BIOLGy AND DYNAMICS OF PAGELLUS COUPEI (DIEUZ. 1960), PAGRUS EHRENBERGI (VAL. 1830) AND DENTEX CANARIENSIS (POLL. 1954) IN GHANA WATERS

by L. Rijavec

RESUME

Les résultats concernant la biologie et la dynamique de trois espèces de sparidae sont présentés dans cet article. L'étude est basée sur les données obtenues à partir de campagnes de chalutages entreprises en 1969 et 1970 dans le cadre du programme UNDP, du Fishery research Unit du GHANA.

L'habitat optimum pour les espèces étudiées était un fond dur entre 20 et 30 bras, avec une biomasse benthique élevée et une température inférieure à 20°C. Pagrus ehrenbergi était moins isotherme que les deux autres espèces.

Dentex canariensis et Pagrus ehrenbergi montrent une distribution bathymétrique des tailles bien caractérisées en toutes saisons, les plus gros individus occupant les eaux les plus profondes.

Il existe deux périodes de ponte par an pour les trois espèces et les nouvelles recrues apparaissent dans la population exploitées pendant leur première année. Les trois espèces atteignent la maturité sexuelle au début de leur deuxième année.

Les fluctuations du facteur de conditions suivent un cycle saisonnier identique pour les 3 espèces, en relation avec la période de ponte et les conditions hydrologiques.

Il n'existe que deux groupes d'âges abondants dans la population, i.e. I+ et II+ qui forment plus de 80% des prises.

Le régime alimentaire est surtout à base de poissons. L'alimentation semble plus intense en période d'upwelling.
ABSTRACT

The results of the work on biology and dynamics of three species of Sparidae are given in this paper. The study is based on the data obtained from trawling survey carried out in 1969 and 1970 under the programme of UNDP - Fishery Research Unit, Ghana.

The optimum habitat for the studied species was found to be a hard bottom between 20 and 30 fathoms, rich in biomass and with a sea temperature below 20°C. Pagrus ehrenbergi was less isothermic than the other two species.

Dentex canariensis and Pagrus ehrenbergi showed a distinctive size distribution by depth in all seasons; bigger fish were found in deeper waters.

There are two spawning periods in a year for all three species and the new recruits come into the exploited population within the first year of life. All three species mature in the beginning of their second year of life.

The fluctuations of condition factor showed a similar seasonal cycle for all three species and they were in relation to spawning period and hydrographic conditions.

There are only two abundant age groups in the population e.g. I and II which formed more than 80% of the catch.

Fish was the main diet for the studied species. Feeding seems to be most intensive during upwelling period.
INTRODUCTION

During our trawling survey (Rijavec - manuscript) it was shown that Sparidae represent the steadiest and the most abundant part of demersal fish stocks on the shelf of Ghana between 10 and 40 fathoms. Three species, i.e. Pagellus coupeii, Pagrus ehrenbergi and Dentex cannieriensis were the most important, their participation in the total catch being 8.15, 5.06 and 6.51% respectively. Fisheries statistics for Ghana inshore waters for 1970 have shown that 14.7% of the total trawl catch were sea breams.

Very little research has been done on the biology of these sparids in the tropical Eastern Atlantic. Some data on their distribution can be found in the publications of ORSTOM (ROSSIGNOL et al., 1960, CROSNIER, 1964, CROSNIER and BERRIT, 1966, POINSARD and TROADEC, 1967, DURAND, 1967, TROADEC et al., 1969, BOUILLON et al., 1969) as well as in the papers of LONGHURST (1964, 1965) and POSTEL (1954). The report of Guinean Trawling Survey (WILLIAMS, 1968) and the paper of SALZEN (1957) are the only sources of this kind of information for the Ghana waters. Some biological observations were done on Pagellus coupeii (SKORNYAKOV, 1963a) and Pagrus ehrenbergi (LONGHURST, 1963, MATTA, 1965).

MATERIALS

The data for the present study were collected during the regular trawling survey programme of which the detailed description is given elsewhere (Rijavec - manuscript).

There were accomplished 22 monthly transects off Tema from January 1969 to December 1970, each consisted of 5 stations at 5, 10, 15, 20 and 25 fathoms depth respectively. In addition, seven trips were
Fig. 1  TRAWLING STATIONS 1969-1970

Key
- Pagellus coupeii
- Pagrus ehrenbergi
- Dentex canariensis

Fig. 2  Relative Abundance of Pagellus coupeii, Pagrus ehrenbergi, Dentex canariensis in relation with depth.
made between August 1969 and December 1970 and data were collected from 21 stations on the transsects off Axim, Cape Coast, Winneba, Tema and Keta at depths between 10 and 40 fathoms (Fig. 1).

From the samples obtained the following number of specimens was examined for various studies:

<table>
<thead>
<tr>
<th>Species</th>
<th>Pagellus coupezi</th>
<th>Pagrus ehrenbergi</th>
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<td>Stomach content</td>
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**METHODS**

Length measurements corresponding to total length were made to the nearest centimetre. The fish investigated for length-weight relationship, condition factor and gonosomatic index were measured to one millimetre/gramme accuracy. The gonads were weighed to one decigramme.

From each catch random samples were taken for length measurements and 250 fish were measured. If the number of fish caught was smaller than 250 (but not smaller than 20) all fish were measured. From these samples, subsamples for biological studies were taken - at most five fish from each cm group.

Sex ratio was tested by chi-square index of dispersion. Minimum length at first reproduction was estimated by using the same methods as for mesh selectivity experiments. The investigation of the
reproductive cycle was based on the monthly fluctuations of gonosomatic index (expressed for each sex as the percentage of gonad weight in relation to the total body weight). Calculations of length-weight parameters were done in the standard manner by regression analysis of logarithmic values of average weights in each cm length group.

Condition factors were calculated for both sexes of *Pagellus coupeoi* while only for females in the other two species. As a power for length in the equation the parameter obtained from length-weight relationship was used. Monthly averages of condition factors were calculated and were plotted together with monthly averages of the gonosomatic index.

Modes were selected in the monthly length frequency distributions for each species according to similar criteria to those established by HENNEMUTH (1961). The modes were joined along the most probable growth lines to trace the growth of individual broods. Growth rate parameter and asymptotic length were calculated by using the linear form of Von Bertalanffy's equation:

\[ l_{t+1} = e^{-K_l} + L (1 - e^{-K}) \]

Only full stomachs were examined for main taxonomic groups.

RESULTS

1. DISTRIBUTION AND ABUNDANCE

In 168 comparative trawling tows 3086 kg of *Pagellus coupeoi*, 1915 kg of *Pagrus ehrenbergii* and 2463 of *Dentex canariensis* were caught. The average catch per hour was 18.4, 11.4 and 14.7 respectively. These relatively small values of catch rates are due to many nil catches on the stations in shallow waters where these three species seldom penetrate. Maximum catches per one hour's towing were 52863 and 118 kgs taking the same order of species as above.
Fig. 3 *Pagellus coupej*—Catch rates (kg/h) as a function of temperature and trawling depth.

- $\bar{C}$—Average catch per water layer and depth; $+$ = less than 0.25 kg.
Fig. 4  *Pagrus ehrenbergii*—Catch rates (kg/h) as a function of temperature and trawling depth.  
\( \bar{C} \)=Average catch per water layer and depth; + = less than 0.25 kg.

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**Fig. 5** Dentex canariensis—Catch rates (kg/h) as a function of temperature and trawling depth.

- **C** = Average catch per water layer and depth, + = less than 0.25 kg.
1.1. - Ecological limiting factors

1.1.1. - Depth:

On figure 2 are shown the curves of relative abundance of fish in relation to the depth. For all three species the highest catch rates occurred at 30 fathoms. *Pagellus coupei* showed a decline in density at 25 fathoms. On the other hand, at 40 fathoms *Pagellus coupei* was still relatively abundant while *Pagrus ehrenbergi* and *Dentex canariensis* were scarce (Fig.3-5).

1.1.2. - Temperature:

All three species were found in the range of 16.10° to 28.58°C. The distribution of fish showed, however, a distinctive pattern within this range. From the bathythermograph records we noticed that the lowest limit of the thermocline lay between 19 and 21°C, but most of the time was around 20°C. On this basis we divided the water column into three temperature-layers, i.e. below thermocline (20°), thermocline or discontinuity layer (20 - 25°) and surface layer (25°). We split the layers according to trawling depths and fitted into the resulting subdivisions the catch rates of each individual haul and their average values (Fig.3-5). The following results can be deduced:

*Pagellus coupei*: Although there is a certain overlap in the distribution of this species between two lower layers, the fish is evidently more abundant on the grounds where the temperature is below 20°C and very seldom penetrates through the upper limit of the thermocline.
Dentex canariensis: This species shows the same temperature distribution as the previous one. In addition, it can be noticed that the bathymetric factor is here very important and very little fish can be found above 20 fathoms.

Pagrus ohrenbergi: This fish is equally abundant in both lower water layers and sometimes is to be found even in warm waters above 25°C. On the other it is rather restricted to the depths between 20 and 30 fathoms.

1.1.3.- Oxygen:

The oxygen content where all three species were caught ranged between 2.22 and 6.25 ml/l. Within this range the species distribution is very similar to that in relation to the temperature i.e. the fish were more associated with lower values of oxygen. This certainly does not mean that optimal values of oxygen content in the water must be low, but that low temperatures above the bottom are correlated with low values of oxygen content and vice versa. The positive correlation coefficient between these two values was highly significant (r=0.89). Because the cooling of the sea water on the bottom is due to upwelling i.e. inshore movements of deep Central Water of South Atlantic (BERRIT, 1964) with low oxygen content, this correlation was normally expected.

1.1.4.- Salinity:

All three species were found within the salinity range of 33.52 to 36.10%. No distinctive distribution pattern of the fish within this range could be found. Although very few fish of all three species were found in the water below 34%, these values occurred on the stations at 10 and 15 fathoms where, as we have seen, these fishes were scarce or absent throughout the year.
Fig. 6 Correlation between quantity of invertebrate fauna (q) and density of Sparidae (kg/h).
1.1.5.- Nature of bottom:

On table 1 the catch rates and percentage occurrences of studied species are presented as a function of the nature of the bottom. The highest catch rates for all three species are found on hard gorgonian grounds while very low ones on soft muddy ones.

1.1.6.- Quantity of Invertebrate Fauna:

On figures 3-5 it can be seen that in what is apparently the most convenient environment for the investigated species, as far as temperature and depth are concerned i.e. at 25 and 30 fathoms below the thermocline, we find together with big catches the ones where very few or no fish were caught at all. This goes especially for Pagrus c. and Dentex c. In all these cases, without exception, the ground on which these negative catches occurred was pure mud (stations 1, 2, 3, 21). It was shown before (Rijavec - manuscript) that on the muddy grounds of Ghana shelf only very small quantities of invertebrate fauna can be found. If we assume that the quantity of invertebrate caught in the net is the indicator of the richness of the biomass of the ground, and as such the indicator of the abundance of the available food for most fish, we can expect some relation between this factor and the density of a particular fish (within the limits of other ecological limiting factors). On figure 6 the average values of the quantity of invertebrates (the method of calculating the density index of invertebrates is described elsewhere; Rijavec - manuscript) obtained during three cruises (May, October, December - 1970) were plotted for each station together with catch rates of each species separately. Positive correlation coefficients were significant on 1% level for Pagrus c. and Dentex c. (r=0.85 and 0.77) and on 5% level for Pagellus c. (r=0.47).

For the tables 1 to 8 mentioned in the texte, see at the end of the volume.
Summarizing it can be said that in Ghana waters the optimum habitat for the three species was a hard bottom between 20 and 30 fathoms, rich in biomass, and with temperature below 20°C.

1.2.- Seasonal migrations

Inshore-offshore movements of all three species follow a distinctive pattern in accordance with the temperature optimum of their habitat. At the end of December and especially, in August when the cool deep water moves inshore (upwelling), Pagellus c. and Pagrus e. penetrated inshore up to 10 fathoms depth Dentex c. was most abundant at 20 fathoms. In February, May and October, i.e. during hydrographic stability with sharp thermocline (the base of which is between 20-23 fathoms) all three species were restricted to the depth of 25 and 30 fathoms (Table II). However, Pagrus e. is more eurythermic than the other two species as we have already mentioned before. On the Tema transect, which was sampled monthly, intensive inshore movements of this species were recorded in September in both years i.e. during its main spawning period.

1.3.- Seasonal fluctuations of the catch

The above migrations should be reflected in the catch fluctuations of these species in inshore waters. The commercial statistics for the inshore trawling fleet show in 1970 rather clearly that the biggest catches of Sparidae were during the main upwelling season (July to September) and in December (Table III).

However, the increase in abundance is not as spectacular as it appears from the table. The effort index in these statistics (trawling trip) is a very bad measure because the whole trawling fleet is combined together. The upwelling season is also the time of the main sardine fishery. During this period all small boats (27' - 49'), which
normally trawl at other times, fish for sardines with purse seines. Only the big trawlers (60' - 100') maintain their trawling operations and normally the catch per trip would increase regardless of the quantity of available fish (their trip usually lasts 4-5 days against one day only for small vessels). Nevertheless the absolute landing data of sea breams (Table III) reveal the same trend of fluctuations, whereas the differences in catches between the cold and warm season are not so big as with the density index (catch/trip).

The December peak in catch could also be caused by the recruitment of the new generation of Pagrus e. and Dentex c. into the fisheries (see later).

2.- LENGTH DISTRIBUTION

Pagellus coupei:

The size range of all specimens caught on Tema transect in 1969 was 6-27 cm. In 1970 they were within the 4-28 cm group. On all the transects of the shelf of Ghana this range was 4-30 cm. The combined length-frequency curves were mostly unimodal or bimodal, and only occasionally polymodal (Figures 7, 8). The length-frequency curves of individual samples were almost always unimodal, which might suggest that the shoals were grouped by age.

The newly recruited generation came into the population in 1970 in September with modal length of 5 cm. In 1969 recruitment was apparently later, probably in October. Although this is only an estimate as we did not sample in October and November, we can not be much mistaken. In December 1969 this new generation was very distinct and its modal length was similar to that of 1970. This generation is thought to be the brood from the main spawning in June. The brood from the "small" spawning period (January) could not be traced from length-frequency histograms.
Fig. 7 *Pagellus_coupeii*. Percentage length frequency distribution by month off Tema.
On the whole the males were slightly bigger than the females. In some months (around the spawning season) the difference in mean length between sexes was very small and even reversed (Table IV). The size range of females was smaller too. The biggest female caught was in the 25 cm group.

The mean length for the whole population was 15.54 cm in 1969 and 15.72 cm in 1970. The monthly and seasonal fluctuations of mean lengths were very dynamic (Tables IV, V). The minimal values were found in September and October when recruitment occurred.

There seems to be a size distribution by depth. Apart from August, when the biggest fish were found in shallow waters, the highest values of mean size were always at the depth of 20 and 25 fathoms. As will be shown later these were also the depths where the sex ratio was constantly in favour of males.

**Pagrus ehrenbergi:**

The overall size range of this species on Tema transect was 4-40 cm in 1969 and 5-43 cm in 1970. During seven trips on the whole shelf of Ghana the fish measured 4-43 cm. The length-frequency curves representing all samples together were always polymodal (Figures 9, 10). It was noticed, however, as with the previous species, that very often the schools were grouped in presumably age groups, length-frequency curves having been unimodal on individual stations.

The new recruits from the main spawning season came into the population in December in both years of investigation. In 1969 their modal length was 5 and 6 cm while 7-8 cm in 1970. The reason for this discrepancy may well be that in 1969 the main spawning took place later than in 1970 perhaps in October, but again we have no data for this month. However, the low value of the gonosomatic index in September 1969 in comparison with that of September 1970 (Figure 15), might suggest
Fig. 9 Pagrus ehrmani: Percentage length frequency distribution by month, off Terns.

Fig. 10 LENGTH FREQUENCY DISTRIBUTION

Page 1969

JAN.
FEB.
MAR.
APR.
MAY.
JUN.
JUL.
AUG.
SEP.
OCT.
NOV.
DEC.

LENGTH GROUP

0 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 cm

N-581
Aug. 1969

N-973
Dec. 1969

N-387
Feb. 1970

N-939
May 1970

N-572
Aug. 1970

N-482
Oct. 1970

N-833
Dec. 1970
that the peak spawning in 1969 occurred one month later. The brood from the small spawning period could be traced in 1969 in July while in 1970 in August (all transects) and September (Tema transect). The modal length of these recruits was 10 cm.

In all months and at all depths the males were bigger than females (Table IV). The size range of females was 7 cm smaller than that of males. From 38 cm on we did not catch females anymore.

The mean length for the whole population was 18.62 cm in 1969 and 25.37 cm in 1970. The reason for this difference is the fact that in 1969 the juvenile generation was very strong and remained so throughout the year on the investigated fishing ground. In both years the seasonal changes in mean size were frequent and rather erratic (Tables IV, V). They were due to recruitment, migration of different age groups and changes in sex distribution.

There was a distinct size distribution by depth in all seasons; the mean size increased with depth. This was especially remarkable during recruitment time (December).

**Dentex canariensis:**

In 1969 the size range of this species on Tema transect was between 7 and 68 cm. In 1970 the fish caught measured 11-70 cm. The overall size range on all transects was 7-70 cm. Length-frequency curves of all samples bulked are mostly polymodal but dominant mode is very often clearly distinctive (figures 11, 12). Individual samples showed the same characteristic as the other two species i.e. their length-frequency distribution being mostly unimodal.

In 1969 and 1970 the newly recruited generation came into the population in December with modal length 14-15 cm. The size suggests that this brood was from January spawning. In August we can trace
Fig 12 LENGTH FREQUENCY DISTRIBUTION.

Fig 11 Gentia canariensis — Percentage length frequency distribution by month off Tema.
another generation coming into the population (this is especially evident in the August 1970 histogram where data from all the transects are combined (figure 12) with no distinct mode with the size range 12-17 cm. This is probably the brood from the previous year's main spawning in August.

With few exceptions the males were bigger than females (Table IV). The biggest female caught measured 63 cm.

The mean length of the whole population was 29.07 cm in 1969 and 26.87 cm in 1970. The monthly and seasonal fluctuations of mean size do not show such big variations as the other two species. A distinct drop in mean length values of the whole population occurred in August and December during recruitment (Tables IV, V). In those months there was also observed a remarkable size distribution by depth, the mean size increasing with depth. This phenomenon, although less marked, was found in all trips except in October 1970 (Table V).

3. REPRODUCTION

Determination of sex was done macroscopically without difficulty. With Pagellus coupei sex could be determined for specimens as small as 10 cm while for the 15 cm - group the determination was 100%. The smallest specimen of Pagrus ehrenbergi sexually identified were within 14 cm (females) and 16 cm (males) groups. For every fish bigger than 22 cm the sex was identified with certainty. For Dentex canariensis this range was from 17 to 22 cm.

3.1. Sex ratio (Table VI)

Pagellus coupei:

In both years of the survey the number of males in the samples was significantly bigger than that of females. The exception was the cruise in August 1970.
Fig. 13 Determination of size at first maturity in *Pagellus coupei*, *Pagrus ehrenbergi* and *Dentex canariensis* off Tema. Data from both spawning periods combined.
Pagrus ohrenbergi:

In 1969 and in 1970 we found more males than females in the samples population off Tema, but the difference was significant only in 1970. On the whole shelf the sex ratio did not show significant differences.

Dentex canariensis:

No significant differences of the sex ratio were found in this species.

No seasonal characteristics in sex distribution could be found in any of the studied species. However, with Pagellus coupei the predominancy of males over females was in general limited to the depths of 20 and 25 fathoms, while in shallower and deeper waters it occurred only occasionally.

3.2. Mean length at first maturity

For each species and both sexes we calculated the number ratio of mature fish (maturity stage III to VII-II) against the total sampled within each cm group. For each species this was done separately for both spawning periods so that samples from three months (month of peak spawning plus two neighbouring ones) were pooled together. The values of the resulting were plotted as a function of size. Curves similar to those of mesh selectivity experiments were obtained. For all three species there was no apparent difference in two spawning periods, so we bulked the data from all six months together (Figure 13). The curves were more or less symmetrical for Pagellus coupei and Pagrus ohrenbergi but very skewed for Dentex canariensis.

The length of mature fish at 50% level - $L_m (50\%)$ was calculated by using the formula:
\[ L_m = L_{n+1} - \sum y_i \]

where \( L_{n+1} \) is the length when all the fish are at least at the beginning of their gonadal maturity and \( \sum y_i \) is the sum of ordinate values within the range of the curve. The results obtained were as follows:

<table>
<thead>
<tr>
<th></th>
<th>Lm (50%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>males</td>
<td>females</td>
</tr>
<tr>
<td>Pagellus coupeii</td>
<td>13.06 cm</td>
</tr>
<tr>
<td>Pagrus ehrenbergi</td>
<td>20.98 cm</td>
</tr>
<tr>
<td>Dentex canariensis</td>
<td>22.31 cm</td>
</tr>
</tbody>
</table>

Our values could be, naturally, bigger if we had used only maturity stages V, VI and VII for the analysis. Using this method however, the dots tend to be very scattered and we never reach the 100% point, because there is always in the sample a certain percentage of fish in maturity stage VII-II or IV during the whole period of spawning.

The age of Pagellus coupeii and Pagrus ehrenbergi when 50% of them first reproduce or are about to spawn is 14 months. Dentex canariensis the growth pattern could not be determined satisfactorily but we believe that they mature in their second year of life too.

3.3. Spawning period

For all three species there was evidence of some reproduction activity throughout the year. It soon became clear that it was not possible to determine the peak of the spawning season merely by using the percentage of fish with advanced sexual maturity in the sample. The distinction between maturity stages was found to be much too subjective for a correct analysis. Moreover the specimens we examined were very
Fig 14  PAGELLUS COUPEI  MONTHLY FLUCTUATIONS OF GONOSOMATIC INDEX (R.G.S) AND AVERAGE BOTTOM TEMPERATURE — 1969 AND 1970

Fig 15  PAGRUS EHRENBERGI  MONTHLY FLUCTUATIONS OF GONOSOMATIC INDEX (R.G.S) AND AVERAGE BOTTOM TEMPERATURE 1969 AND 1970.
seldom fresh as they had stayed several hours or even days in deepfreezers. After the fish had been defrozen it was impossible to distinguish maturity stages IV and VII. From May 1969 on we used therefore a quantitative method for reproduction cycle studies i.e. we calculated for each month the gonosomatic index (RGS) for both sexes in all three species. The monthly variations of average values of RGS together with average bottom temperatures of the stations from where the samples were taken are shown on figures 14-16.

The main spawning season for Pagellus couperi was in June, just before the principal upwelling season. Another smaller peak of gonad activities was found in January. Both sexes showed remarkably parallel development. The highest values of bottom sea water temperature were associated with minimal gonad activity.

For Pagrus ehrenbergi the main spawning occurred in 1970 during September, at the end of the cool period. We believe that in 1969 this peak period was postponed till October, but unfortunately no data were available to prove this assumption. However, the small value of RGS and prolonged period of low bottom temperature in September 1969 might suggest that the above assumption is correct. Another small peak of reproductive activity occurred in February. Although the average RGS values of males are small they show similar fluctuations to those of females.

Dentex canariensis spawned in 1969 in August i.e. during the main upwelling period. In 1970 the maturity development was abruptly interrupted in July by a sharp decline in temperature (note the similar interruption with Pagrus ehrenbergi) and later it was renewed in August. However, the value of RGS was smaller than the previous year. Another smaller spawning period could be detected in January.
Fig. 16 DENTEX CANARIENSIS MONTHLY FLUCTUATIONS OF GONOSOMATIC INDEX (RGS) AND AVERAGE BOTTOM TEMPERATURE — 1969 AND 1970.

\[ W = 0.01336 L^{3.0043} \]

\[ N = 1684 \]

Fig. 17: Pagellus couperi, length/weight relationship (x=sample values)
3.4. - Spawning ground:

*Pagellus coupei* was limited during spawning time to the depth between 20 and 30 fathoms. RGS values did not show any difference within this bathymetric range.

*Pagrus ehrenbergi* migrated into shallow waters during spawning and RGS values decreased with increasing depth (10 fathoms - 4.3, 30 fathoms - 2.6).

*Dentex canariensis* was distributed more or less evenly between 20 and 30 fathoms during reproduction, but RGS values were the highest at 25 fathoms.

From the above results it seems that *Pagellus coupei* and *Dentex canariensis* spawn in deeper waters while the spawning ground of *Pagrus ehrenbergi* is in shallower waters.

4. - LENGTH-WEIGHT RELATIONSHIP

The parameters of the equation $W = aL^n$ were calculated for each sex and for all the specimens together (including sexually undetermined) for all three species. The differences of the exponent values of length between sexes were tested by Student t distribution using the formula:

$$t = \frac{n_f - n_m}{S_{nfnm}}$$

Where $S_{nfnm}$ is the pooled standard deviation of the regression coefficients of the logarithmic values of $W$ and $L$ for both sexes.
Pagellus coupei:

The length-weight relationship for all specimens examined was expressed by the equation:

\[ W = 0.01336 L^{3.00} \]

Confidence limits for the exponent of \( L \) were \( 3.00 \pm 0.03 \). The adequate values for females were:

\[ W = 0.01314 L^{3.01} \text{ (conf. limits: } 3.01 \pm 0.06) \]

and for males:

\[ W = 0.01528 L^{2.96} \text{ (conf. limits: } 2.96 \pm 0.05) \]

Pagrus ehrenbergi:

All specimens:

\[ W = 0.02442 L^{2.85} \text{ (conf. limits: } 2.85 \pm 0.04) \]

Females:

\[ W = 0.02424 L^{2.85} \text{ (conf. limits: } 2.85 \pm 0.09) \]

Males:

\[ W = 0.02392 L^{2.86} \text{ (conf. limits: } 2.86 \pm 0.08) \]

Dentex canariensis:

All specimens:

\[ W = 0.01736 L^{2.91} \text{ (conf. limits: } 2.91 \pm 0.03) \]

Females:

\[ W = 0.01651 L^{2.93} \text{ (conf. limits: } 2.93 \pm 0.03) \]

Males:

\[ W = 0.01893 L^{2.88} \text{ (conf. limits: } 2.88 \pm 0.04) \]

Only Pagellus coupei showed the cubic relationship between weight and length. For the other two species, the exponent values of length were significantly different from 3.
Fig. 18: *Dentex caneriensis, Pagrus ehrenbergi*, length/weight relationships.

Fig. 19: *Pagellus couperi* monthly fluctuations of somosomatic index (RGS) and condition factor (CF) in 1970.
With all three species the sexes did not show significant differences in their length-weight relationship. It is therefore sufficient to present the resulting curves for all specimens combined (Figures 17, 18).

5.- CONDITION FACTOR

Condition factor (C) is classically expressed by the formula 
\[ C = \frac{W}{L^3} \]
multiplied by a convenient constant factor (usually 100 is used). This equation can be used only in cases where the power of L in length-weight relationship is not significantly different from 3. In this case the condition factor of fish is independent of the length and is affected only by ecological (abundance of food, inconvenient temperature) and physiological (spawning, disease) factors. If, on the other hand, the length-weight relationship is not cubic, the condition factor becomes also a function of L and does not only reflect the influence of the above factors.

In our case the classical formula could be used only for Pagellus coupeai for which the relation between weight and length was found to be cubic. For the other two species we had to use as a power of L the values obtained in the length-weight equation. The condition factor was calculated for each fish and the values obtained were averaged for each month and plotted together with monthly variations of gonosomatic index. Only the samples from Tema transect were used in this analysis.

Pagellus coupeai (Figure 19):

Monthly variations of condition factor showed the same pattern for both sexes. Maximum values of C were obtained in January-February, from September-November and in May - just before the main
spawning. Minimum values were found in June during the spawning and in July after the sharp drop in bottom temperature.

**Pagrus ehrenbergi** (Figure 20):

Condition factors were calculated only for females. The gono­somatic variations of males are not sufficiently distinct to be used for comparison. There was one small peak of average C found in January and two big ones in August and October, i.e. before and after the main spawning period. Another peak was also observed in May. The lowest value of C was found in July. There was a short decline in September during main spawning.

**Dentex canariensis** (Figure 21):

For this species also the condition factors were calculated only for females. Peak values of C were found in January, May and November. The biggest decline in the value of C occurred again in July.

6. GROWTH RATE AND ASYMPTOTIC LENGTH

Several methods were tried to determine the age groups and growth rate of the studied species.

At first age determination was tried by scale reading which proved unreliable. The number of rings on the scales did not reveal any correlation with the length of the fish. It seems that Longhurst's claim (1963) that most of demersal fishes in tropical waters showed no cyclical change in feeding intensity during the year, was correct.

Several trials were made by using Cassie's (1950) method of dissecting polymodal length-frequency curves into normal distributions by use of probability paper. This method, however, failed to give more than mean lengths of first two year classes.
Fig. 20 PAGRUS ENHRENBERGI ♀ MONTHLY FLUCTUATIONS OF GONOSOMATIC INDEX (R.G.S) AND CONDITION FACTOR (C.F) IN 1970.

Fig. 21 DENTEX CANARIENSIS ♀ MONTHLY FLUCTUATIONS OF GONOSOMATIC INDEX (R.G.S) AND CONDITION FACTOR (C.F) IN 1970.
Another method was tried therefore which proved to give rather good results on growth studies with Pacific tuna (Hennemuth - 1961) and tropical Scienidae (Longhurst - 1964) i.e. by analysis of monthly progressions of modal lengths. Modes were selected from the monthly length-frequency distributions for Pagrus ehrenbergi according to similar criteria to those established by Hennemuth (1961). With Pagollus coupeii and Dentex canariensis we selected modes from seasonal length-frequency distributions using the same method as Barro (1968). The growth of individual broods was traced by joining the modes along the most probable growth lines. A linear form of von Bertalanffy's growth equation was used and parameters were calculated by standard regression analysis. The time period between \( t+1 \) and \( t \) was one year for Pagrus ehrenbergi and 3 months for the other two species.

**Pagrus ehrenbergi:**

Both broods (from September and February spawning) were easily traced (Figure 22) and growth equation was as follows:

\[
\begin{align*}
l_{t+1} &= 0.61 \cdot l_t + 17.24 \\
K &= -\log_{e} 0.61 = 0.49 \\
L &= \frac{17.34}{1 - e^{-K}} = 44.76 \text{ cm}
\end{align*}
\]

Asymptotic weight was calculated, using the length-weight relationship of this species:

\[
W = 0.0244 \cdot L^{2.8496} = 1247 \text{ g}
\]

The biggest specimen caught measured 43.1 cm with weight 1196 g which is very close to our estimated asymptotic values.
Fig. 22 Growth of individual broods of Pagrus ehrenbergii from progression of modes identified in monthly length frequency distributions. See text for explanation.
To get the theoretical growth curve we would need parameter $t_0$ which we could not calculate from our data. Taking for $t_0 = 0$ we can use however our growth equation and result will be the theoretical modal lengths at each birthday. The theoretical weights were calculated in the same manner as the asymptotic weight. Theoretical growth curves for length and weight are given on figure 23.

From the above results can be concluded that Pagrus ehrenbergi lives in these waters 6-7 years. The exploited population is, however, composed mainly of age groups I+ and II+. Of all fish caught, 97.24% measured less than 34 cm which is the length the fish reaches at its 3rd birthday.

Pagellus coupe:]

The monthly length-frequency histograms on Tema transect were too erratic for tracing the progression of modal length. Therefore we used the data from seven trips on all the transects. It was mentioned before that Pagellus coupe: was found very often grouped by size (or age) on a particular station and length-frequency curves were mostly unimodal. All modal lengths from the samples with more than 50 specimens were plotted for each cruise, together with the major mode of all the samples combined, and joined in such a way that the curves represented the growth of individual broods (Figure 24). Both the broods of January and June were clearly detected. The modal length for the June brood in December 1969 was apparently too high to fit into the curve. We believe that this is probably due to the selectivity of the gear which retained only larger fish of the age group O. From both curves of June brood the modal lengths at three-monthly intervals were deduced. With the regression analysis the growth equation was obtained as follows:

$$l_{t+1/4} = 0.896 \, l_t + 3.19$$

and growth parameters were
\[ \frac{K}{4} = -\log e 0.896 = 0.11 \quad K = 0.44 \]

\[ L = \frac{3.19}{1-e^{-K/4}} = 30.76 \text{ cm} \]

From the equation of length-weight relationship we calculated

\[ W = 0.01336 L^{3.0043} = 395 \text{ g} \]

The biggest specimen caught measured 30.2 cm and weighed 357 g which correspond well with our estimate of asymptotic length and weight.

Taking as before \( t_0 = 0 \), and using the above length-weight relationship the theoretical growth curves of length and weight were obtained (Figure 23).

The life span of Pagellus coupeii is, similarly, to the previous species 6-7 years. The only important part of the population are those fish of I\(^+\) and II\(^+\) age groups. Of all fish caught during the period of our survey 97.21% were smaller than 23 cm which is the estimated modal length of age group at its third birthday.

**Dentex canariensis:**

The same method was used as with the previous species. Two broods were determined clearly, both presumably from the main spawning period (August), although it is very difficult to trace the curve accurately as far back as from 18 cm mode (Figure 25).

The growth equation from the regression analysis was:

\[ l_{t+1/4} = 0.945 l_t + 3.31 \quad \text{and} \]

\[ \frac{K}{4} = -\log e 0.345 = 0.06 \quad K = 0.24 \]

\[ L = \frac{3.31}{1-e^{-K/4}} = 59.96 \text{ cm} \]
Fig. 23 Pagellus couperi Pagrus ehrenbergii—Growth curves of length (solid line) and weight (broken line).
We could not be satisfied with these results. We can still tolerate that estimated asymptotic length is 10 cm lower that the biggest fish caught and that 0.5% of fish captured measured more than 60 cm. However the theoretical modal length at first birthday, obtained from our growth equation (12.8 cm) is in rather big discrepancy with the empirical length-frequency distribution. We have seen earlier (chapter 2) that 11 months old recruits had modal lengths of 14 and 15 cm. It is therefore believed that our estimation of growth parameters is not correct and the most probable reason is insufficient material and consequently the modal lengths of age groups did not truly represent the population.

7. FOOD AND FEEDING

Only full stomachs were examined for main taxonomic groups. The results expressed in percentage composition of food of all three species are given on Table VII.

Fish was the main diet in all three species. Dentex canariensis was especially piscivorous, its second important food item were Cephalopoda. Pagrus chrenbergi feeds very often on slow moving shelled benthic animals such as molluscs, crustaceans and ophiuroids. Pagellus coubei appears to take a wider range of available food organisms.

No study could have been made on the feeding habits of these species in relation to their size as the number of specimens was too small. In all samples only about 3% of stomachs were full, mainly due to the captured fish regurgitating the stomach contents during their ascent to the surface. This is an important handicap when the feeding intensity is investigated on the basis of the amount of fish with full stomachs in the sample. If it is assumed, however, that the rate of regurgitation is more or less constant then the highest feeding intensity for all three species occurred in both August trips, i.e. during the main upwelling time (Table VII). Moreover in Pagellus coubei there was higher percentage of specimens with full stomachs in December.
Fig. 24: - Growth of individual broods of Pagellus coupei from progression of modes identified in seasonal length frequency distributions. (figures indicate the number of samples with the same mode)

Fig. 25: - Growth of individual broods of Dentex canariensis from progression of modes identified in seasonal length frequency distributions. (figures indicate the number of samples with the same mode)
DISCUSSION

Several years ago LONGHURST (1963) described two main communities of demersal fish fauna in tropical West Africa: a Sciaenid community above the base of thermocline on soft deposits, and a Sparid community which inhabits hard bottoms above the base of thermocline (shallow Sparid sub-comm.) and all deposits below that level (deep Sparid sub-comm.). All trawling surveys carried out in different regions of West Africa confirmed that theory more or less. As for the species dealt with in this paper Pagrus ehrenbergi belongs to so-called shallow Sparid community while Pagellus couperi and Dentex canariensis are typical representatives of the deep Sparid community.

Pagellus couperi seems to be a rather important demersal species in almost every region of the tropical East Atlantic between 30 and 70 metres (GTS report-1968). Some authors report maximum catch rates of this species between 30 and 50m (CROSNIER and BERRIT, 1966; GTS, 1968; BOUILLON, TROADEC, BARRO, 1967-1969) while others in deeper waters i.e. between 50 and 70 m (SKORNYAKOV, 1963a; CROSNIER, 1964; DURAND, 1967; SALZEN, 1957). We believe that these differences are caused largely by the time at which the survey was carried out. Optimal temperature for this species seems to be below 20°C (LONGHURST, 1963; DURAND, 1967; BOUILLON et al., 1969) and as we have seen, the inshore-offshore migrations of this species depend on this temperature optimum. If the survey is carried out during the stable warm period with a distinct thermocline at 30-50 m, the fish will be found in deeper waters (SALZEN, SKORNYAKOV, CROSNIER), and vice versa (GTS - area 7 - Ghana). CROSNIER and BERRIT (1966) found this species, however, rather eurithermic and abundant between 19 and 25° on the shelf of Togo and Dahomey.

Our results agree with those of the above authors that Pagellus couperi inhabits all grounds regardless of the nature of the bottom, although it is more abundant on hard deposits (four times according to our data). This is also in agreement with the general definition of the deep Sparid sub-community as regards the nature of the bottom they inhabit.

Pagrus ehrenbergi has a wide distribution and was reported to be found in all regions in tropical West Africa (GTS, 1968). In some regions
it occurs very occasionally (Ivory Coast: TROADEC, BOUILLON, BARRO, 1967, 1969; Nigeria: LONGHURST, 1965; Cameroon: CROSNIER, 1964; Congo, DURAND, 1967) while in the others, especially in north-western part of the Gulf of Guinea, may sometimes represent 25-63% of total catch (LONGHURST, 1963; POSTEL, 1954). Most of the authors report this species as having shallower distribution than the other two species (LONGHURST, 1963; CROSNIER, 1964, CROSNIER & BERRIT, 1966). In Ghana waters the biggest catch rates were found at 25-30 fathoms (SALZEN, 1957; GTS, 1968) which corresponds well to our data. Only in Congo (DURAND, 1967) was this species not found at shallower depths than 50 m.

As the representative of the shallow Sparid sub-community, Pagrus e. is supposed to be found in warm waters on hard deposits. It seems, however, that this species inhabits equally abundantly the cold deep waters, preferring there hard grounds as well (CROSNIER and BERRIT, 1966). In our deeper muddy stations off Axim we did not find this species but only a few specimens on two occasions.

Dentex canariensis is reported to be distributed over a wide depth range in the tropical West Africa (GTS, 1968). It seems as if there is a geographical break in the distribution of this species off Nigeria (ibidem). Very poor density was also recorded in Ivory Coast (TROADEC, BOUILLON, BARRO, 1967), Cameroon (CROSNIER, 1964) and Congo (DURAND, 1967). During the Guinean Trawling Survey, bigger catch rates than 5.5% of the total catch were found only in Ghana and Dahomey. The highest catch rates found during the above survey were at 40-50m with the exception of Ghana where the best catches were recorded at 15-20 m depth which is quite exceptional. SKORNYAKOV (1963a) found this species in abundance between 40 and 60 m. In our 53 hauls accomplished at depths of 10 and 15 Fathoms (18 and 27 m) on only one occasion was the catch bigger than 10 kg (17.5 kg) while in 34 tows the catches were nil or only in traces (less than 0.25 kg).

According to LONGHURST's conception of the deep Sparid sub-community this species should be expected on all grounds below the thermocline. CROSNIER and BERRIT (1966) found this species on hard or sandy grounds in the
vicinity of the rocks. Our data showed practically a total lack of this species on soft deposits. Out of 21 tows carried out on the above mentioned stations off Axim, the total of 13 specimens were caught on only 3 occasions.

The data collected hitherto on size distribution of the species in question are rather inadequate for comparison purposes as the boats, gears and the measurement technique (including total length-LT, standard length-LS and fork length-LF) were not standardized and differ by author and region. Nevertheless, some conclusions could be drawn from our data and those of different authors in tropical West Africa.

Pagellus coupei is the smallest of the three species with rather small overall size range. LONGHURST (1965) found bigger specimens in Togo than in Nigeria (size range 15-30 cm against 14-23 cm). CROSNIER and BERRIT (1966) recorded in Togo and Dahomey size range 9-25 cm (LF), SKORNYAKOV (1963a) in Ghana 10-23 (LS) and CROSNIER (1964) in Cameroon 9-25 (LT). All these data including ours show that the biggest specimens found were not bigger than 30 cm total length. Only GTS reports the size range of this fish as 6-42 cm and Ghana the only region where the fish was bigger than 34 cm; unfortunately no records on depth were represented. It might be presumed that these large specimens were caught in deep waters as we found in two years of survey only three specimens larger than 28 cm LT between 10 and 40 fathoms depth. The mean value of LT was around 16 cm (CROSNIER, 1964) and a little less for LF and LS (CROSNIER, 1966, SKORNYAKOV, 1963b).

Overall size range of Pagrus ehrenbergi was reported in GTS as 6-74 cm. MATTA (1965) found it in Mauritania as 29-66 cm LT, LONGHURST (1965) recorded again with this species smaller fish in Nigeria (5-38 cm) than in Togo (12-48 cm). For the latter region CROSNIER and BERRIT (1966) report the size range of this species as 9-42 cm (LS), and CROSNIER (1964) in Cameroon as 16-43 cm LT. Our data correspond quite well with those of the other authors, only during GTS II they found bigger specimens in Ghana waters than we did.
There was a wide range of mean sizes recorded in GTS (from 11.1 to 42.5 cm). The results of mean length reported by the other authors also differ considerably: SKORNYAKOV (1963b) in Ghana - 28.1 cm (LS), CROSNIER and BERRIT (1966) in Togo and Dahomey - 23 cm (LF) and CROSNIER (1964) in Cameroon - 29 cm (LT). Considering the unequal size distribution within the populations, i.e. the fish grouped by size and/or the different size distribution by depth (see later), such differences in observed mean lengths are not surprising. In our case we found the difference of 6.8 cm between the mean lengths in two consecutive years of survey, the decline of mean size being caused by the strong newly recruited generation in the first year of the survey. This case shows that detecting overfishing by the data on length distribution and on mean size becomes very questionable in a region where the fish population is mainly composed of two young year classes and the older and bigger specimens are always scarce. The recruitment can therefore influence much more the mean size of the population than the excessive exploitation.

The widest size range of all three species was found with Dentex canariensis (GTS-1968) i.e. 11-96 cm (12-69 cm in Ghana which corresponds well with our data). A much smaller range was reported from Togo and Dahomey (CROSNIER and BERRIT, 1966) i.e. 19-47 cm (LF) and from Ghana (SKORNYAKOV, 1963b) - 32-61 cm (LS). It is also evident that mean sizes from different regions differ considerably (GTS - 14.3 to 46.9 cm).

There are only few data available about the size distribution by depth. Although it was found that all three species shoal by size groups there was no indication of size distribution by depth (GTS-1968). SKORNYAKOV (1963a) found in Ghana small specimens of Pagelluscoupeii (7-8 cm LS) in shallow waters, while CROSNIER and BERRIT (1966), on the contrary, recorded the young specimens farther from the coast and assumed that the spawning of this species probably takes place in deeper waters. Our results showed, however, that the newly recruited generation of all three species first occurred in shallow waters (10 and 15 fathoms) during both years of the survey.
During this season size distribution by depth was very distinct for all three species, i.e. mean size increased with depth. In the other periods of the year Pagrus ehrenbergi always kept the same size distribution by depth and Dentex canariensis in all but one occasion, while the highest mean lengths of Pagellus courei were recorded at the intermediate depths of 20 and 25 fathoms. Bearing in mind the optimum temperatures of these species such a size distribution by depth as was found than the young ones. The reason for size distribution of Pagellus c. could also be due to its particular sex distribution by depth, bigger males prevailing over females at depths where the highest values of mean size were obtained.

There are only few available data from tropical Eastern Atlantic, concerning the reproductive cycle of the species in question. SKORNYAKOV (1963a) supposed that Pagellus c. spawns from December to March and that larvae must be eurythermic and euryhaline as sexually mature specimens off Dakar and off Takoradi (Ghana) were found in waters with temperature from 18-30°C and salinity from 32.0% to 35.5%. During GTS they found mature Pagellus c. in November in Cameroon and in May in Gabon and Congo. MATTA (1965) put very strict limits of spawning period for Pagrus e. off Mauritania, i.e. 15th May to 15th June. LONGHURST (1963) assumed that in Guinea waters (south of Isles de Los) spawning of this species occurred in September or from September onwards. GTS found running ripe individuals off Nigeria in October and mature females in Bissagos area in May. As for Dentex c. there are data from Gabon and Congo (GTS-1968) where the fish was found mature in May.

There may be several reasons for these seemingly erratic results of spawning period. It is possible that there exist different populations of studied species with different reproductive cycle. The seasonal hydrographic conditions can surely affect the outburst of spawning in different periods in a particular region. However, the main reason for these discrepancies is, in our opinion, the particular sexual pattern of fish in tropical waters where the distinction between rest-period and spawning is not
clear and spawning time is very difficult to detect if sampling is not continuous over a longer period. During 18 months of our observations only Dentex canariensis showed a more or less distinct rest-period against a period of reproductive activity. The other two species showed a moderate sexual activity throughout the year especially evident in females. In only four months was there more than 50% of females of Pagellus c. in maturity stage VII – II and none in stage IV. In all the other months we found from 11.1 to 40.6% of females with gonads in advanced maturity (stage IV). With Pagrus c. this was even more explicit. In all but one month there was less than 40% of females in the rest-period and all the time we were catching females with gonads in stage IV (3.3 - 30.3%) and VII (1.2 - 57.6%). The only way to detect the spawning time was therefore by following the fluctuations of gonosomatic index. The specimens with running ripe gonads were very scarce and we agree with Matta's statement (1965), that the actual release of sexual products has to be accomplished in very short time.

It appears quite evident that spawning alone does not affect the condition factor value. It is remarkable that the fluctuations of C showed a very similar pattern in all three species. The fish were in the "best condition" in January (despite small spawning), May and after the upwelling season i.e. in October and November. The peak production of zooplankton in August (MENSAH, 1969) probably causes a later peak production of zoobenthos upon which these fish feed and which is reflected in the maximum values of C in October and November. A similar explanation could be applied to the peak in May as there is a minor peak of plankton production during the smaller upwelling at the beginning of the year. Apart from the decline of the condition factor during the main spawning, which is a normal feature, the lowest C in all three species occurred in July, when the temperature on the bottom dropped sharply by more than 5 degrees. The reason for this striking loss of weight in connection with this unusually cold water (the average temperature for all stations was below 18°C) might be either a direct influence of low temperature on metabolic processes or an indirect one through an adverse effect on the zoobenthos production. However, knowing that optimum tempora-
tures for all three species are below 20°C this second possibility seems more plausible. A similar double effect can also be produced by the sudden drop in oxygen which accompanies the upwelling but the study of this effect is beyond the scope of the present paper.

Very little research has been done in tropical West Africa, concerning the age distribution and growth rate of the species studied. Age determination by using the number of rings on the scales proved to be rather difficult if not impossible (LONGHURST, 1963), SKORNYAKOV (1963a) was the only author who claimed that age determination of Pagellus coupei by scales reading was easy. However, this results, based on such determination, are not convincing. Mean lengths of age groups seem to be much too low and when the length increments between consecutive age groups are plotted against their average lengths, the obtained asymptotic length is only 18.5 cm.

Regression analysis, of modal increment, although the selection of modes and their joining in apparent growth curves is unavoidably subjective, seemed to give at least for Pagellus coupei and Pagrus ehrenbergi rather satisfactory results. It is interesting to note that LONGHURST (1963), using a similar technique, estimated for Pagrus ehrenbergi off Sierra Leone lengths at first and second birthday in close agreement with our results.

From the length-frequency distributions recorded by different authors for several regions of the tropical Eastern Atlantic, as well as from our results, we may conclude that only two age groups represent more than 80% of the total exploitable population of these three species. Consequently, overfishing can very quickly deplete the stocks. On the other side, with such a particular population structure, with the first maturity in the second year of life and sexual activity over a longer period it is expected that the recovery of the stock will be more rapid than in temperate sea fisheries. The overfishing would therefore be mainly of economical and much less of biological consequences.

Although the percentage of full stomachs in the samples of all three species was always small, we never found samples in which all the
specimens would have empty stomachs. This means that the fish feed the whole
year around. To the same conclusion came SKORNYAKOV (1963a) for Pagellus c.,
while MATTH (1965) found out that Pagrus e. did not feed during spawning,
but he meant only the actual time of releasing the sexual products.

We emphasized above that the method we used for estimating the feeding intensity on the basis of the amount of full stomachs in the samples is rather questionable when the fish regurgitate the stomach content during their ascent to the surface. However, our finding of maximum feeding intensity in August agreed well with the observations of fat content and fluctuations of condition factor. In October the visceral cavity of Pagellus c. and Dentex c. was full of fat. Lack of such fat with Pagrus e. was expected in this period considering that this species just accomplished spawning. It was mentioned before that in the months after the main upwelling season, the condition factors reached their peak values in all three species.

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