth of the smallest fish caught in August, 1965, could be followed for 20 months.

Growth

The combined growth parameters for males and females appear in Table I. Data from 961 sexed fish showed that throughout the year males were larger than females, and that the sexes occurred in approximately equal numbers. In random samples taken from January to March, the average length of 58, 1+ males was 17·4 cm and 40, 1+ females 15·9 cm. Males 2+ and older averaged 24·6 cm whilst corresponding females averaged 21·8 cm (137 fish).

Although growth in winter appeared slower than in summer, the expanded von Bertalanffy formula which allows for seasonal growth did not fit the observed data significantly better than the regular formula ($P < 0{\cdot}05$). Therefore only the growth parameters for the regular formula are presented (Table I). The asymptotic length, L_∞, (30 cm) was only exceeded by 0·5% of the fish measured.

TABLE I. Growth parameters calculated for *Priacanthus tayenus* and *P. macracanthus*, the latter with fish from spring and autumn spawnings both separated and combined. Shown with their 95% confidence limits are: L_∞ (asymptotic length), k (exponent of the growth formula), t_0 (hypothetical age of zero length) and W_∞ (the asymptotic weight). Also given are n (number in sample) r^2 (the coefficient of regression)

	P. tayenus	*P. macracanthus*		
		All	Spring only	Autumn only
n	44 696	28 256	13 360	14 896
L_∞	30	32	28	34
	(27·4–32·6)	(27·8–36·0)	(25·7–30·3)	(29·3–38·9)
k	0·8	0·7	1·0	0·7
	(0·58–1·01)	(0·45–0·93)	(0·69–1·33)	(0·43–1·03)
t_0	0·6	1·0	1·1	2·1
	(0·51–0·76)	(0·84–1·15)	(0·93–1·20)	(1·05–1·46)
r^2	0·98	0·96	0·97	0·95
W_∞	282	512	348	620
	(221–353)	(342–729)	(271–439)	(397–914)

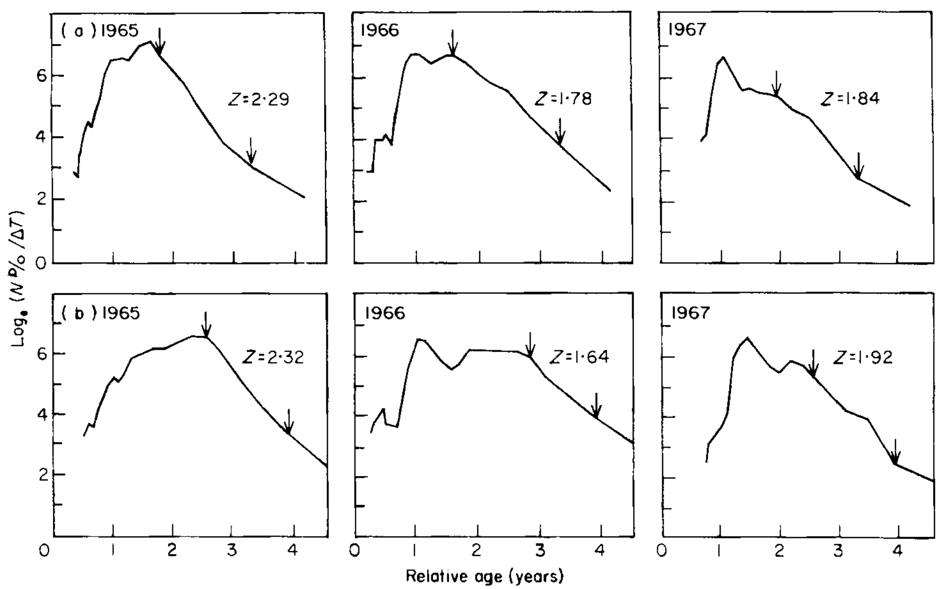


FIG. 2. Estimates of total mortality (*Z*) using adjusted catch curves for (a) *Priacanthus tayenus* and (b) *P. macracanthus*. The portion of the curve delineated by arrows was used in the calculation of total mortality.

Mortality

Estimates of total mortality made by using adjusted catch curves (Fig. 2) were similar to those obtained using Beverton & Holt's (1956) equation (Z^1, Z^2; Table II). Both estimates indicated a marked reduction in total mortality after 1965.

TABLE II. Estimates of the critical length of full recruitment (l_c), mean length of fish between l_c and $L(\bar{L})$, total mortality (Z), natural mortality (M), fishing mortality (F) and exploitation rate (E)

Species	Year	n	l_c	$\bar{L}$	Z^1	Z^2	M	F^1	F^2	E^1	E^2
P. tayenus	1965	13 798	22	23·7	2·29	2·87		0·88	1·46	0·38	0·51
	1966	26 217	21	23·8	1·78	1·73	1·41	0·37	0·32	0·21	0·18
	1967	4618	21	24·0	1·84	1·56		0·43	0·15	0·23	0·10
	Average				1·97	2·05		0·56	0·64	0·28	0·26
P. macracanthus	1965	9715	25	26·5	2·32	2·52		1·05	1·25	0·45	0·50
	1966	13 316	23	26·1	1·64	1·36	1·27	0·37	0·09	0·23	0·07
	1967	5225	24	26·0	1·92	2·14		0·65	0·87	0·34	0·41
	Average				1·96	2·01		0·69	0·74	0·35	0·33

[1] Z based on adjusted catch curves.
[2] Z based on equation of Beverton & Holt (1956).

Estimates of fishing mortality, F, and the exploitation rate or ratio of fishing to total mortality, E, are shown in Table II. Only a single estimate of natural mortality, M, is given as all study years were used to make the estimates of L_∞ and k from which M was calculated.

Yield per recruit

The parameters for the weight–length relationship, $W=aL^b$, were $a=0{\cdot}03$, $b=2{\cdot}7$ ($r^2=0{\cdot}93$). Growth of *P. tayenus* could not be shown to differ significantly ($P<0{\cdot}05$) from isometric growth ($b=3$).

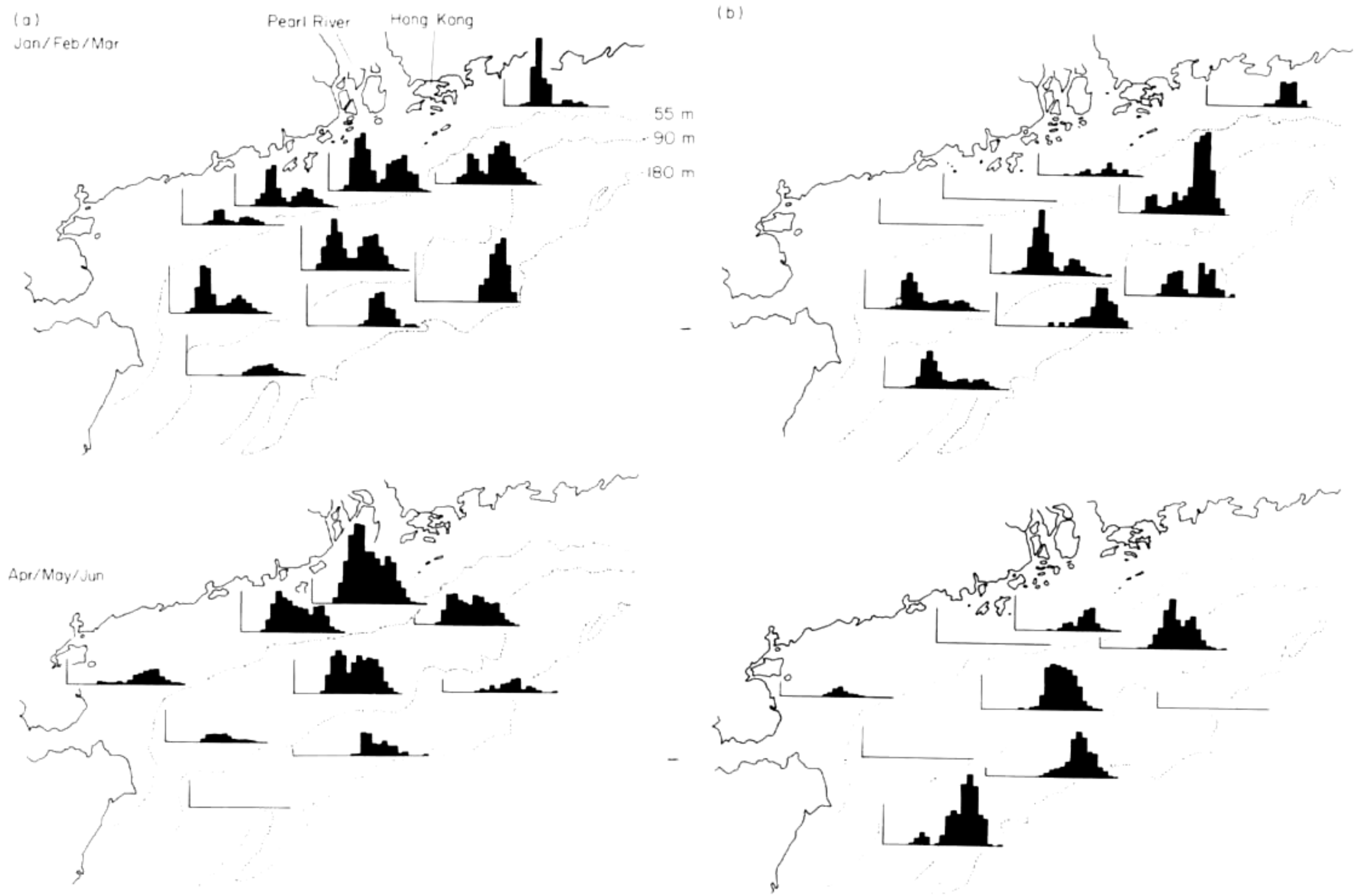
Potential yields of *P. tayenus* were estimated for a range of fishing mortalities using Marten's (1978) yield equation. The maximum predicted yield was 22% of the asymptotic weight of a recruit or 62 g/recruit. This yield was predicted when the fishing mortality was 5·4 and the calculation assumed a critical recruitment time (t_c) of 0·71 (based on an average recruitment length of 21 cm), a natural mortality of 1·4, and an asymptotic weight of 282 g.

Distribution

Priacanthus tayenus was the predominant priacanthid in catches from less than 55 m (Fig. 3). Fish less than 20 cm long were restricted to waters of less than 90 m. In January, February and March, the 2+ fish were fairly evenly distributed over the shelf. In April, May, and June, the highest catch rates of all age groups were from boats fishing adjacent to the Pearl River estuary in less than 55 m. Later the fish dispersed over the shelf, and by the end of the year were mostly in over 55 m, except for the newest recruits which were predominantly in shallow water.

Parasitisation

Priacanthus tayenus was heavily infected with the microsporan, *Pleistophora priacanthicola*. This parasite was not found in *P. macracanthus*. Spore sizes were


(a)
Jan/Feb/Mar
Pearl River
Hong Kong
55 m
90 m
180 m
Apr/May/Jun
(b)

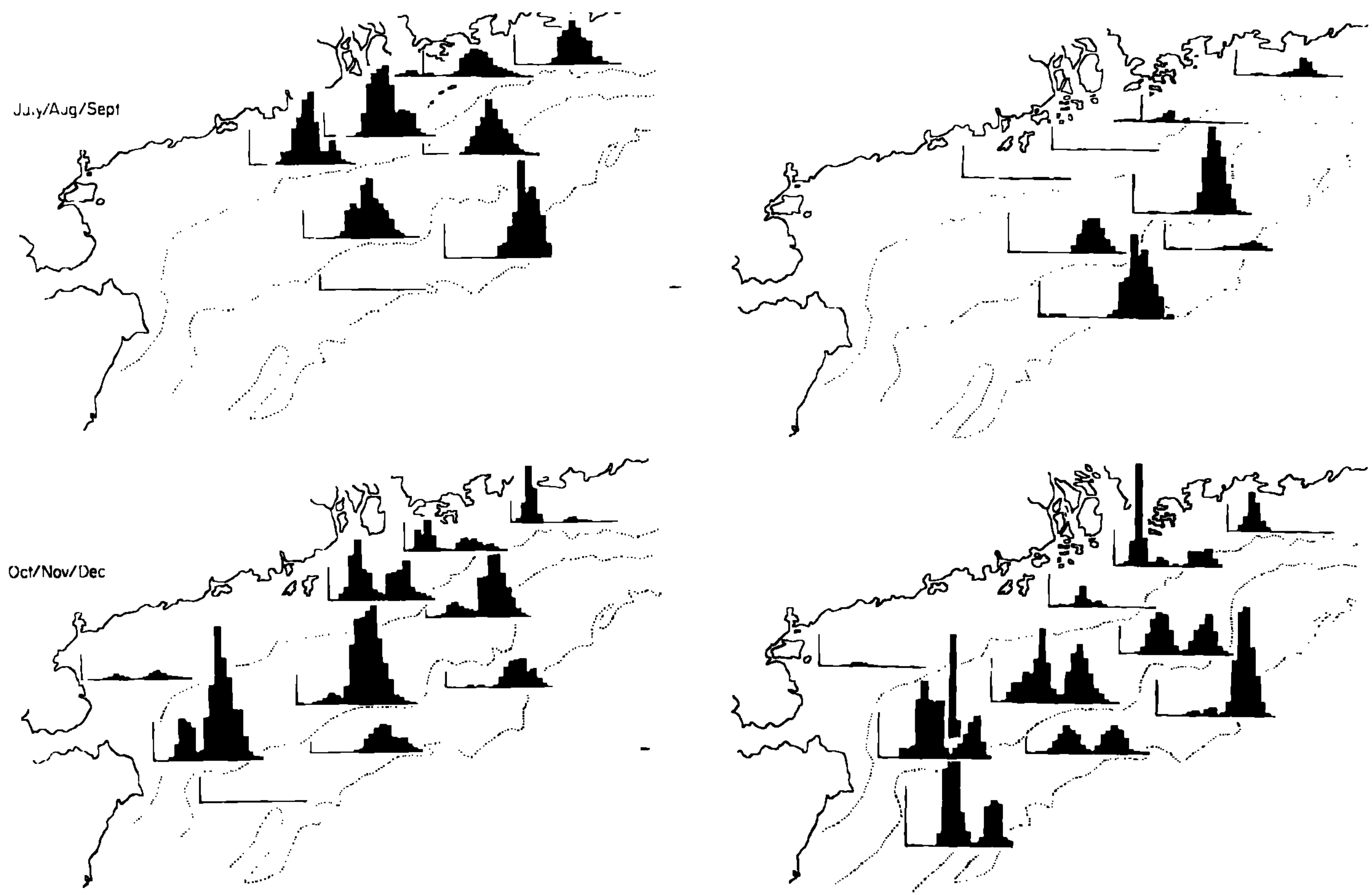


FIG. 3. Relative abundance of different size classes of (a) *Priacanthus tayenus* and (b) *P. macracanthus* on the Hong Kong shelf, South China Sea, for 3-monthly periods. The horizontal axis represents fish length. It is in 1 cm increments and the vertical line intersects it at 10 cm. The vertical axis represents catch rate × percentage length frequency. Its scale is the same for all histograms. Distant-water samples were not available during the typhoon season (July/August/September). Note the concentration of *P. tayenus* near the mouth of the Pearl River in April/May/June, the inshore recruitment of *P. tayenus* and the offshore recruitment of *P. macracanthus*.

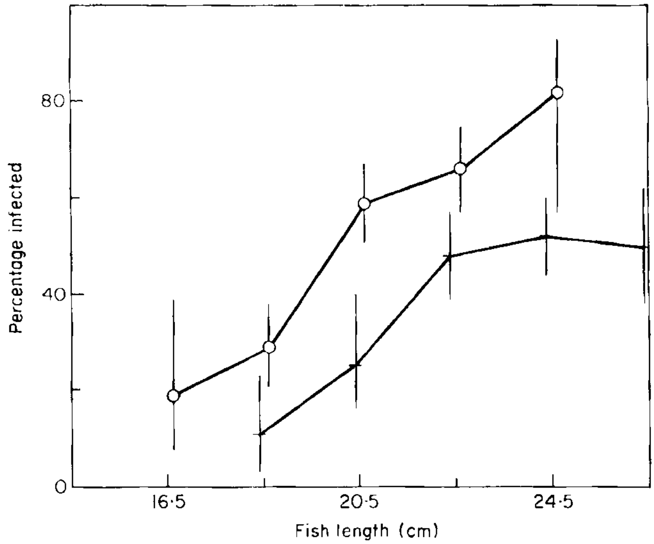


FIG. 4. Prevalence of macroscopic cysts of *Pleistophora priacanthicola* in 427 males and 485 females (circles) of *Priacanthus tayenus* taken south of Hong Kong. The 95% confidence limits are indicated.

variable. In a fixed smear they measured from 4·2 to 7·0 μm by 2·8–4·2 μm, and were found in groups of 12 to 20.

The microsporan was first noticed as a small, thin-walled cyst 2–3 mm in diameter filled with a milky fluid. Cysts were in the body cavity, either on the serosal surface of the gut or in the mesentery or on the peritoneum. They grew to 20 mm across. Thirty or forty such cysts so distended the abdomen that heavily parasitized fish could be distinguished without dissection. Prevalence of infection increased with the size of the fish (Fig. 4). The gonads of heavily infected fish, approximately 15% of the population, were partly or totally destroyed by cysts developing on and in them.

In many of the larger fish the parasites were found in a different form, always in light or medium infections, and rarely at the same time as the milky cysts. These modified cysts were firm, yellow, and angular in shape, fitting around the internal organs of the fish. They appeared to be dead or dormant cysts.

(b) PRIACANTHUS MACRACANTHUS

Reproduction

Fish in spawning condition were found throughout the summer, though there appeared to be two peaks, the first in May/June and the second in September. From October to March, inclusive, ovaries were white to red, and measured less than 0·25 of the length of the body cavity. From March to August, they were bright yellow, and up to 0·7 of the length of the body cavity. In May, June, September, and to some extent in July, the eggs were clear, visible through the gonad wall, and easily extruded. In all months from May to October, shrunken, flaccid, red or orange ovaries were frequently found, though this stage was less common in August. In July, small, yellow ovaries were found containing developing ovarian tissue and a few fully-developed eggs. This suggested that some fish spawned twice in the same year.

Testes often contained milt, even in the winter. From April to August, milt was present in over half the fish examined. In May, June, September, and to some extent in August, the vas deferens was filled with sperm. Spent testes, grey, shrunken, and covered in fine blood vessels, were found from May to October.

Females first spawned when they were about 20 cm long. A ripe female 25 cm long contained about 150 000 eggs.

Length frequency

A progression of modes was evident in the length frequency data (Fig. 1). These plots supported the conclusion above that there were two spawning periods, one in spring (May/June), and a second in autumn (September). The growth analysis described below indicated that the spring fish entered the fishery in July at 8 cm in length and at 15–16 months of age, while the autumn fish were first caught in July and August, at 11–13 cm and at 21–22 months of age.

In all seasons, females appeared to be slightly larger than males. From January to July the lengths of 1+ and 2+ fish partly overlapped making a statistical comparison difficult. However, from July to December, the 2+ frequency was distinct and approximately normally distributed. The average lengths of 510, 2+ males and 349, 2+ females measured during this period were significantly different ($P<0{\cdot}05$) and the values were 24·7 and 25·0 cm respectively.

Growth

As with *P. tayenus*, *P. macracanthus* appeared to grow slower in the winter than in the summer. The expanded von Bertalanffy formula which allows for seasonal growth did not, however, fit the observed data significantly better than the regular formula ($P<0{\cdot}05$) and therefore only the growth parameters for the latter are presented (Table I). The asymptotic length, L_∞, was 32 cm. It was only exceeded by 0·6% of the fish measured.

Mortality

Estimates of total mortality (Z; Table II) indicated that a marked reduction in this parameter occurred from 1965 to 1966, followed by an intermediate value in 1967.

The empirical estimate of natural mortality (M) was 1·27 (Table II). Calculated for the spring and the autumn fish separately, it was 1·66 and 1·25 respectively. The estimates of fishing mortality and exploitation rates were based on the single estimate of natural mortality from the combined sample, and these generally showed a reduction from 1965 to 1966, with intermediate values in 1967.

Yield per recruit

The parameters for the weight–length relationship, $W=aL^b$, were $a=0{\cdot}02$, $b=2.9$ ($r^2=0{\cdot}98$). Growth of *P. macracanthus* could not be shown to differ significantly ($P<0{\cdot}05$) from isometric growth ($b=3$).

Potential yields of *P. macracanthus* were estimated for a range of fishing mortalities using Marten's (1978) yield equation. The maximum predicted yield was 26% of the asymptotic weight of a recruit or 132 g/recruit. This yield was predicted when the fishing mortality was 5·8 and the calculation assumed a critical recruitment time (t_c) of 0·75 (based on an average recruitment length of 24 cm), a natural mortality of 1·3, and an asymptotic weight of 512 g.

Distribution

Priacanthus macracanthus was primarily a deep-water species, few fish apart from juveniles being taken in less than 55 m (Fig. 3). No specific spawning areas were identified, though fish distribution from April to September suggested that the fish spawned in much deeper water than *P. tayenus*. Young fish were recruited at all depths, suggesting that inshore nursery grounds are not as important for *P. macracanthus* as for *P. tayenus*.

IV. DISCUSSION

PARASITISATION

The parasite *Pleistophora priacanthicola* (He, 1982) was described from *Priacanthus tayenus* north of Hainan Island. He (1982) found that the milky cysts contained dividing stages and the solid cysts contained mostly mature spores. In the following year Hua & Dong (1983) described *Pleistophora priacanthusis* from similar cysts in the same host from the same locality. The two species appear to be synonymous, and *P. priacanthicola* is the senior synonym. Hua & Dong noted the wide range in the size of the spores. Contrary to our observations, both papers reported finding the parasite in *Priacanthus macracanthus*. Evidently its absence, at least macroscopically, in *P. macracanthus* south of Hong Kong results from environmental factors rather than the unsuitability of the host.

GROWTH

Growth of *P. tayenus* and *P. macracanthus* in the South China Sea was expected to show some seasonal variation because of the marked change in the average bottom temperature between winter and summer. Williamson (1968) reported that the cold north-east monsoons produced an annual range of 8° C at 55 m depth. For neither species, however, did the von Bertalanffy growth formula which allows for seasonal growth fit the data significantly better than the regular formula. This was possibly because the sexes were not treated separately though their growth rates were different, at least in *P. tayenus*; and in *P. macracanthus*, spring and autumn fish of the same relative ages were combined regardless of the season, thus confounding asynchronous seasonal growth cycles.

Priacanthus tayenus from the demersal trawl fishery of the Gulf of Thailand had an L_∞ of 29 cm and a k of 1·2 (Pauly, 1980*a*). These appear to be smaller, but faster growing fish than those from the South China Sea where for the same species $L_\infty = 30$ cm and $k = 0{\cdot}8$, though the differences are not significant ($P < 0{\cdot}05$). Chomjurai & Bunnag (1970) estimated a maximum length of 30·8 cm for *P. tayenus* from the Gulf of Thailand. This is similar to our estimated maximum (30 cm) for the South China Sea.

MORTALITY

Priacanthus tayenus had a lower estimated natural mortality in the South China Sea than in the Gulf of Thailand. Pauly (1980*a*) used an early version of his empirical equation to calculate a natural mortality of 1·8 for *P. tayenus* from the Gulf of Thailand trawl fishery. His equation was later revised using data from additional fish stocks (Pauly, 1980*b*). We used this revised equation to recalculate *P. tayenus* natural mortality in the Gulf of Thailand. It is estimated to be 2·0, compared to 1·4 for the South China Sea. The difference may be due to the higher temperature of the Gulf of Thailand, which averages 5° C above that of the South China Sea.

Both *P. tayenus* and *P. macracanthus* showed a marked reduction in fishing mortality in 1966 and 1967 compared to 1965. This coincided with the onset of the Chinese Cultural Revolution and the rise of the Red Guards in August, 1966, following which industrial production in many spheres was seriously disrupted (Houn, 1973).

YIELD PER RECRUIT

The fishing mortalities of both species which correspond to the maximum yields predicted by Marten's (1978) equation are eight to nine times those estimated to occur during the study period. It has been reported by Gulland (1971) and others that the ideal exploitation rate occurs when the fishing and natural mortalities are equal. However, the fishing mortalities predicted by Marten's (1978) equation are four to five times those of the estimated natural mortalities. Marten (1978) cautioned that his yield formula did not allow for the effects that high fishing mortalities would have on the recruitment rate. In view of this, stocks of *P. tayenus* and *P. macracanthus* may not be able to sustain the high fishing mortalities necessary to achieve the maximum yields predicted by Marten's formula.

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