

Bionomics of the Sciaenidae of Tropical West Africa

By

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Introduction

The most important genera in the tropical West African trawl fisheries belong to the family Sciaenidae ("croakers"), the taxonomy of which has recently been put on a sound basis by TREWAVAS (1962), whose system is followed here. Within the zone of permanently warm equatorial water under the influence of the Guinea Current, the tribe Pseudotolithinae is dominant. It mainly occurs in the warm water above the base of the thermocline (p. 100 and LONGHURST, 1963) where it is present ubiquitously on muddy deposits, and extends seasonally into the oceanographic transitional zones to the north and south, reaching Mauretania and Angola during the northern and southern summers respectively.

Of the nine Pseudotolithinae species recognized by TREWAVAS, only four are economically important above the base of the thermocline while a fifth, *Pentheroscion mbizi*, probably represents an unexploited resource in South Atlantic Central Water below the thermocline, where it is at times very abundant. Of the four warm-water species, two, *Pseudotolithus senegalensis* and *P. typus*, form approximately 30% of the catch of the trawl fishery on the continental shelf, while *P. brachygnathus* and *P. elongatus* occur in estuaries and saline creek-systems, the latter species being, perhaps, commercially the most important demersal fish in the large estuaries of the Guinea Coast. Of the two open-sea species, *P. typus* regularly penetrates into estuaries, while *P. senegalensis* very rarely does so.

The abundance of *Pseudotolithus typus* appears to increase progressively to the south both absolutely and relative to the other species. Between Senegal and Sierra Leone it seems to be relatively rare (ARNOUX, 1957; LONGHURST, 1963); from Ivory Coast to Nigeria it appears to occur in about the same numbers as *P. senegalensis*; off the Congo it is the dominant species according to POLL (1954), though COLLIGNON (1960) and COLLIGNON, ROSSIGNOL and ROUX (1957) indicate that the two species are equally abundant. The relative abundance of *P. senegalensis*, of *P. brachygnathus* and of *P. elongatus* is apparently rather uniform throughout the area, wherever suitable ecological conditions occur.

This study is concentrated on three species since the estuarine *P. brachygnathus* has not been available in great enough numbers, nor has the deep *P. mbizi* been

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taken regularly enough for study; other genera are represented in the catches only rarely, or do not grow to a useful size even if abundant, and have been ignored. The present paper reports the results of a two year study of *P. typus* and *P. senegalensis* off Nigeria, with which are compared the results of a study on *P. elongatus* in the Sierra Leone estuary (LONGHURST, 1963) which has been re-appraised in the light of the Nigerian data.

Materials

In the absence of a proved method of ageing individual fish, reliance had to be placed on the interpretation of whole-catch length frequency distributions; these were taken with the research vessels "Apese" (9.2 m), "Kingfisher" (12.0 m), "Explorer" (14.5 m) and "Kiara" (21.3 m); all trawls were fitted with a fine mesh lining inside the cod-end, so that the effective mesh size was 1.5 cm. All mesh measurements were made with vernier callipers, and were taken as internal and diagonal measurements of a stretched mesh, using an approximately standard tension of 1.5 kg.

The following number of fish were measured:—

Species	Year	Samples	Specimens	Totals
<i>Pseudolithus typus</i>	1961	74	42,948	
	1962	117	38,318	= 83,256 = 56.3 %
<i>P. senegalensis</i>	1961	72	30,358	
	1962	118	34,304	= 64,662 = 43.7 %
Grand total, January 1961 – December 1962				= 147,918

Monthly samples averaged 3,469 (915–8,732) and 2,694 (308–5,765) for the two species respectively. Such large samples were found necessary due to schooling by size groups so that peaks in trip length frequencies were of schools rather than broods and often varied widely from day to day.

From these fish, smaller numbers of randomly selected post-juveniles were taken between October 1961 and December 1962, for examination of the gonad state and of the gonad weight/body weight ratio. The number examined were as follows:—

Species	Sex	Number	
<i>Pseudolithus typus</i>	Males	11,138	= 52.88 %
	Females	9,923	= 47.12 %
<i>P. senegalensis</i>	Males	12,678	= 56.56 %
	Females	9,738	= 43.44 %

Subsidiary data, comprising length frequency distributions from exploratory trawling along the eastern Gulf of Guinea shelf, were collected from several vessels:—

Year	Vessel	Locality	Number of fish	Mesh size, cm
1952	"Cape St. Mary"	Cameroun to Togo	506	5.0
1963	"Akindeko"	Forcados River	1,227	2.5
1963	"Kiara"	Port Harcourt to Cotonou	9,019	2.5

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Data were also available from the following sources: landing statistics from the commercial trawling fleet working out of Lagos during the period October 1959 to February 1963; the results of some preliminary biological investigations on the feeding regime and the fecundity of the two species carried through in 1961 by the Federal Fisheries Service, and the results of mesh selection experiments by the Federal Fisheries Service and by Fisheries Development and Research Unit, Freetown.

Methods

All measurements were made to the nearest centimetre using a measuring board calibrated so that the centimetre groups were centred around whole centimetres, and no adjustment was necessary before using the data; only the fish investigated for the gonad weight/body weight ratio were measured to the nearest millimetre and decigram below.

All measurements were made as total length (LT), defined by BAYAGBONA (1963), and subsequent transformations to standard length (LS) and total weight (WT) were made according to his regression equations.

The individual trip length frequencies were transformed into monthly length frequency distributions and these expressed as percentage distributions and as 3-period running means; a trial was made with the Harding-Cassie use of probability paper to dissect the polymodal curves into normal distributions but this failed to elucidate the right-hand limb of the distributions and a visual selection of modes appeared to be at least as satisfactory: it must be recognized that there is some subjectivity in the selection of modes on which the later analysis is based, but this appears to be inherent to a greater or lesser degree in any study based entirely on PETERSEN's method.

Modes were selected in the monthly length frequency distributions for each species according to similar criteria to those established by HENNEMUTH (1961) and then plotted as a scatter diagram (Figures 1a and b). The modes were joined along the most probable growth lines, with constant reference to the form of the peaks in the original frequency distributions, to trace the growth of individual broods. Using an arbitrary origin three months previous to the attainment of $LT = 10$ cm, the growth of the individual broods was meant to produce a single average growth curve for each species, the origin then being adjusted according to the form of the curve fitted above $LT = 10$ cm. This process was less satisfactory in the case of *P. typus*, probably as a result of the relatively heterogeneous nature of the sampled stocks (p. 110).

From this curve, LT -for-age at six monthly intervals were deduced and these were subsequently transformed to LS and WT -for-age. Extrapolation beyond three years was performed by a Walford plot of LS , from which a value for asymptotic length (L_{∞}) was derived.

The spread of the individual monthly length frequency distributions for each brood was not closely analysed since it could not be determined, in any case, to what extent such spread was due to non-synchronous spawning or to differential individual growth rates.

However, for each species it was possible to dissect graphically individual broods from the general monthly length frequency distributions and to determine their range between the points at which numbers of fish in each centimetre class fell below 0.2% of the sample total. As was expected, the spread was found

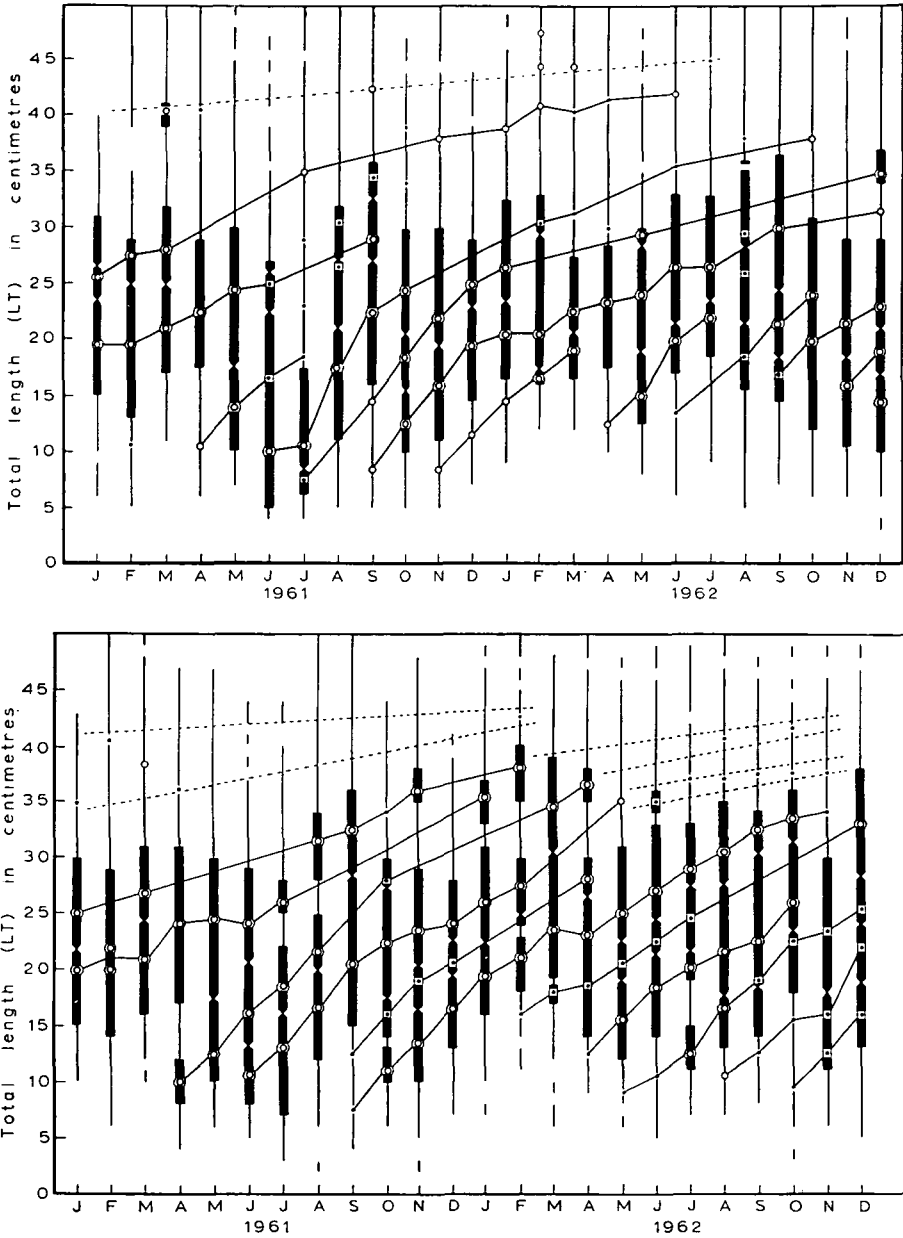


Figure 1. Upper Figure: Growth of individual broods of *Pseudotolithus senegalensis* from progression of modes identified in monthly length (LT) frequency distributions. Open circles are major modes; closed, smaller circles are minor modes; the heavy section of the lines indicate those parts of the LT distribution where individual cm classes form over 2% of sample total. Constrictions in the heavy lines indicate divisions between modes. (Original data filed at the Federal Fisheries Service, Lagos.)

Lower Figure: Growth of individual broods of *Pseudotolithus typus*.

to be higher in those broods whose members dominated a monthly sample and was smaller in those which contributed less to the total. The mean spread was 14.7 cm in each species and the maximum observed for each was 19 cm. There was no clear indication that spread increased with age, perhaps because younger broods tend to dominate the samples. The mode appears to be close to the mean in most cases and few skewed distributions were observed. Thus, although all the calculations which follow are based upon modal fish, it may be assumed that individual fish in a brood may vary up to 9 cm on either side of the given modal values.

The investigation of the reproductive cycle was based on a series of gonad maturation stages set up by ANYA (unpublished) which appears to be applicable to all West African sciaenids so far examined, and which is set out below.

Females

Stage 1. Sex indeterminable.

- 2. Ovary transparent and filamentous, membrane very delicate, vascularization slight.
- 3. Ovary opaque, membrane firm and vascularized, oocytes not visible to the eye.
- 4. Ovary contents granular, membrane transparent.
- 5. Ova clearly visible within the ovary, some ova transparent and ripe.
- 6. Ova ripe and running from vent on pressure.
- 7. Ovary spent and resting.

Males

Stage 1. Sex indeterminable.

- 2. Testis rather rounded in section, of a pale cream-white colour.
- 3. Testis milky-white and flattened in section.
- 4. As stage 3, but sperm running from vent on pressure.
- 5. Testis spent, translucent, especially at the edges.

Some difficulty was experienced in separating spent females which had returned to rest in stage 3, from virgin stage 3 fish, and this has resulted in some anomalies in the determination of first and mean maturity lengths.

Results

The parameters determined by the methods described above are summarized in Table 1, together with similar parameters, similarly determined, for *P. elongatus* in the Sierra Leone estuary.

Geographical variation in fish size and stock density

The 1963 "Kiara" resource survey produced samples of *P. senegalensis* and *P. typus* from about 350 miles of the coastline from the Bonny River off the southern Niger Delta to Cotonou on the non-deltaic Dahomeian coast to the west of Lagos (Figure 2). The catch rate of *P. typus* showed a general increase towards the east, and reached highest values in area 5 off the southern Delta

Table 1
Basic parameters for *P. senegalensis* and *P. typus* off Lagos and *P. elongatus* off Sierra Leone; for symbols, see text except for *g* and *h*, instantaneous and relative growth rates of *LS* (standard length); *i* and *a*, instantaneous and annual rates of total mortality; *s*, annual rate of survival

Growth	<i>P. senegalensis</i>						<i>P. typus</i>						<i>P. elongatus</i>						
	<i>LT</i>	<i>LS</i>	<i>a</i>	<i>s</i>	<i>N</i>	<i>Y</i>	<i>LT</i>	<i>LS</i>	<i>a</i>	<i>s</i>	<i>N</i>	<i>Y</i>	<i>LT</i>	<i>LS</i>	<i>a</i>	<i>s</i>	<i>N</i>	<i>P</i>	
1 Year	29.4	23.7	226.4	5.42	—	—	30.3	24.2	174.3	5.16	—	—	15.0	—	—	—	22.0	3.09	—
2	39.6	32.6	566.8	0.92	1.51	—	41.7	34.0	483.4	1.02	1.78	—	24.5	—	—	—	109.0	1.60	3.95
3	44.2	36.6	794.8	0.34	0.40	—	48.8	40.3	805.0	0.51	0.66	—	31.5	—	—	—	222.0	0.71	1.03
4	46.3	38.5	874.5	0.09	0.10	—	53.5	44.4	1076.6	0.29	0.34	—	36.0	—	—	—	337.0	0.42	0.52
5	47.3	39.6	979.8	0.11	0.12	—	56.4	47.1	1285.2	0.18	0.18	—	39.2	—	—	—	403.0	0.17	0.19
6	—	—	—	—	—	—	—	—	—	—	—	—	41.2	—	—	—	439.0	0.09	0.09
<i>L</i> _∞	47.8	40.4	1011.0	—	—	—	61.2	52.6	1789.5	—	—	—	45.0	—	—	—	—	—	—
<i>L</i> _{maz}	60.0	—	—	—	—	—	93.0	—	—	—	—	—	47.0	—	—	—	—	—	—
Mortality (<i>Z</i>)																			
0-1 Years	7.45	0.99	0.01	1000	—	—	7.18	0.990	0.010	1000	—	—	—	—	—	—	—	1000	22.0
1-2	1.73	0.82	0.18	180	216.7	—	2.33	0.903	0.097	97	192.1	—	2.05	0.87	0.13	—	—	130	14.2
2-3	1.55	0.79	0.21	38	65.7	—	1.05	0.650	0.349	20	34.0	—	1.45	0.76	0.24	—	—	31	6.9
3-4	1.04	0.65	0.35	13	14.4	—	1.17	0.689	0.310	7	8.5	—	1.45	0.76	0.24	—	—	7	2.3
4-5	0.69	0.50	0.50	6	0.5	—	0.44	0.356	0.644	3	3.2	—	0.99	0.62	0.38	—	—	3	1.2
Maturity (<i>L</i> _m)	1%	22.0	10%	25.0	50%	35.0	1%	30.0	10%	38.0	50%	48.3	1%	19.0	10%	24.0	50%	32.6	—
<i>L</i> _m / <i>L</i> _∞	0.46	—	—	—	0.73	—	0.49	—	—	—	(0.79)	—	0.42	—	—	—	—	0.72	—
Selection factor, <i>S</i>																			
Cotton 3.76; hemp 3.85; nylon 4.57																			
<i>K</i> = 0.71; <i>t</i> ₀ = -0.44; <i>f</i> = 623/g																			
Cotton 4.26 predicted																			
<i>K</i> = 0.37; <i>t</i> ₀ = -0.47; <i>f</i> = 573/g																			
Cotton 3.25; nylon 3.64																			
<i>K</i> = 0.61; <i>t</i> ₀ = +0.10; <i>f</i> = 96/g																			

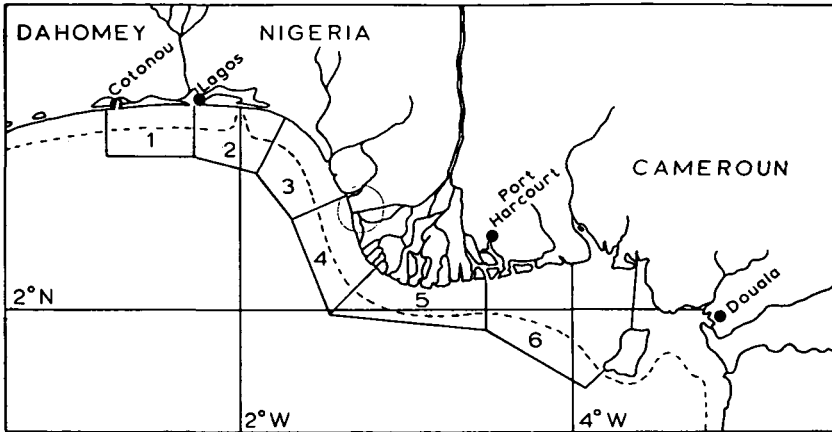


Figure 2. Chart of Nigerian statistical areas to indicate coverage of the 1963 "Kiara" survey.

coast, while that of *P. senegalensis* varied less consistently and showed highest values off the western Delta coast and minimal values further to the south in area 5. There was also a discontinuity in the percentage of large fish of total length equal to or greater than 30 cm in the catches of *P. senegalensis* between areas 2 and 3, that is at the point of change from a non-deltaic to a deltaic coast; to the east of this point, on the Delta coast, the percentage of large fish was relatively very low. The same phenomenon apparently occurs in *P. typus*, but (as so often occurs with this species) the effect on the results of a single sample in area 5 in which very many large fish were taken has been to obscure the general pattern in, for example, Table 2 and Figure 3 in which the general results are set out. These results are consistent with what is known of the general ecology of the species and with what has been reported by commercial trawlers of the "small fish areas" off the deltaic coasts; almost all the fishing effort of the trawling fleet is concentrated on the non-deltaic coast where it is known that in the last five years the percentage of large fish has seriously declined (LONGHURST, 1964b), suggesting that prior to the start of trawling the size distributions of the two areas must have been even more different.

Using the "swept-area" method it is possible to deduce values (Table 2) for stock density in terms of numbers of fish/hectare. The limitations of this method of extrapolation are obvious, for it is in any case only a minimal figure and is influenced by avoidance and escapement. Rather more tenuous is the further extrapolation from this to arrive at an estimate of stock density on those parts of the survey area on which the two species occur; this suffers not only from the same limitations but also from the more serious one of the effects of uneven stock densities on the grounds.

Ecological limiting factors

The distribution of *Pseudotolithus typus* and *P. senegalensis* within the warm surface waters of the Gulf of Guinea can be correlated rather closely with the 18°C isotherm. In the horizontal sense their distribution along the coast is limited by the zones of transition to the northern and southern cold-water

Table 2

Size composition and catch rate of *P. senegalensis* and *P. typus* by statistical area, "Kiara" 1963 survey

Area 1 – Cotonou to Lagos; 2 – Lagos to Lekke; 3 – Lekke to Escravos; 4 – Escravos to Kulama; 5 – Kulama to Bonny; n = number of specimens taken in each area; N × 10⁶ = stock size.

Area	1	2	3	4	5
	<i>Pseudotolithus senegalensis</i>				
n	615	431	2327	2367	717
n/60 mins	77	54	211	296	96
10–19 cm	17.0 (%)	5.0	25.1	33.5	14.1
20–29	34.7	41.0	63.4	59.4	74.2
30–39	41.5	48.5	9.7	4.4	8.4
40–49	9.4	3.2	0.3	0.1	0.5
Kg/100 fish	30.5 (kg)	27.5	19.7	10.60	14.30
Kg/60 mins	23.5	14.8	41.5	31.7	13.7
Fish/hectare	6.4	4.5	17.6	24.6	8.0
N	0.41 (× 10 ⁶)	0.64	3.28	9.55	2.48
	<i>Pseudotolithus typus</i>				
n	69	46	749	813	885
N/60 mins	23	12	107	116	147
10–19 cm	26.1	4.3	37.9	32.1	16.8
20–29	56.5	41.3	45.2	60.7	31.1
30–39	10.2	39.4	12.5	5.9	41.2
40–49	5.6	8.7	0.5	0.5	10.1
50–59	2.8	4.3	0.0	0.0	0.7
Kg/100 fish	16.2	24.9	8.8	8.6	22.4
Kg/60 mins	3.7	2.9	9.4	9.9	32.9
Fish/hectare	1.9	1.0	3.2	9.6	12.0
N	0.12 (× 10 ⁶)	0.14	0.59	3.72	3.72
	<i>Combined</i>				
Fish/60 mins	100	66	318	412	243
Kg/60 mins	27.2	17.7	29.8	41.3	47.2
Fish/hectare	0.83	0.55	2.08	3.42	2.00
(% <i>P. senegalensis</i>)	77	82	71	72	39
(% <i>P. typus</i>)	23	18	29	28	61

In October 1963, the "Kiara" was able to work in area 6 in the Bight of Biafra where very sparse stocks of croakers were found, consisting mostly of very small individuals; the following Table, which is supplementary to Table 2, summarizes the important data from area 6.

	n	n/60 mins	% length frequency (LT, cm)			
			0–19	20–29	30–39	40–49
<i>Pseudotolithus typus</i>	331	33	51.9	43.8	5.9	0.1
<i>P. senegalensis</i>	324	36	41.8	54.9	4.0	0.0

areas. Off the Congo mouth COLLIGNON (1960) shows that the fishery for these species declines during the winter when the bottom temperature on the trawling grounds falls to about 17.5°C. At the northern transitional zone, off Cape Verde, the fishery similarly occurs only during the summer, at which time the fish migrate from the south and appear in water shallower than 10 m, at temperatures of between 18° and 28°C (BLACHE, 1957; ARNOUX, 1957), the higher temperatures being comparable with those off the Congo in summer when the fishery is at its peak.

In the central zone of permanently warm surface water (BERRIT, 1962) the species occur the year round in surface waters of 29°C down to the base of

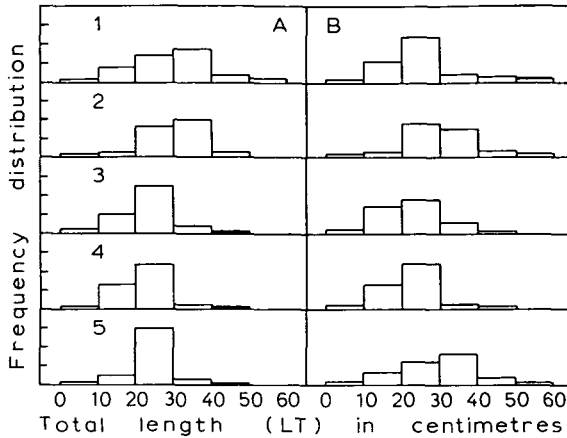


Figure 3. Percentage length (*LT*) frequency distributions by statistical areas, "Kiara" survey, 1963. A – *P. senegalensis*. B – *P. typus*.

the thermocline at about 18°C. The 1963 "Kiara" survey recorded them down to 19.9°C, while off Sierra Leone the "Cape St. Mary" surveys recorded the species down to 17.5°C (LONGHURST, 1963). In this central zone the 20 m temperature ranges from about 25–28°C, except in the region of coastal upwelling from Ivory Coast to Western Nigeria where the August upwelling may reduce surface temperatures to below 20°C. Off Ghana, where the upwelling is strongest, beach temperatures may fall to 18°C, and the 20 m bottom temperature to 17°C, and at such times in some years the fish may leave the bottom and may be caught only with hand-lines near the surface (Anon., 1963). The catch rate of the trawl fishery in shallow water off Ghana at this time falls to a minimum in each year. Off Nigeria, where the upwelling is never so profound (BERRIT, 1962; LONGHURST, 1964a) the 20 m temperature does not fall below 19°C and the day-to-day trawl catches are in fact independent of the irruption of cold upwelled water across the shelf. It has been suggested by DEVOLD (Anon., 1963) that the upward migration off Ghana is caused by the movement across the shelf of subthermocline oxygen-free water; off Nigeria the bottom water at this time never has less than 1.5 ml/l of oxygen which is not a limiting value ecologically, and during non-upwelling periods even higher minima are normal for the water immediately below the thermocline.

Although the year-round spawning of varying intensity found on the Nigerian coast (p. 105) is probably typical of the whole warm-water zone, the situation is evidently different in the transitional zones; off the Congo, COLLIGNON (1957) records that breeding occurs only from October to April, during the summer, when the 15 m temperature exceeds 22.5°C, and a similar situation will probably be found in the north at Cape Verde. Off Nigeria, it is clear that peak spawning (p. 105) coincides with the period of maximum water temperatures and occurs only when these exceed 27.5°C at the surface, or about 27.0°C at 20 m. The relationship between temperature and spawning cycles is indicated in Figure 4.

To what extent temperature is the proximate factor in determining the distribution of the continental shelf species is not clear. In the vertical sense,

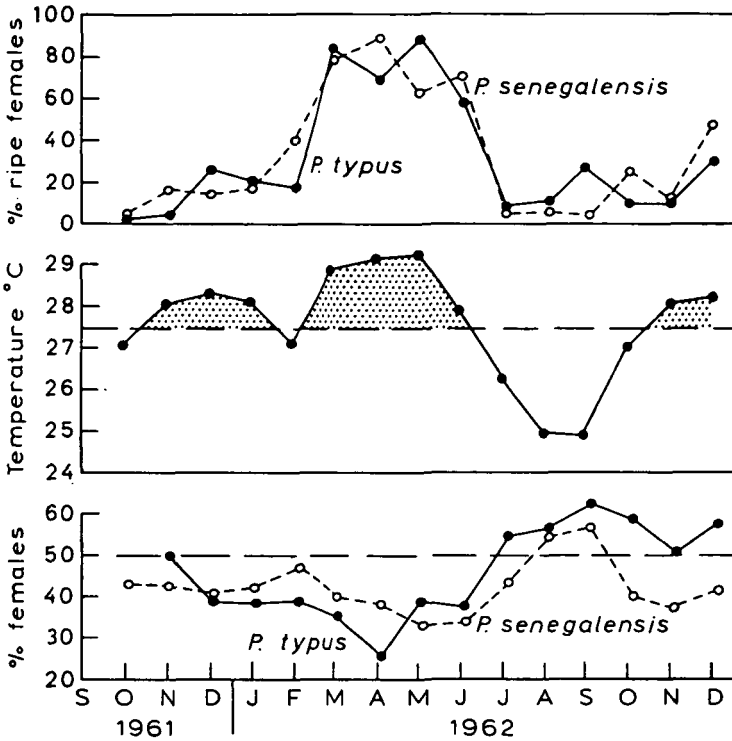


Figure 4. Reproductive cycle off Lagos. Broken line = *P. senegalensis*, complete line = *P. typus*. The percentage of females over L_m at the 10% level which are ripe; the mean monthly temperature of the water above the thermocline; and the percentage of females in the landings.

the 18°C isotherm corresponds not only with the base of the thermocline and the transition from Tropical Surface Water to South Atlantic Central Water, but also with the salinity maximum of about 35.7–35.9‰. Below this level, salinity falls very gradually with increasing depth, while above it may, at times of heavy rain, fall quite rapidly, although the region of maximum dilution does not effectively extend so deep. Certainly at times of strong surface dilution the bottom salinity on the inshore trawling grounds falls as low as 33.0‰ and though these species do not suffer the same salinity fluctuations as the estuarine *P. brachygnathus* and *P. elongatus*, they must still be relatively euryhaline. If salinity itself was an ecological factor of importance one would expect, at times of surface dilution, to find *P. senegalensis* deeper than *P. typus*, but this has not yet been demonstrated.

Length frequency comparison between sexes

The length frequency distributions of all sexed fish showed for both species a slight preponderance of males in the mid-range of sizes from $LT = 20$ cm to about $LT = 40$ cm, above which size females were in slightly greater numbers, this effect being rather more marked in *P. senegalensis* than in *P. typus*. The various modes in the frequency distributions of each sex were approximately

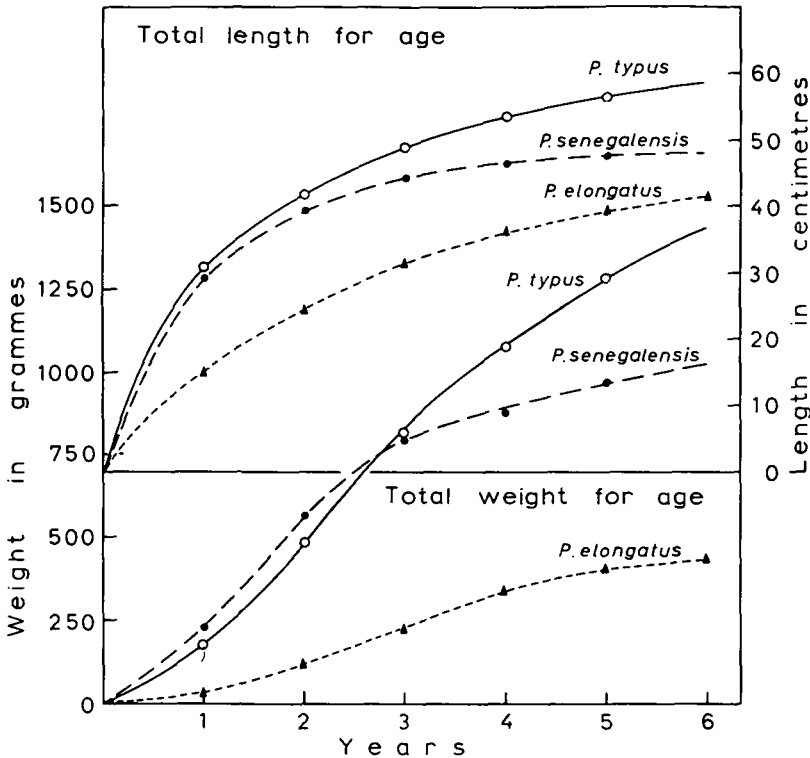


Figure 5. Growth curves in *LT* and *WT*, modal values at each birthday.

coincident and there was no evidence to suggest differential growth rates between sexes which might invalidate growth parameters derived from the basic data in which specimens were not sexed. COLLIGNON (1957) found a similar situation at Pointe-Noire.

Effect of vessel size on length frequencies

During May, June and July 1962 the research vessel "Kiara" contributed a few samples from the same grounds as those worked by the three smaller research trawlers which contributed the bulk of the samples; comparison between the "Kiara" samples and the others for the same months showed relatively larger quantities of fish of $LT = > 30$ cm, but the same modes were readily identifiable in the two sets of data. Thus, the addition of the "Kiara" samples to the total is justified and enabled objective evidence to be obtained for the supposition that the small vessel samples were biased against large fish active enough to be able to escape from the relatively slowly moving trawls of the three small boats.

Growth rate and asymptotic length

Basic data for growth in length (*LS*, *LT*) and weight (*WT*) are set out in Table 1 and Figure 5. It can be seen that the rates, both in absolute and relative

terms, for *P. typus* are a little higher than those for *P. senegalensis*. COLLIGNON (1957) studied the growth rate of *P. senegalensis* at Pointe-Noire by comparable methods, but his derived growth curve is of rather different form from that presented here. His $LT = 44$ cm at age 3 years is very close to the Lagos figure, but his values for years 1 and 2 are somewhat lower than the Lagos values and give a much straighter profile to the growth curve and, consequently, a very low value of K of only 0.20.

The overall length frequency distributions for the two species shows that *P. typus* grows considerably larger than does *P. senegalensis*. The maximum length observed for *P. typus* was 93 cm, while that for *P. senegalensis* was 60 cm or somewhat less, the scattered records of fish larger than this certainly, in fact, pertaining to the sibling *P. brachygnathus*. These figures are in accordance with published records (e.g. POLL, 1954; COLLIGNON, 1957).

The values of LT_{∞} derived from the Walford plot corresponds, in each species, rather closely with the point at which the right-hand limbs of the total length frequency distributions flatten out. The considerable extension of the right-hand limb more or less parallel with the abscissa in both curves suggest that the asymptotic length may be set too low. The numbers of fish taken in the flattened limb of the distributions are, however, too small to allow of further analysis of this point.

Values for the von Bertalanffy growth coefficient (K) were derived from the LS_t and LS_{∞} data, and correspond with expectation, that for *P. senegalensis* being considerably higher than that for *P. typus*. Values for t_0 were rather similar in the two species (Table 1).

Size at first and mean maturity

From a regression of percentage of ripe (stage 6) females against LT an estimate was obtained of first maturity and of mean maturity (Figure 6). This presented no problem in the case of *P. senegalensis* for which values of L_m at the 1%, 10% and 50% levels were readily determined, but in *P. typus* the points above about 30% mature became so scattered as to be apparently meaningless and the value of L_m at the 50% level had to be extrapolated from the form of the maturity curve of the previous species; this appears to be due to the fact that the sampled population of *P. typus* is much less homogeneous than of the other species (p. 110).

These estimates of the onset of maturity are confirmed indirectly by the biometric study of BAYAGBONA (1963) in which he showed rate changes in the allometric growth of several structures at values for LT corresponding with those at which 1–10% maturity occurs; thus the biometric indices for pectoral, ventral and caudal fins, and for the orbital diameter, change in *Pseudotolithus senegalensis* between $LT = 20$ and 25 cm, and in *P. typus* between $LT = 25$ and 35 cm. It is very likely that such changes in the growth patterns of the species are connected with the onset of first maturity.

Seasonal reproductive cycle

Stage 6 gonads occurred in the females of both species in every month of the sampling period, and some small fish of $LT = < 10$ cm were present in the catches in almost every month: thus, spawning is virtually continuous throughout the year. However, there are clearly marked cyclical changes in

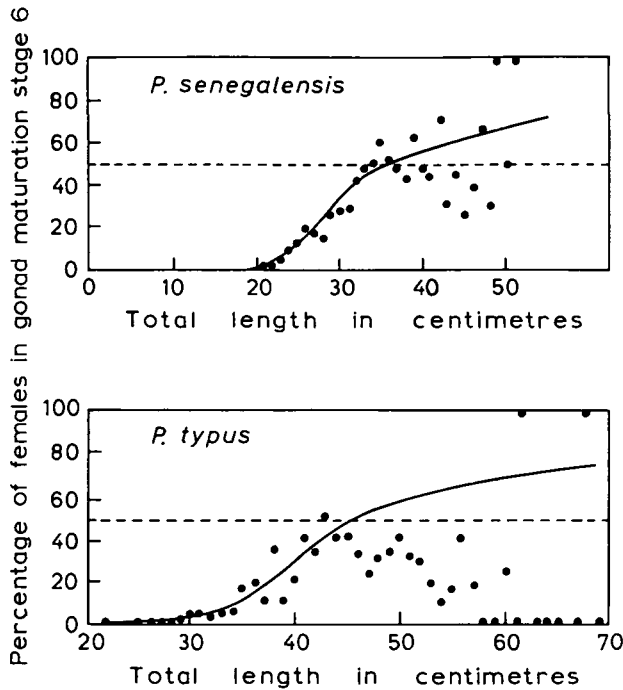


Figure 6. Attainment of maturity from the percentage of all females in gonad maturation stage 6 by cm classes. All data bulked.

the percentage of potentially ripe females which are actually in stage 6, in the number of stage 6 females caught per standard day's trawling, and in the *WG/WT* ratio. These cycles suggest that the year may be divided into two periods, the one of peak spawning activity, the other of minimal spawning activity. In both species, peak spawning occurs in the first six months of the year and especially between February and June (Figure 4). Gonad development begins very soon after the minimal spawning period of July to September and continues during the last few months of the year. Although the cycles are not precisely synchronised in the two species, they clearly both follow a similar general pattern which can be correlated with the oceanographic cycle (p. 100).

The correspondence between the overall sex ratios in the Lagos samples and those determined by COLLIGNON off the Congo is fairly close and the sex ratios of the two species differ comparably in the two localities. An analysis of monthly sex ratios at Lagos shows a clear cycle which is followed synchronously by the two species (Figure 4) and which can be correlated with the spawning cycle, maximum abundance or availability of females corresponding to the period of low spawning intensity. LOWE (1963) has studied a similar croaker fauna in the western tropical Atlantic and found that spawning fish occur only very close inshore, generally in untrawlably shallow water. Subjective evidence suggests that the same occurs at Lagos, where it is rare to find a fish on the point of breeding in the trawl catches. Ova can be extruded from ripe, stage 6 fish only with considerable pressure and all attempts to artificially fertilize these ova have so far failed. It is suggested that the increased availability of

females as represented by the increased percentage of females in the non-breeding season catches represents an offshore movement of resting females. This is to an extent supported by the careful observations of DOWSON (MACLAREN, 1948) on the Lagos beach-seine fishery. He showed a very clear cycle in the catch of croakers in which high catches occurred between November and April, 1943–46, a season corresponding approximately to the period of peak spawning in 1961–62. Such a cycle in the catch of other demersal genera was not recorded.

It is possible, in the case of a few broods, to follow the pattern of reproduction during the first year or so of the life of the broods. In the case of *P. senegalensis*, broods E and G, the following table summarizes the observations on female fish:—

Brood	Month	Age (months)	Mode (LT)	Gonad state
E	April 1961	0	0	—
	October 1961	6	22.5	All fish in stages 2–4, maturing.
	December 1961	8	24.0	First appearance of stage 5 fish.
	January 1962	9	25.0	About 20% of fish which are larger than mode in stages 5 and 6.
	March 1962	11	30.0	About 75% of all fish are in stage 6.
	May 1962	13	35.0	More than 95% of all fish are in stage 6.
	July 1962	15	37.0	Less than 10% in stage 6, remainder resting in stage 3.
G	July 1961	0	0	—
	January 1962	5.5	19.5	All in stages 2–4, maturing.
	May 1962	9.5	25.0	About 50% of the fish in stages 5 and 6, mostly larger than mode.
	June 1962	10.5	27.0	No change.
	July 1962	11.5	29.0	Less than 10% in stage 6, remainder resting in stage 3.

In this example, brood E has an origin in the middle of the peak spawning period, while brood G was spawned at the very end of the period; both contributed to the spawners in the following spawning period, the earlier brood contributing relatively more heavily than the later.

From the available data (Table 1) on growth rates, maturity sizes and spawning seasons it is possible to construct a theoretical reproduction cycle for each species (Fig. 7), which indicates that a brood spawned early in the season will contribute more heavily to the spawning stock in the subsequent season than will a late brood. The cycle is not precisely similar in the two species and though it is probable that all broods of *P. senegalensis* will breed in the first spawning season after their origin, it seems likely that broods of *P. typus* which have their origin very late in the spawning season will not breed in large numbers until the second spawning season after the origin of the brood. In each case, evidently, the larger fish in each brood will commence to spawn before the smaller fish. The low intensity spawning which occurs in all months may derive from broods which mature too late or too early at their first maturity to participate in a major spawning period. Thus, it seems that there is a reason-

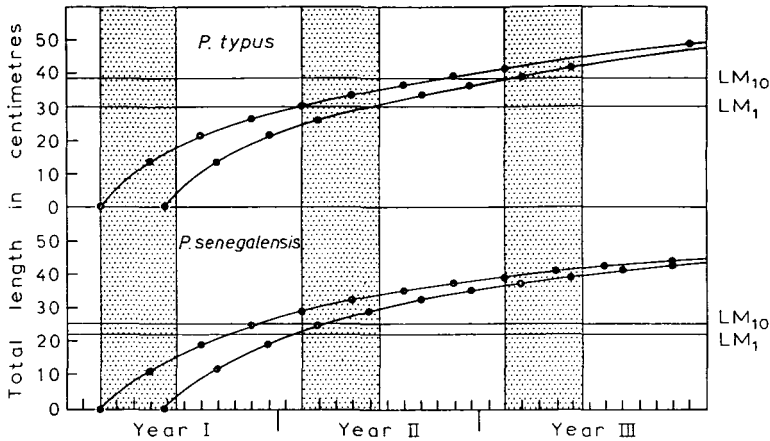


Figure 7. Hypothetical reproductive history of a brood spawned early or late in the period of peak spawning (indicated by stippled areas); lengths of attainment of 1% and 10% maturity indicated by horizontal lines.

able coincidence between the hypothetical spawning cycle of a single brood and that actually observed in the few broods in which it was possible to trace it satisfactorily in the data from the gonad examinations.

Fecundity

A preliminary estimate of fecundity (f) was made by counting ova within a weighed sub-sample of apparently mature ovaries on a small number of fish, less than 10 for each species. Results (Table 1) were of course widely varying, but showed that fecundity on an ova/g of body weight for the two species was similar within the size range examined, and was nearly an order of magnitude higher than for *P. elongatus*. The ova appear to be planktonic and of about 0.50 mm diameter at the time of formation of the oil globule, but have not yet been identified in the plankton (EZIUZO, personal communication).

Recruitment

Because of the fine mesh cod-end lining, recruitment to the samples was virtually complete for both species by a total length of 10 cm. In 1961 four broods of *P. senegalensis* and five of *P. typus* were identified, while in 1962 there were apparently five broods of each species. That the apparent origins of all major broods fall within the period January to July confirms the correctness of the reproductive cycle outlined above. MANN (1962) and LONGHURST (1959; 1960) have studied escapement of these species from trawls and enabled theoretical recruitment patterns to the commercial catch to be deduced.

Mortality

Tagging experiments on West African demersal fish including sciaenids (WATTS, 1959) have failed because of fouling and mutilation of tags by other fish, and mortality estimates have perforce depended on less direct methods. The multiplicity and frequency of broods in *Pseudotolithus senegalensis* and *P. typus* precludes the derivation of total mortality rates from single large

samples as was possible for *P. elongatus* (LONGHURST, 1963) and an estimate was only possible by an analysis of the right-hand limb of the overall length frequency distribution for the sampling period, from which were derived numbers of fish caught at lengths corresponding to the modal lengths for each completed year's growth. This is clearly less than completely satisfactory particularly because of the bias against large fish which are thought to avoid the net, but will give an approximation (Table 1) of total mortality, $Z = F + M$, under current conditions of fishing pressure. The results are consistent between the two species and similar to those obtained for *P. elongatus* by a more satisfactory method at Freetown. It appears that in *P. typus* the mortality rate of larger fish is considerably lower than in *P. senegalensis*.

It has not been possible to separate fishing (F) and natural mortality (M) by a study of their effect under differing values of fishing effort since the effort of the Lagos fleet has remained remarkably steady during the two study years (1961 = 484,000; 1962 = 451,000 horsepower hours per month), nor were sufficient numbers of specimens taken from the relatively unexploited stocks of areas 3, 4 and 5 for a satisfactory comparison with the exploited stocks to the west.

An indication as to the nature of the relationship between F and M can be obtained by a calculation based upon the estimates of Z , on the estimates of stock numbers for each area (Table 2), and from estimate of the numbers of fish landed per annum by the Lagos trawling fleet. During 1962 this fleet landed 709.1 metric tons of croakers from areas 1-3, which represents a total in the region of 3.41×10^6 fish if the calculation is based on the length frequency distributions of croakers in the same areas found during the "Kiara" surveys; to this figure should be added the fish landed by the indigenous canoe set-netters operating from villages along the coast, but it has so far proved impossible to estimate these landings even approximately, and the catch of these canoes is, in any case, heavily biased towards small numbers of large fish, generally of $LT = > 30$ cm. For the present calculations, therefore, these catches have had to be ignored.

The numbers of fish per hectare shown in Table 2 are based on the assumption of no avoidance of the trawl in using the swept-area method of stock determination, and in the table below are re-calculated at three levels of avoidance. For each of the resultant stock estimates a value of F has been suggested, from which follows, by subtraction from the average value of Z for the exploited phase, an estimate of M .

Hypothetical avoidance, %	Stock size ($\times 10^6$)	Z	Mortality (a) F	M
0	5.18	0.67	0.69	0.00
25	7.77	0.67	0.55	0.12
50	10.36	0.67	0.34	0.38

Ignoring the recruitment to the catches of fish spawned during the year, it is possible to deduce from the above figures the probable levels of F and M ; clearly, at the level of no avoidance an impossible result is reached in which $F > Z$. On the other hand, it seems unlikely subjectively that the level of avoidance is as high as 50%; at this level F is approximately equal to M . These two levels give limits of probability to the estimate and suggest that fishing mortality under current levels of fishing effort is somewhat higher than

Table 3

The diet of Sciaenidae off tropical West Africa

Small crustacea = Mysidacea, Cumacea and larval forms;

Natant crustacea = Penaeidae, Caridea.

Benthic crustacea = Brachyura, Anomura, Stomatopoda.

(Numbers are occurrences)

Species		Small crustacea	Natant crustacea	Benthic crustacea	Poly-chaetes	Cephalopods	Fish	Locality
<i>P. typus</i>								Off Lagos
N = 50	LT = 0-10	78	18	-	-	-	4	
33	11-20	42	44	-	-	-	3	
111	21-30	22	60	-	-	1	14	
68	31-40	22	48	-	-	3	26	
<i>P. senegalensis</i>								Off Lagos
N = 61	LT = 0-10	75	11	-	-	5	5	
35	11-20	33	46	-	-	-	14	
97	21-30	21	55	-	-	-	22	
26	31-40	16	54	-	-	-	23	
<i>P. elongatus</i>		38.1	44.5	6.0	5.4	-	24.6	Sierra Leone River
<i>P. elongatus</i>		16.7	50.0	-	-	-	33.3	West African shelf
<i>P. brachygnathus</i>		-	16.9	2.4	0.6	0.2	75.0	Sierra Leone River
<i>P. mbizi</i>		-	-	-	-	25.0	75.0	Continental edge

natural mortality, and if the 25% avoidance level is accepted as being reasonable then may as well be as much as five times higher. It must also be remembered that if it had been possible to include the indigenous fishing mortality in these calculations, then the estimates of F relative to M would have been even higher.

It would not be justifiable on the nature of the present evidence to pursue this line of enquiry further.

Food and feeding

It is well known that the sciaenids under consideration are active predatory species, largely taking natant crustacea and fish. Table 3 shows the progression, during growth, of the diet of *P. senegalensis* and *P. typus* off Lagos from small to large crustacea and then to fish, and compares it with that of the principally ichthyophagous *P. brachygnathus*, the estuarine shrimp-feeding *P. elongatus*, and the sub-thermocline *P. mbizi* which feeds on cephalopods and fish. LONGHURST (1957) showed that off Sierra Leone no seasonal cycle in feeding intensity could be detected, though BAYAGBONA (personal communication) has demonstrated a cycle in condition factors off Lagos, with a seasonal peak occurring in the last three months of the year just before the onset of the peak breeding season.

Discussion

To the extent that these calculations are unchecked by independent data, they must be considered preliminary. It is expected that the parameters calculated for *P. typus* will be more modified by future work than will those for *P. senegalensis*, in which the sampled populations, and hence the length frequency distributions, were more homogeneous and hence satisfactory of analysis. It is hoped that work in progress by BAYAGBONA on growth rings in

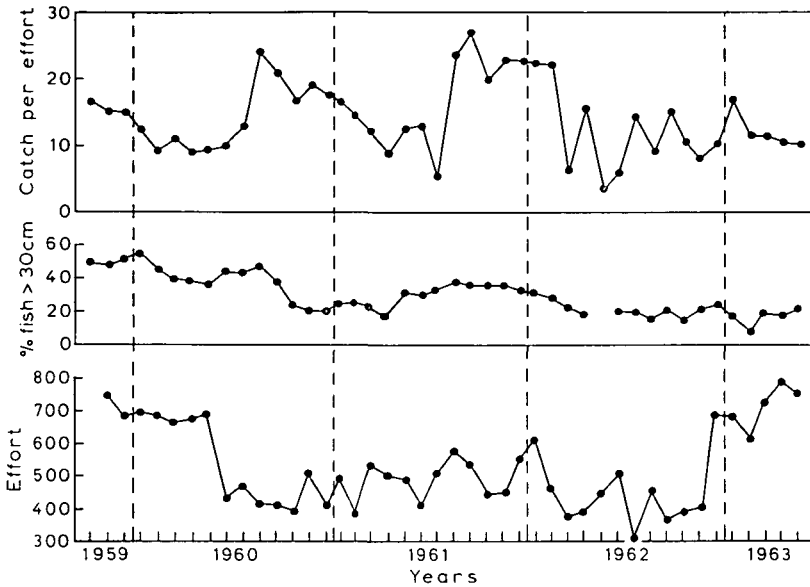


Figure 8. General features of the trawl fishery for croakers out of Lagos. Catch per unit effort = $100 \times \text{kg/h.p./hours absence}$; effort = $\text{h.p. hours absence}/1000$.

skeletal structures will confirm the correctness, or otherwise, of the growth parameters presented here.

From the values of the von Bertalanffy growth coefficient (K) given in Table 1 and from the small numbers of year-classes or year-groups present in the samples, and, presumably, in the commercial landings, it is clear that the species under investigation follow the general pattern now emerging for tropical demersal fish and that their growth and mortality rates are very different from those of fish of colder seas. It has not been possible to make direct comparisons with many other species of Sciaenidae, but from the small amount of published data it appears that, as with the West African species, K can vary quite widely for members of the family even from the same area. For instance, RAO (1961) presents data for *Pseudosciaena diacanthus* in the Indian Ocean from which it is possible to derive an approximate value of $K = 0.87$; KUTTY (1961) gives data on the growth of *Otolithoides brunneus* in the same area which indicates a value of $K = 0.25\text{--}0.28$. In much colder Californian waters, JOSEPH (1962) has analysed the growth of *Roncador* and *Menticirrhus* and from his data it is possible to deduce values of $K = 0.32$ and $K = 0.51$ respectively. Thus, there is apparently nothing unusual in the variation of K from 0.37 to 0.71 in the species under analysis in the present paper.

The relationship between the parameters L_m and L_∞ is quite close to that predicted by BEVERTON and HOLT (1959). It is seen from Table 1 that L_m/L_∞ varies from 0.45 to 0.75 according as to how L_m is calculated and it may be that the difficulty of estimating L_m in a standard manner, or of deriving it in a standard manner from published data, accounts for the great variation observed by these authors in this ratio. The relationship between the point of inflection in the WT growth line and the value of WT_∞ is very close to the value of 0.3

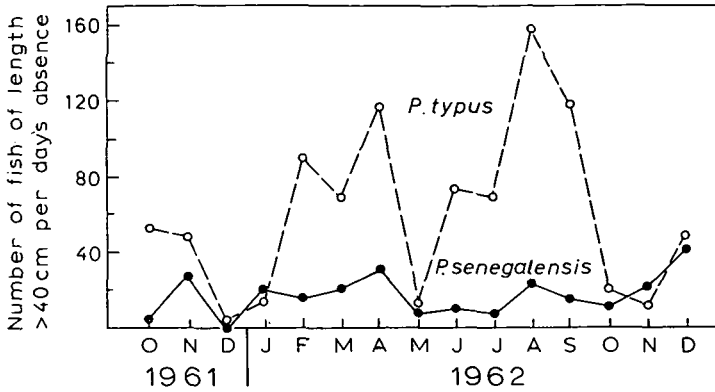


Figure 9. Number of fish of $LT = > 40$ cm per day's absence, "Kingfisher", 1961–1962.

which BEVERTON and HOLT found to be common in the species reviewed by them. It is approximately 0.25 in *P. senegalensis* and 0.30 in *P. typus* and this may be taken to indicate the general correctness of the values calculated for the asymptotic lengths and weights for these species.

From the results of this investigation and from the commercial landing statistics some deductions may be made concerning the biological basis of the West African sciaenid fishery. Commercial trawling has been established for about a decade on the tropical West African coast and the reports of WATTS (1962), LONGHURST (1963, 1964b) and others make it clear that within this period catch rates have declined, and size and species composition of the stock changed. Ghana, Sierra Leone and Ivory Coast have found it necessary to impose restrictions on the number of trawlers or on mesh size, while in other countries administrative inertia and disinterest have prevented the enactment of any fisheries regulations. Off Lagos, therefore, we are presented with an example of a fishery controlled only by economic factors.

The general characteristics of this fishery can be seen from Figure 8. During this period the effort has fluctuated around a mean value of 571,000 h.p. hours fishing/month, held at this level by limitations of berthing facilities, cold storage and market capacity. This represents a fishing effort of about 1000 h.p. hours/mile²/month (LONGHURST, 1961) on the trawling grounds. The progressive decline in the percentage of fish of $LT = > 30$ cm is probably both an effect of fishing on local stocks and also of the very recent extension of trawling onto the "small-fish" areas off the Niger Delta (p. 99).

The available stocks of the two species have rather different compositions throughout the year. For *P. senegalensis* the number of very large ($LT = > 40$ cm) fish remains approximately constant, while for *P. typus* the number fluctuates very considerably (Figure 9) as recorded in the research vessel landings. The commercial trawlers do not separate the two species, and record a cycle (Figure 8) in the landings of large fish ($LT = > 30$ cm) in which high percentages of such fish occur particularly during the second half of the year, coincident with the period of highest catch rates for croakers. These cycles are not easy to explain but it is clear that *P. typus* stock is less homogeneous than that of *P. senegalensis* and is probably considerably influenced by rapid and relatively short distance migrations in and out of the area. The arrival, for instance, of very large *P. typus* in non-breeding condition in such numbers as to dominate

the landings for a few days or weeks is typical and may be, as during March 1961 and 1963, accompanied by unusual quantities of the estuarine *P. elongatus* including fish of unusually large size (to $LT = 47$ cm) for that species. These facts suggest the movement onto the Lagos grounds of unexploited estuarine stocks of sciaenids, perhaps from the western delta. This certainly occurs during the August irruptions when specimens of other typically estuarine sciaenids (*P. epipercus*, *P. moorii*) occur together with the others in unusually large, but still commercially insignificant, numbers.

It has been suggested above that there is an increased availability of females during the second half of the year connected with the period of low spawning intensity and this may also contribute in some measure to the high catch rates of this period. But perhaps the most significant factor is that during this period the broods spawned during the previous breeding season begin to be recruited to the catches. The mesh size used by the uncontrolled Lagos fleet is commonly below 50 mm and the table below will show that 50% retention for a mesh size of 50 mm falls at about $LT = 20.0$ cm for *P. senegalensis* and $LT = 22.7$ cm for *P. typus*, or at an age of about seven months in each species.

If, as seems probable because of the high fecundity, recruitment is independent of stock size at stock densities which remain economic, then an estimate of the mesh size necessary to produce the optimum sustained yield is more likely to be obtained from a consideration of the relative biomass (P_t) of the survivors and of the yield (Y_t) under present levels of fishing intensity than by a consideration of the necessary numbers of escapees to maintain an adequate breeding stock. Values of Y for current fishing intensities are tabulated in Table 1, from which it can be seen how great a percentage of the yield is derived from fish of from one to two years old, that is $LT = 30$ to 40 cm approximately. The 50% retention levels, calculated from known mean values of the selection factor (S), for a trawl with a mesh of moderately flexible twine, for example hemp, would be:—

	Mesh (cm)				
	S	2.5	5.0	7.5	10.0
<i>P. senegalensis</i>	4.01	10.0	20.0	30.0	40.1
<i>P. typus</i>	4.55	11.4	22.7	34.1	45.5

This would indicate that a mesh size of between 75 and 100 mm is necessary to place a sufficient degree of fishing intensity upon the fish of between one and two years old, and that a larger mesh would allow of very little exploitation of this age-group. For reasons which have been discussed previously (LONGHURST, 1960; MANN, 1962) it is not good practice in these fisheries to use a cod-end of which the 50% escapement length falls on an abundant age-group of large fish, since excessive meshing leads to excessive attack of the cod-end by large sharks, and for this reason it is suggested that the 75 mm mesh should be adapted, and that the level of fishing intensity should be controlled rather through the regulation of fishing effort, than by attempting to rationalize escapement. This is the more true since the fishery, besides croakers, includes very many other species with very diverse mesh selection factors.

It would appear that the rather rapid growth rate revealed for these species would lead to two effects on the fishery. Firstly, that recovery from a severe decline in the stocks due to heavy fishing would be more rapid than in demersal stocks of temperate seas, and secondly, that it would lead to the occurrence of only a very small number of year-classes in the fishery which would itself lead

to instability. The first supposition is probably correct, but cannot be demonstrated at present, though the writer feels that it may well be soon if the present trends in the fishery are allowed to continue, but the second supposition is perhaps not true. The effect of a very large number of discrete broods from each year being present in the stocks at any one time may to some extent damp out any instability in stock strength. That this is so may be indicated by the very stable level maintained by the catch rates over the five years during which landing statistics have been maintained.

The greater part of the discussions in this paper have been concerned only with the two commercial species at Lagos, and it is perhaps interesting to compare these species with the results obtained for *P. elongatus* in the estuary of the Sierra Leone River (LONGHURST, 1963). This species has a considerably smaller maximum size ($LT_{max} = 47.0$ cm) than the other two species but the relative growth and mortality rates, set out in Table 1, are not dissimilar. The major difference to be noted appears to be that in *P. elongatus* the pattern of spawning does not include a number of discrete broods in each year but much more approaches the case of a single year-class spawned over a relatively short period in the middle of the dry season at a time when salinities and temperatures in the estuary are at their annual maxima. This difference from the cases of the sciaenids of the open continental shelf off Lagos is perhaps to be related to the considerably greater and more regular changes that occur in the physical environment in the Sierra Leone River (WATTS, 1958) which may much more than on the open shelf restrict spawning within narrow temporal limits. It is unfortunate that a population of *P. elongatus* sufficiently abundant and regular in occurrence for bionomic study has not been available at Lagos for comparison with the other species studied here.

Acknowledgements

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Summary

1. This paper reports a two year investigation of the bionomics of the exploited sciaenids off Lagos, Nigeria, and compares the results with what is known of sciaenid bionomics elsewhere in the tropical Atlantic.

2. The two species which form the most important constituent of the trawl catches on the continental shelf occur only in the warm tropical surface water and do not extend below the thermocline into South Atlantic Central water, nor do they extend into cold water to the north and south.

3. Breeding is continuous throughout the year off Nigeria, but reaches a peak at the time when the surface water is warmest, from January to June.

4. Growth is rapid, growth coefficients varying from 0.37 to 0.71 in the species examined; the total mortality coefficient averages 2.03 in the second, and 0.71

in the fourth year of life. Fishing mortality may comprise up to 80% of this total mortality under current fishing intensity.

5. It is suggested that a 75 mm mesh may be the most suitable for this fishery, taking steady state yields into consideration, and in view of certain practical difficulties connected with the fishery.

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