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The Azorean squid *Loligo forbesi* (Cephalopoda: Loliginidae) in captivity: feeding and growth

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Abstract

Two sets of feeding growth experiments were carried out (EXP94 and EXP95). Squid were fed mainly with *Trachurus picturatus, Scomber japonicus* and *Pagellus bogaraveo.* During the first trial feeding and growth was assessed for all the squid as a group. Daily feeding rate (DFR) was low (0.39%) and almost all the squid showed negative daily growth rates (average DGR = -0.5%). Squid maintained during EXP95 were significantly smaller than those kept in EXP94. The majority of them fed on a regular basis. The average DFR was 4.09% and the average DGR was 0.06%. However, when considering only squid that showed a considerable growth (DGR>0.5%) the average DGR increase to 0.99%. Maximum DGR (1.42) was achieved by a squid with initial body weight of 270.5g. Daily feeding rate for maintenance was very high (3.78% DFRM), when compared with other cephalopods in captivity. The average food conversion rate (FCR) was 10.6% and the conversion of efficiency (CE) was 32.7%.
Feeding behaviour is described. High percentage of fish heads rejection was observed. The number of the ingested otoliths, eye lens and fins were recorded. Concerning head rejection a relationship between fish (prey) and squid (predator) size seems to exist.

Introduction

The Azorean population of *Loligo forbesi* contain the larger loliginid squid known even when compared with the conspecific populations of the European shelf (see Boyle & Pierce, 1994). Male squid can reach a dorsal mantle length (DML) close to one metre and more than 8 kg of body weight (Martins, 1982; Martins & Porteiro, 1988; Porteiro & Martins, 1994). A preliminary study of ageing has been done by Martins (1982) who found and a maximum of 450 statolith rings for a male with 75 cm DML. This value roughly fits an average growth rate of 5 g/day. Recent work using statoliths showed to similar results (Estácio, *et. al.*, 1995).
Culture experiments have been used for growth estimation of some squids, both ommastrephids (O'Dor *et al.*, 1980; Sakurai *et al.*, 1993) and loliginids (Hurley *et al.*, 1976; Hanlon *et al.*, 1983; Turk *et al.*, 1986; Yang *et al.* 1986). Some of these authors contemplated the entire life cycle of the target species while others aimed at a particular phase of development. Based on culture of the younger stages, it is accepted that exponential growth is a characteristic of the first stages of cephalopod's life cycle followed by a power or logarithmic growth (Forsythe & Van Heukelem, 1987). Previous studies on growth of captive *L. forbesi* were carried out by Forsythe *et al.*, 1989 (see also Hanlon *et al.*, 1989 and Forsythe, 1993). However, squid size attained during that experiment was very small, compared with the wild population.

Cephalopods are active opportunistic carnivorous. Their diet change during ontogeny (Boucher-Rodoni *et al.*, 1987) and adult loliginids prefer fish as food. Several studies on the diet of *L. forbesi* have been published (Martins, 1982; Ngoile, 1987; Collins *et al.*, 1994; Pierce *et al.*, 1994; Rocha *et al.*, 1994) and all of them were based on stomach contents analysis. Feeding behaviour of adult *L. forbesi* was reported by Porteiro *et al.* (1990).
A high food conversion rate and efficiency is a characteristic of cephalopods. Their energetic demands are analysed comprehensively by O'Dor & Wells (1987). Recently, laboratory calibration of the energetic expenses (metabolic rates) of adult *L. forbesi* has been done aiming at the interpretation of the squid eco-behaviour in the field (O'Dor et al. 1994). A tracking research programme was performed using acoustic telemetry techniques. Life style and energetic expenses for such activity were described.
Presently, a closed sea-water system for squid culture was built up at the University of the Azores (see Gonçalves et al., 1995). It gave the opportunity to carry out this study on feeding and growth of captive squid.

Material and Methods

Two sets of experiments were performed. Experiment 1 (EXP94) started on 23.10.94 and finished on 27.12.94 and the second trial (EXP95) was executed between 09.02.95 and 18.04.95. All the squid were caught by jigging and transported ashore into black plastic bags with a flow-through water. Squid were numbered, weighed (nearest 0.1g up to 1500g and to 1g for heavier squid), measured (nearest 1 mm) and sexed. The close sea water system used for the experiments is composed by 3 circular tanks (T1, T2 an T3) each 3.6 m diameter and 0.90 m high (see Gonçalves et al., 1995 for details of transport, handling and design of the close sea water system).
Thirty-three adult squid were submitted to observation during EXP94 and 23 during EXP95. However, accurate data of squid weight on EXP94 were obtained only after 21.11.94 where 19 squid were studied. Therefore, growth was estimated only after that day (EXP94a). The squid of EXP94a had an average initial body weight of 1489.7g (587.4 g- 3880g BW) which was about three times more than squid maintained during EXP95 (529.0g, ranging from 95.0 to 2854g). During EXP95 squid were marked with a heated rod for individual identification. The number of animals inside each tank was variable (1 to 7) and different combinations of sexes were maintained. In EXP94a an average of 5.7 squid was maintained simultaneously in captivity (2 to 13 squid) and the average survival was 9.6 days (4 to 26 days). During EXP95 we kept an average of 6.7 squid (1 to 10) squid and the average survival was 21.4 days (3 to 47).
Feeding data were recorded differently during the two assays.
EXP94 - *group squid study*. Fish were provided every day. Freshly dead *Trachurus picturatus* were the main food item used. However, few juveniles of *Pagellus bogaraveo*, *Trachynotus ovatus*, *Scomber japonicus* and slices of *Lepidopus caudatus* and *T. picturatus* were also provided. The amount of fish furnished to each tank were weighed (nearest to 0.1g) and the food not eaten by the squid removed, weighed and deep-frozen. In general, feeding took place at 1800 hr.
EXP95 - *Individual squid study*. Predominantly frozen fish were used. Squid were fed 2 times a day, at 0900H and 1800H, with *Trachurus picturatus*, *Pagellus bogaraveo* or *Scomber japonicus*. Fish were weighed and measured individually before being introduced into the tanks. They were supplied one by one to allow the identification of the squid that ate them. Afterwards, the parts of fish rejected by each squid were removed from the tank, weighed, labelled and deep frozen.

In both experiments the rejected portions were recorded as number of entire fish, heads and fins (pectoral, pelvic and caudal). A sub-sample of the rejections was analysed. Heads were dissected and the number of otoliths and eyes recorded.
After death squid were measured, weighed and deep frozen for posterior biological sampling.
Daily growth rate (DGR), daily feeding rate (DFR), daily feeding rate for maintenance (DFRM), food conversion rate (FCR) and conversion efficiency (CE) were calculated according to O'Dor *et al.*, 1980.
Temperature was recorded daily and several water nutrients (N-NH4, N-NO2, N-NO3, % DO) were performed on a regular basis. Average temperature during EXP94, EXP94a and EXP95 was 15.2 ± 1.7 (sd) °C, 13.2 ± 0.8 (sd) °C and 18.3 ± 0.8 (sd) °C, respectively (see Gonçalves *et al.*,1995 for more information).

Results

Squid ate all the fish species furnished, even when supplied in slices. The average weight of the fish was 33.3g (7.7 - 69.0g) during EXP94 and 52.8g (18.6 - 275.0g) in EXP95.
Data concerning the features of the food supplied during both experiments is presented in Fig1.

Feeding and Growth

EXP94. Only 48.3% of the food added were ingested. The average meal size taken by one squid was 27.5 g/squid/day (g/s/d). However, squid often do not feed on a daily basis (starvation during several days was observed mainly by large squid) and consequently the average quantity of fish ingested by squid by day was considerably less than one average meal (i.e., 14.1 g/s/d). It seems that meal size depends upon the weight of the fish supplied. The data suggest that food intake oscillated within a period of one to several days (after a meal, starvation occurs on the subsequent days and vice-versa). No relationship was detected between the meal size and the starvation period. A slight increase of food intake was detected with higher temperatures (range from 12°C to 18.5 °C).
EXP94a. During this sub-experiment the squid ate notably less than the previous weeks. The average amount of food ingested by one squid was 4.9 g/s/d and the meal size decreased to 9.6 g/s/d. The daily feeding rate (DFR) for the group was 0.39 % and the daily growth rate (DGR) was negative (-0.5%).

EXP95. During this experiment squid showed a more regular feeding behaviour than during the previous trials. Despite the smaller size (compared with EXP94) they ingested an average of 18.6 g/s/d of food (average meal size of 28.6 g/s/d). The amount of fish ingested and the DFR were independent of the quantity of food furnished. The average DFR was 4.09% (0.00 - 7.46%) and the maximum value was 18.9%. High DFR was normally achieved when squid fed twice a day. Squid that grew satisfactory (DGR> 0.5%; see Table 1) took two meals during 28% of the days in captivity and starved for 22% of the days. The DFRs of some squid are shown in Fig 2. The average DGR was low (0.06%) but considering only those with a DGR>0.5%, that value increase to 0.99%. The maximum DGR attained was 1.42% and the highest food conversion rate was 21.20% (Table 1). The relationship between DGR and DFR was calculated (Fig. 3). This estimation did not involve the squid B2 and B3 (see Table 1) since they spawned previously in the tanks which influenced their final body weight. From the regression, the daily feeding rate for maintenance (DFRM) is 3.78%. The average food conversion rate (FCR) was 10.6% (14.5% for squid with DGR>0.5%). The net conversion efficiency (CE) was calculated for some individuals (Table 1). The average CE was 32%. Influence of temperature oscillation on DFR was not detected.

Table 1. Results of the feeding growth experiment EXP95 for captive squid *L. forbesi*. Squid A was kept in tank A (TA), squid B in TB and squid C in TC. Shaded columns indicate squid with positive growth. * refer to squid with a daily growth rate higher than 0.5% (DGR>0.5%).

Squid ref.	A2	A3	A4	A5*	A6*	A7*	A8*	B1	B2	B3	B4*	B5*	B6*	C1	C2	C4	C5	C7
Survival	7	13	6	39	9	9	9	21	20	8	28	28	28	22	8	17	7	28
Initial body weight	95.0	135.0	129.4	162.1	354.4	385.2	354.8	1582.6	885.0	607.9	393.0	381.2	270.5	853.5	810.6	555.2	932.5	805.4
Final body weight	86.6	140.7	113.6	204.4	388.5	431.8	374.0	1593.2	729.2	551.5	473.5	558.9	405.0	874.3	728.4	505.8	858.8	820.4
Increment	-8.4	5.7	-15.8	42.3	34.1	46.6	19.2	10.6	-155.8	-56.4	80.5	177.7	134.5	20.8	-82.2	-49.4	-73.7	15.0
Daily increment (g/day)	-1.2	0.4	-2.6	1.1	3.8	5.2	2.1	0.5	-7.8	-7.1	2.9	6.3	4.8	0.9	-10.3	-2.9	-10.5	0.5
Daily growth rate weight	-1.3	0.3	-2.2	0.6	1.0	1.3	0.6	0.0	-1.0	-1.2	0.7	1.4	1.4	0.1	-1.3	-0.5	-1.2	0.1
Total ration (g)	7.1	75.2	12.1	507.4	223.1	270.8	197.0	540.2	504.5	213.3	849.8	838.4	676.5	486.9	135.2	92.5	0.0	854.3
Mean daily ration (g)	1.0	5.8	2.0	13.0	24.8	30.1	21.9	25.7	25.2	26.7	30.4	29.9	24.2	22.1	16.9	5.4	0.0	30.5
Mean daily feeding rate	1.1	4.2	1.7	7.1	6.7	7.5	6.0	1.6	3.1	4.6	7.0	6.4	7.2	2.6	2.2	1.0	0.0	3.8
Food conversion rate		7.6		8.3	15.3	17.2	9.7	2.0			9.5	21.2	19.9	4.3				1.8
Conversion efficiency (net)				17.8	35.3	34.5	26.3				20.6	52.2	42.2					
No. of meals	1	6	1	32	7	9	6	6	10	9	33	35	28	10	4	4	0	29
No. of starving days	6	7	5	8	3	3	5	15	12	2	5	3	6	14	4	13	7	4
No. of days with two meals	0	0	0	10	1	3	2	0	2	2	10	10	6	2	0	0	0	5
Mean ration				16.4	31.9	30.1	32.8	90.0	50.5	23.7	25.8	24.0	24.2	48.7	33.8	23.1	0.0	29.5

Feeding behaviour

In this study squid ate the majority of the guts of the fish even from those where only a small fraction of the entire fish was consumed (e.g. *P. bogaraveo* from EXP95). Squid refused the majority of the heads of the fish (Table 2).

Table 1. Percentage of the body structures rejected by captive *L. forbesi* for the species eaten during EXP94 and EXP95 (sub-sample). n - number of fish sampled; fw - average fish weight in grams;

	EXP94						EXP95					
Species	n	fw (g)	% head	% caudal	% * pectoral	% * pelvic	n	fw	% head	% caudal	% pectoral	% pelvic
T. picturatus	295	35.4	79	37	16	12	26	38.4	96	96	93	96
P. bogaraveo	53	17.2	7.5	2	0	0	21	151.0	100	73	81	77
S. scombrus	4	35.4	75	50	75	75	8	69.5	100	75	44	33
S. pilchardus	0						5	78.1	100	100	0	100

* - based on a sub-sample of 168 *T. picturatus*

This behaviour was quite consistent except when small *P. bogaraveo* were furnished during EXP94 (see Fig 1). The average weight of the heads collected was around 20% of the average fish weight. Larger squid rejected fewer heads than smaller squid.The position of the "neck bite" is always the same. However, the squid can eat almost the whole head (rejecting only the jaws) showing a gradual behaviour to throwing away the head intact with the jugular area and paired fins. Some of the complete heads had several clean vertebrae attached. The heads in this condition were normally from large fish. Also, often, the squid ate exclusively the viscera and the muscle of the dorsal area of a large fish (e.g. *P. bogaraveo* during EXP95).

Table 3. Percentage of eye lens and otoliths (*sagittae*) in the heads rejected by *L. forbesi*, during EXP94 and EXP95 (Species with less than 5 heads rejected are not included).

	EXP94						EXP95							
	T. picturatus		*P.bogaraveo*		*S. scombrus*		*T. picturatus*		*P.bogaraveo*		*S. scombrus*		*S. pilchardus*	
otoliths lens	% lens	% otol.	% lens	% otol.	% lens	% otol.	% lens	% otol.	% lens	% otol.	% lens	% otol.	% lens	% otol.
0	28	39	-	-	-	-	0	0	9.5	0	0	14	-	-
1	19	19	-	-	-	-	11.5	4	9.5	0	0	0	-	-
2	53	42	-	-	-	-	88.5	96	81	100	100	86	-	-

The majority of the paired fins were consumed. These fins when rejected were normally attached to the head. However, some isolated pectoral fins were refused. When squid from the EXP95 were fed with *P. bogaraveo* they often rejected the spiny part of the dorsal fin. The caudal fin rejections were most commonly observed. Normally, only the caudal fin was refused but a variable part of flesh associated with that fin may also be discarded. Few of these parts had clean vertebrae.The percentage of the heads that contains 0, 1 or 2 otoliths and eyes was calculated (Table 3).

Discussion

Squid maintained during the first experiment EXP94 fed proportionally less (small DFR) than squid kept during EXP95. Also, the frequency of meals was smaller for EXP94 squid. That behaviour probably is related mainly to squid size since squid of EXP94 was roughly 3 times heavier than those of EXP95. Differences of squid feeding rates (and consequently metabolic rates) during their ontogeny are referred by O'Dor & Wells (1987) as a natural feature of the majority of cephalopods; that is, "No ecosystem could sustain large squid that fed at the rates of small ones". Moreover, male-male agonistic interactions were most common during EXP94 due to squid size and courtship (see Porteiro *et al.* 1995) and the stress produced by such behaviour affect greatly feeding (Hanlon, 1990). However the temperature during EXP94 was remarkably lower that in EXP95, which can influenced the feeding activity. Temperature seemed to affect the feeding in EXP94 but no correlation between them could be detected in EXP95 (probably due to small temperature variation, 3°C). Other factors such as intraspecific interactions, prey size, stress caused by transport and handling, lesion provoked by collision on the tank wall, are also important in regard to feeding, growth and survival.
The average daily feeding rate (4.09%) obtained during EXP95 is probably lower than of wild squid, with the same size. This value at a mean temperature of 18.3°C correspond to a daily growth rate (DGR) of 0.1%. However, if we only considering squid that showed positive growth (see Table 1) the DFR increase to 5.8% and the DGR to 0.7%. For squid with an average body weight of 438.3 g the latter rate allow an increment of 3.07g a day. Squid in such conditions, would attained 1kg (average body weight of mature female squid, Porteiro & Martins, 1994) in 183 days (note that the majority of squid were female). Following the same thinking, squid that showed the maximum DGR would achieve the same weight only in 91 days. This rough approach seems to be quite reasonable since squid were caught at February-March and by July the fishery decrease as a consequence of low abundance of mature squid (Porteiro, 1994).

The results obtained put in evidence some differences between *L. forbesi* and the ommastrephids *Tadarodes pacificus* and *Illex illecebrosus*, whithin similar range of weight (Sakurai *et al.*, 1993; O'Dor et al., 1980, respectively). Lower values of DFR and DGR were achieved by the specimens of *T. pacificus* (2.60% to 3.72% and 0.42% to 0.81%, respectively) when compared with the values attained by some individuals of *L. forbesi*. However, the food conversion rate (FCR) achieved by squid of both species is similar (14.53% to 24.2% for *T. pacificus*). Despite the fact that individuals of *L. forbesi* showed a DFR as high as *Illex illecebrosus*, the DGR (as the FCR) of that ommastrephid was significantly higher. The conversition efficiency of *L. forbesi* (with a positive DGR and a DFR >DFRM) was smaller than those calculated for the two ommatrephids (39% for *T. pacificus* and 40% for *I. illecebrosus*), but it also shown a high variation. The daily feeding rate for maintanence (DFRM) calculated for *L. forbesi* (3.78%, see Fig. 2) is very high when compared with the DFRM of *T. pacificus* (1.67%) and that of *I. illecebrosus* (1.1%). However, the experiments done by Sakurai *et al.* (1993) and O'Dor *et al.*, (1980) were carried out at 15.6°C which can compromise these comparisons. However, these results should be regarded with some reserve since some squid starved (and consequently lost weight) during few days prior to dying (e.g. squid A8 in Fig. 3)

The speed-respiration of *L. forbesi* has been assessed in laboratory using a combination of video records, telemetered mantle pressure and repirometer by O'Dor *et al.* (1994). This information was used for inferences about the costs of different behaviours telemetered in the field as well as to suggest a life style for this squid in nature. In this study an average food equivalent of 1.9% BW d^{-1} of metabolic rate maintenance (DFRM) was calculated from 4 squid. Also a food equivalent of 0.21%, 1.45% and 0.47% was computed for resting, climbing and hovering, respectively. Unfortunately, the costs of fin swimming was not assessed. All the previous estimations presented low values compared with the results obtained in captivity. Swimming is required to avoid sinking (squid have negative bouyance) and although jetting was observed, fin propulsion accounted for more ca. 99% of the squid motion in the tanks. The high DFRM calculated is related with high metabolic rate. The energetic demands of the squid should be associated with high stress levels or with the costs of permanent use of fins. The latter explanation seems unlikely since low costs of fin swimming should be expected. The first assumption is sustained by a weak squid survival (average survival was 21.4 days during EXP95).

Several times fatty faeces were observed floating on the surface reflecting the high lipid contents of the food furnished and the inability of those animals of lipid absorption and metabolization (see O'Dor & Wells, 1987).

T. picturatus, were chosen for diet because that species are important items of *L. forbesi* in the Azores waters as recorded by Martins, (1982) and Pierce *et al.*, (1994). Also, wild squid can eat *S. japonicus* and *P. bogaraveo*. When fishing for demersal fish with a bottom long-line, in coastal water, those species came to the surface bitten and eaten by squid (observation by FMP).

Some aspects of feeding behaviour of captive adult *L. forbesi* has been previously described by Porteiro et al. (1990). The rejection of hard structures such as head, vertebrae and caudal fin, has been observed in several species (e.g., Hanlon et al., 1983, for loliginids; by O'Dor et al., 1980; for *Illex illecebrosus*). However the bulk of the studies of feeding ecology of squid are based on the analyses of hard structures found in stomach contents as otoliths, eye lenses, bones, and rarely teeth (see for example Martins, 1982, Collins *et al.*, 1994, Pierce *et al.*, 1994, and Rocha *et al.*, 1994 for *L. forbesi*).

Martins (1982) concluded that *Loligo forbesi* do not reject the head since otoliths and eye lenses of fish were found frequently in the stomach contents. Although, the ingestion of an entire fish occur, it depends of the relationship between squid size and prey size. Also, the variation of the feeding behaviour probably depends on the prey species and the squid appetite. Subevaluation of some food items at the cost of others can occur if no information of feeding behaviour exists. It is not yet known if preferences of prey size exist in *L. forbesi*, but, as other loliginids, they probably feed on a wide size range of fish. Squid in the wild might have a similar behaviour, since feeding behaviour is stereotyped. If they seize the same sort of prey, the probability of finding statoliths of *T. picturatus* would be 61% and 2%, respectively, for squid within the same range size of those maintained in EXP94 and EXP95. The use of otoliths and other hard structures used to studyto infer about the feeding ecology of aquatic animals has been critically reviwed by Jobling & Breiby (1986).

The ideal methodology when feeding ecology is concerned will be the combination of serological methods, stomach contents analysis (as done by Kear, 1992) and studies on feeding behaviour.

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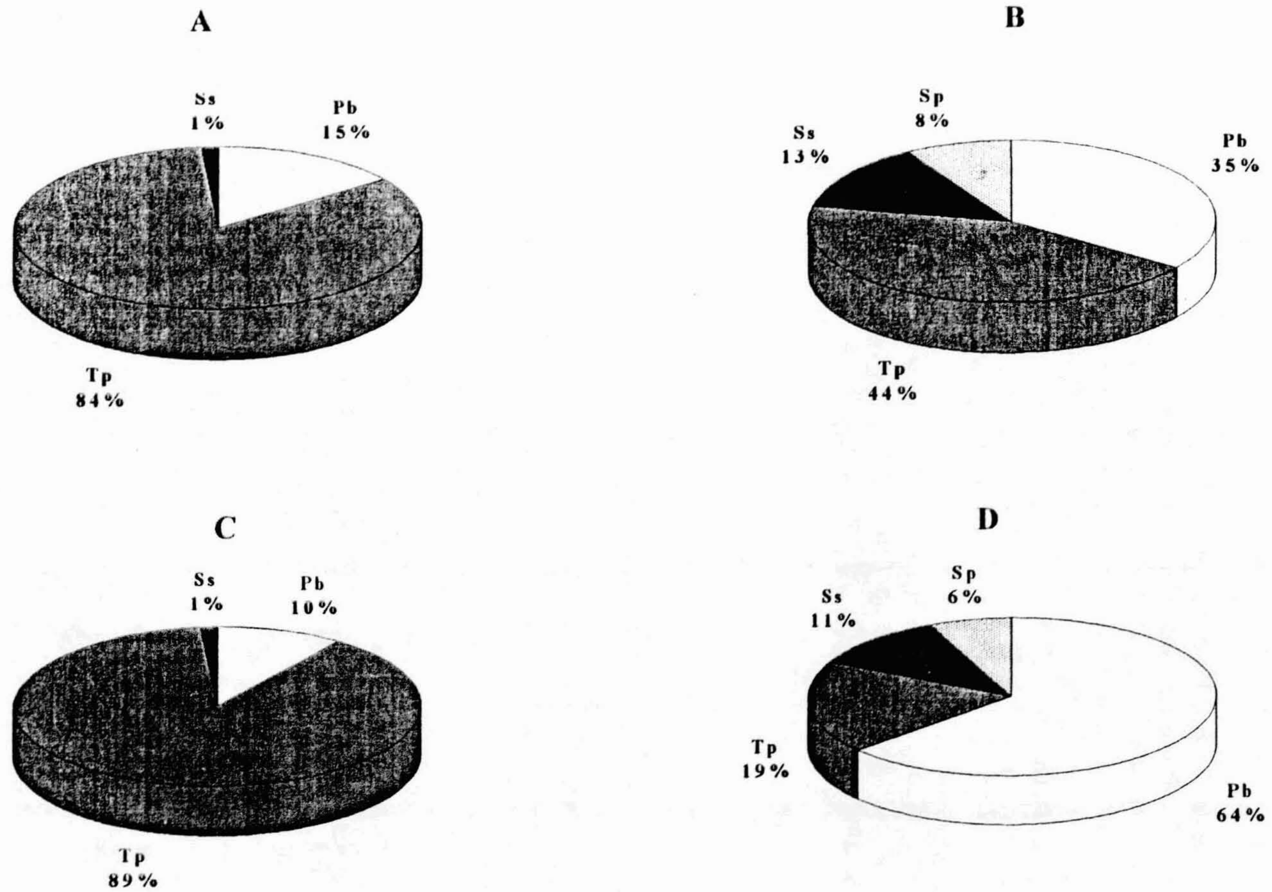

Fig.1 - Relative composition of the food items furnished during the two sets of experiments: A in numbers for EXP94; B in numbers for EXP95; C in Weight for EXP); D in weight for EXP95. Pb - *Pagellus bogaraveo*; Tp - *Trachurus picturatus*; Ss - *Scomber japonicus*; Sp - *Sardina pilchardus*

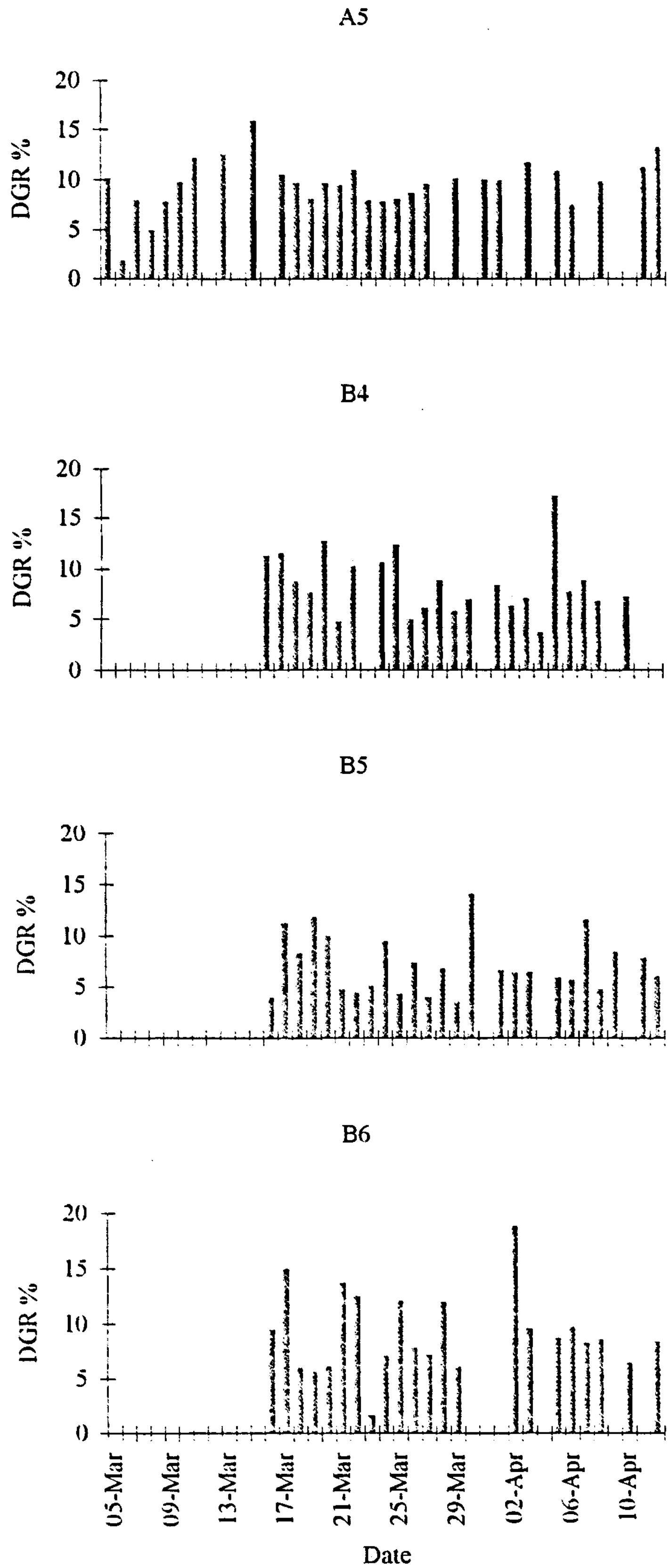

Fig. 2 - Daily feeding rate (DFR) for some squid that grew with an average daily growth rate higher than 0.5% (DGR > 0.5%). See text and Table 1for more information.

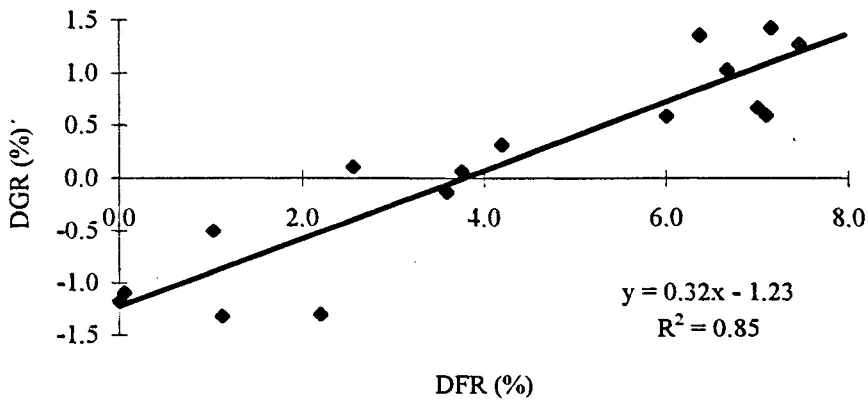

Fig. 3 - Linear regression between daily feeding rate (DFR) and daily growth rate (DGR) of squid group EXP94a and individual squid from EXP95.