International Commission for   the Northwest Atlantic Fisheries

SPECIAL MEETING OF STACRES - FEBRUARY 1979

Feeding and Growth Rates in Capitive Squid (*Illex illecebrosus*) and the Influence of Food Availability on Growth in the Natural Population

by

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INTRODUCTION

Direct studies on feeding and growth rates and conversion efficiency in large pelagic squid of commercial interest have not been possible until now because of the difficulties of maintenance in captivity; however, there is some information on juvenile Loligo opalescens (Hurley, 1976) and considerable data on small decapods (Choe, 1966; LaRoe, 1971; Boletzky, 1974) and octopods (Nixon, 1966; Wells and Wells, 1970, Mangold and Boletzky, 1973; Joll, 1977). In general, it appears that at a single temperature with unlimited food the weight increase in cephalopods is proportional to their weight (i.e., $^{dw}/dt = \propto W$, Wells and Wells, 1970) with weights doubling in as little as 10 to 20 days (LaRoe, 1971; Wells and Wells, 1970). This pattern seems to hold until sexual maturation which usually leads to decreased feeding, a negative growth rate, and death after a short period of reproductive activity (van Heukelem, 1973; Wells, 1978). Higher temperatures usually result in increased feeding and growth, though there are exceptions (Boletzky, 1974).

Growth patterns of commercial squid based on population sampling generally show much less dramatic growth (eg. Summers, 1971; Ishii, 1977) and the pattern for Illex illecebrosus is typical. Squire's (1967) data for I. illecebrosus fit well on a von Bertalanffy-type curve in which growth rates decline well before the squid reach sexual maturity. The experiments described here are a first attempt at studying growth and feeding rates in a captive school of I. illecebrosus under conditions allowing comparison to other studied

cephalopods. The results are also compared to available data on the natural
population of the species.

MATERIALS AND METHODS

On July 18, 1978, 300 squid from a net trap were brought into the
15 m diameter pool in the Aquatron Laboratory by methods previously described
(O'Dor et al., 1977; O'Dor, 1979). The mean mantle length (± Standard
Deviation) for 80 dead squid from the same trap was 19.3 ± 1.6 cm and mean
body weight, 142 ± 43 g. 43% of these squid were males. All dead animals
were immature. Feeding and growth studies were conducted until September 7
when both males and females began, precociously, to reach advanced stages of
sexual maturity under the 15 hour light, 9 hour dark regime used (O'Dor, 1979).
Temperatures in the pool were uncontrolled and rose from 7 to 17°C during
this period (see Table 1 for details).

The principle food used was live Fundulus sp. ranging from 6 to 11 cm
in length and from 2.5 to 17.5 g in weight. This was sometimes supplemented
with slices of whole frozen herring and occasionally with live fish of other
species.

Experiment I: Individual squid

Weight changes in two groups of individual squid were studied; eleven
feeding (A) and eleven starving (B). On July 19, both groups were weighed,
measured, and tagged through the upper mantle, near the head, using anchor
tags (see O'Dor et al., 1979). For Group A these were coded with three 1 cm
sections of colored spagetti tubing and were readily identifiable from the
bridge over the pool. For Group B solid colored, numbered tags of similar
design were used. Weighing was done without anesthesia and required that the
animal be out of water for 30 to 60 seconds. Squid were held vertically and
allowed to empty their mantles before weighing. Initially, feeding during
Experiment I was controlled by threading a knotted line through the backs
of the measured fish (the knot prevented escape of the fish, allowed the feeder
to prevent feeding by Group B, but did not interfere with feeding by Group A
or other squid) and records were kept of the length of each fish taken by
each animal in Group A. After 10 days, Group B was reweighed and transferred to
a 5.5 meter diameter outdoor tank where they were starved for an additional
seven days at 13.5°C before reweighing (Designated Expt. I.C.). Squid in the

inside pool were then fed on measured free swimming fish and records kept
for Group A until August 1.

The weight of food consumed by the squid was calculated from the length
of the fish taken using a standard curve relating length to edible weight.
The squid eat only the fleshy portion of the fish and often leave intact
skeletons including head and tail. The edible portion was calculated from
length-weight relationships for intact fish and recovered skeletons and
averaged about 80%. This figure was also used as a correction factor for
other types of food.

Population Experiments (II to V)

By August 1 it was apparent that the tagged squid of Group A were
feeding less than the other squid. The total number of squid in the large
pool had dropped to 120 and was stabilizing (see O'Dor et al., 1979). At
this time, all of the remaining squid were captured with a seine, weighed,
and returned to the pool. This process was repeated four times giving four
experiments as indicated in Table 1. By the fourth weighing, the squid had
learned to escape from the seine, and during the last two weighings a few
escapees prevented measurement of total weight.

During all experiments except III, an abundant supply of fish was
kept in the pool by daily additions of weighed fish. The pool was vacuumed
every second or third day and the waste recovered in the filter was weighed.
The weight of food consumed over each experiment period was calculated as
the difference between the weight of fish added and the waste removed.
Estimates of the edible portion calculated from these data also averaged
about 80%.

Calculations

Since data were for a short intervals and for animals in the same size
range of individual animal's daily growth rate was calculated as a percentage
of mean body weight during the period from the initial weight (w_i) and final
weight (w_f) as described by Mangold and Boletzky (1973):

$$\text{DGR (daily growth rate, \% day}^{-1}) = \frac{w_f - w_i}{(w_f + w_i)/2} \times \frac{100}{t}$$

Daily feeding rate for individuals was also calculated as a percentage of
mean body weight from the total weight of food consumed (F) over the period.

$$\text{DFR (daily feeding rate, \% day}^{-1}) = \frac{F}{(w_f + w_i/2)} \times \frac{100}{t}$$

Because of the failure to weigh all animals, the removal of animals for other experiments and deaths during the population studies, the DGR was calculated from the mean initial and final weights for the population. This approach should be valid since the animals weighed and those which died or were removed were representative of the population (see results). Since the number of squid feeding varied with time, a term for squid-days (S-t; the cumulative sum of the number of squid present on each day) was introduced into the equation for DFR for these experiments

$$\text{DFR} = \frac{F}{(w_i + w_f)/2} \times \frac{100}{S-t}$$

RESULTS

General Observations on Feeding

Squid in the pool remain in a relatively tight school; those that leave the school usually cease to feed and die within a few days. Squid behaving oddly (eg., irregular swimming in tagged animals) are sometimes attacked and driven, at least temporarily, from the school. When fish are added singly, the largest squid generally feed first, darting across the pool to capture the fish and then returning quickly. Smaller squid, nearer the fish, often give way to the larger squid; and if they fail to do so, may be attacked and and have the fish taken away. When large numbers of fish are added, observations are difficult, but all animals appear to feed, and fighting occurs only when two squid aim for the same fish.

The squid fed readily on a variety of small live fish including caplin, herring, mackerel, smelt, salmon smolts, and _Fundulus_ sp. and on _Crangon_ sp., but rejected eels and crabs after capturing them. In one experiment a small school of herring was added with lengths ranging from 16 to 27 cm (weights from 60 to 375 g). All of the herring of less than 19 cm were captured, but those above 22 cm remained in the pool for several months and were never eaten. It appears that there is an upper limit on the size of prey the squid will attack (roughly equal to their mantle length), and that they are relatively unselective below this limit.

The largest single meal we have observed was 23% of body weight, 70 g of herring consumed by a 260 g tagged squid. This was still visible in the

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gut 24 hours later when the animal rejected its next meal. The next largest
meal for this animal was 27 g at 270 g (10% B.W.) which did not interrupt
its regular feeding schedule. Similarly, a 118 g animal took 26 g (22% B.W.)
and skipped its next feeding, but later took 13% B.W. on one day and fed the
next. Thus, the squid can take advantage of quite large meals, but are
limited by their digestive capacity to a daily intake of less than about
20% B.W. Sustained feeding rates probably do not exceed 10 to 15% B.W. for
an animal in the size range studied at 10°C.

Feeding and Growth Rate

Figure 1 shows the DGR's plots against the DFR's calculated as described
above for each of the individual feeding animals (Expt. IA) and for the four
population experiments. It also shows the average percentage weight loss
per day for the unfed, tagged animals in the pool (Expt. IB) and in the
outside tank (Expt. IC). The solid line represents our "best guess" of the
relationship between feeding rate and growth rate for an "average squid". The
upper portion (A, extrapolated to zero by the dotted line) is the linear
regression for the data from Expts. II, IV, and V and all individuals from
Expt. IA that did not lose weight. The dashed line (B) is a linear regression
for the data from all individuals from Expt. 1A that did not gain weight,
Expt. IB and Expt. III.

A critical value in relating feeding rate and growth rate is the DFR
maintenance (DFRM), the amount of food required per unit body weight to
maintain the animal at a constant weight. Since the feeding rate for the
individuals which showed no weight change ranged from 0.7% to 1.8%, DFRM
appears to be quite variable. The daily consumption of maintenance food is
normally approximated as ζw^j, where ζ is the maintenance food coefficient,
W is the weight, and j has a value near 0.7 (Beverton and Holt, 1957).
Over the weight range in these experiments weight related changes were
masked by individual variation. We have chosen the mid point between the
intersects of the two regressions with DGR = 0 as the best estimate of
DFRM for the weight class. The solid line connects regression line A to the
estimated DFRM (1.1%) and continues to the intersect of regression B at
DFR = 0 (0.95%, the rate of weight loss during starvation).

Although individual variation is high, this line is probably a reasonable
approximation of the relationship of DGR and DFR for a population of squid.

Regression line A, in particular, seems robust since temperature differences
(Expt. V) and the systematic errors (see below) tend to shift points along the
line rather than away from it. The additional point, IIA, recorded on
Figure 1, is the result of a different analysis of the data for Expt. II and
gives some indication of the reliability of the calculations used for the
population experiments. For Expt. II, the total initial and final weights
were known and only dead animals were removed (dead weights were recorded).
Deaths occurred in all experiments at rates of about 3% per day, and their
influence on the results depends on the behaviour of the dying squid.
Observations indicate that dying squid do not feed and it seems likely that
they lose weight at a rate near that of other starving squid. The data for
Expt. II tabulated below show that the average weights of the dead squid
declined during the experiment, but if these weights are extrapolated back
to day 1, assuming 0.95% loss per day (the intercept of line B in Figure 1),
the mean weight on that day is 153.8 g - very close to initial mean weight of
the whole group.

DATE:	1	2	3	4	5	6	7	8
LIVE SQUID (g)	18237							15229
DEAD SQUID (g)			464			1342	1618	666
NUMBER OF LIVE SQUID	120	120	117	117	117	108	97	92
AVG. WT. LIVE	152.0							165.5
DEAD			155			149	147	133

If the estimated initial weight of all dead squid is subtracted from
the initial total, the DGR and DFR calculated by the formulae used for
individual animals are 1.27% and 5.03%, respectively (point IIA, Figure 1).
This suggests that the method based on average weights (point II, Figure 1)
underestimates DGR and DFR by about 20 to 25%. The values for the other
experiments are probable also underestimates since the dead squid showed
similar weight loss patterns; however, not all animals removed in these
experiments were dead so the corrections should be lower. Since both
DGR and DFR are underestimated to a similar degree, these errors would
not significantly alter the curve in Figure 1.

DISCUSSION

Comparison to Other Cephalopods

The growth rate of an animal is determined by its feeding rate, its maintenance energy requirement, and its efficiency in converting food into animal. Feeding rate may be controlled by food availability or by rate limiting physiological processes. The maintenance energy requirement is the sum of a variety of physiological demands which are characteristics of an organism, related to DFRM and which vary with the activities of the organism. The maintenance energy consumption per unit weight usually decreases with increasing weight (typically as a function of $w^{0.7}$) and increases with temperature (typically doubling or trebling with a 10°C rise in temperature). Conversion efficiencies (after deducting maintenance) calculated from wet weight as used here vary widely, depending primarily on the composition of the organism and the food. Even for the same food the efficiency often declines at higher feeding rates because digestive efficiency decreases (Beverton and Holt, 1957).

Although the data we have are few and limited to a relatively short portion of the life cycle, they do form a consistent pattern and provide values for several feeding and growth parameters for comparison with other cephalopods. Mangold and Boletzky's (1973) average DFR, DGR, and food conversion values for Octopus vulgaris in the same weight range as our squid were 1.6, 0.9, and 56%, respectively at 10°C and 3.3, 1.7, and 55% at 15°C. Comparing these figures to Table 1 indicates that at a given temperature squid feeding ad libitum probably grow a bit faster than octopusus and have a lower food conversion rate. This requires them to feed at approximately twice the rate. One might expect this lower conversion rate as a consequence of a higher DFRM for an active pelagic organism, but this does not appear to be the only factor. The estimates of conversion efficiency ($\frac{DGR}{DFR-DFRM}$) in Table 1 average about 40% which is less than half of the 83% calculated by Joll (1977) for Octopus tetricus. This lower efficiency could relate to the fish diet of squid; there is some evidence that octupuses grow less efficiently on fish than on crustaceans (Mangold and Boletzky, 1973) which have a composition more similar to that of cephalopods (O'Dor et al., 1979). There is also evidence that the digestive process in O. vulgaris is considerably longer than that in I. illecebrosus (Boucher-Rodoni, 1975), and haste may make waste.

Boucher-Rodoni (1975) has also shown that digestion rates increase with temperature. Since feeding rates are higher at higher temperatures (Expt. V) digestion rate may be the principle limitation on feeding. It appears that for I. illecebrosus the increase in DFR with temperature is greater than that in DFRM (as indicated by a comparison of Expt. IBand IC) since DGR also increases.

Comparison to Natural Populations

The fact that growth rates are temperature dependent means that caution is required in comparing captive growth rates to those in the field; however, since most of our data were collected near the 10 to 12°C temperature range in which I. illecebrosus is commonly caught (Lu, 1973), the problem may not be a major one. A second consideration, less easily resolved, is the relative activity levels in captive and wild populations which would influence DFRM. Squid in the pool swim continuously at speeds of 2 to 4 km/hr and exhibit all the preditory activities of those in the wild. They also are frequently startled into "fast-swimming" by observers whcih probably creates an energy demand similar to that resulting from predators in the wild. These activities seem comparable to those reported from field observations (Bennet, 1979; Merdsoy, 1979). If temperature and activity levels are comparable, our data suggest that squid in the field are feeding considerably below their ad libitum rates in the latter half of the season. This is consistent with several types of field data. The arguments for and consequences of this hypothesis are discussed the the paragraphs to follow.

Figure 2A shows the seasonal weight changes for female I. illecebrosus in 1977 transformed from lengths given by Amaratunga et al. (1977) with the equation provided and fitted with a von Bertalanffy curve (ℓ_t = 254.6 $(1-e^{-0.164 \ (t+3.2)}$). Also shown are the mean weights for squid from the pool and the weights of the longest lived tagged animal at the indicated dates. The slight decline in this animal's growth rate in August reflects precocious maturation: she was the first female to spawn on September 9. Normal female maturation is not pronounced until November. The temperature during Expt. II and IV should be comparable to the field, but growth rates are more than double those calculated for the 1977 population during the same period. The growth rate during Expt. V is even higher, but these may not be directly comparable since the temperature was higher. It seems likely

that the natural populations are not achieving their full growth potential from about mid June onward and are resource limited. The dashed line (Figure 2A) shows the projected growth of an average squid from the 1977 population if growth had continued at the mid-June rate (DGR = 1.05%). Squid with weights of over 700 g do occur in November in these population so this DGR is not unreasonable. The presence of both large and small squid in late season is a predictable consequence of the hierarchic feeding observed in captivity.

From the actual growth curve in Figure 2A, DGR's for the wild population can be calculated for any biweekly period and can be related to a DFR using Figure 1. The product of DFR and midpoint weight gives an estimate of food consumption for any period. These estimates are plotted in Figure 2B. Even if the entire growth curve were a certainty, the values would likely be underestimates during early development since DFRM is probably considerably higher in small animals; however, the major food of small squid is crustaceans (Squires, 1957; Ennis and Collins, 1978) which may be digested more efficiently resulting in compensating errors. In any case, for the cumulative food consumption curve (Figure 2B), errors when the animals are very small will have marginal effects. It is interesting to note that even with these underestimates, nearly 50% of a squid's consumption before it leaves the fishing grounds in November occurs before mid June during a period when their predominate prey is probably planctonic crustaceans (Squires, 1957). From mid July on, there is a progressive decline not only in DFR but in total consumption. This suggests depletion of prey fish which are significant portions of their diets at this time (Ennis and Collins, 1978). Both the squid and their prey were heavily fished during this period in 1977. If prey are scarce, heavy fishing of squid should increase individual growth rates unless the limiting factor in feeding is spacial distribution rather than abundance. Since fecundity of squid appears to be proportional to body weight (O'Dor et al., 1978) the resulting increase in individual growth should compensate to some extent for the loss of reproductive capacity associated with removal of squid at this time. Over-fishing of prey species may be a more serious problem as declines in the growth rate of squid should be a good indicator of it.

From September on, empty stomachs are common and squid becomes an increasingly important component (often the major component) in the squid's diet (Ennis and Collins, 1978), presumably because other prey are depleted. In one of the starvation experiments in the outside pool the smallest animal disappeared (except for a few ramains), while the largest female in the pool gained weight despite the supposed absence of food. We have observed other instances of cannibalism in previous years but only when food had not been given for several days. While we could not identify the cannibals, the squid eaten were always small males. From these observations, it is clear that the presence of squid bits in squid stomachs is not always the accidental result of fights during feeding frenzies (Bennet, 1979) or a result of predation of one school on another but can be a result of intraschool cannibalism when other foods are not available. If, as appears likely, a significant portion of the late-season growth of the larger individuals which will become the breeding stock for the next year class is based on consumption of other squid, there are several implications. 1) Late-season squid become increasingly valuable in terms of the food they have consumed to reach a given weight. If the larger squid consume smaller squid, the overall efficiency of conversion will be the product each conversion - even at the high estimate, 36%, this is only 13% overall efficiency. 2) Late-season animals that do not themselves spawn may have an important role as a food reserve for the breeding stock during migration. Even though individual females have a high fecundity, the stock size required for successful spawning may be high. 3) Selective removal of smaller squid may affect the mean lengths and apparent growth rates in late season.

SUMMARY

1. Feeding and growth rates of tagged individuals and of the entire population of a captive school of squid were monitored over a two-month period on a live fish diet.

2. The daily feeding rate for maintenance is estimated at about 1% body weight. Average daily feeding rates (ad lib.) ranged from 3.6 to 6.7% and average daily growth rates from 1.1 to 1.9%. Both rates increased with temperature. Food conversion rate (wet weight food to wet weight squid) ranged from 25 to 36% and conversion efficiency (after allowing for maintenance) ranged from 35% to 51%.

3. Feeding and growth rates for these pelagic cephalopods were higher than those for <u>Octopus vulgaris</u> at comparable temperatures. The maintenance requirement was slightly higher, but the conversion efficiency much lower.

4. Growth rates in the field are well below those of captive animals suggesting that the natural population becomes increasingly resource limited as the season progresses.

5. Field feeding rates are estimated from field growth rates. Food consumption (absolute, not weight specific) is higher before July than after. Most of the biomass of squid results from early season feeding when crustaceans are the principle prey.

6. The importance of cannibalism as a food source for the breeding stock is discussed.

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TABLE I. Summary of experimental conditions and results.

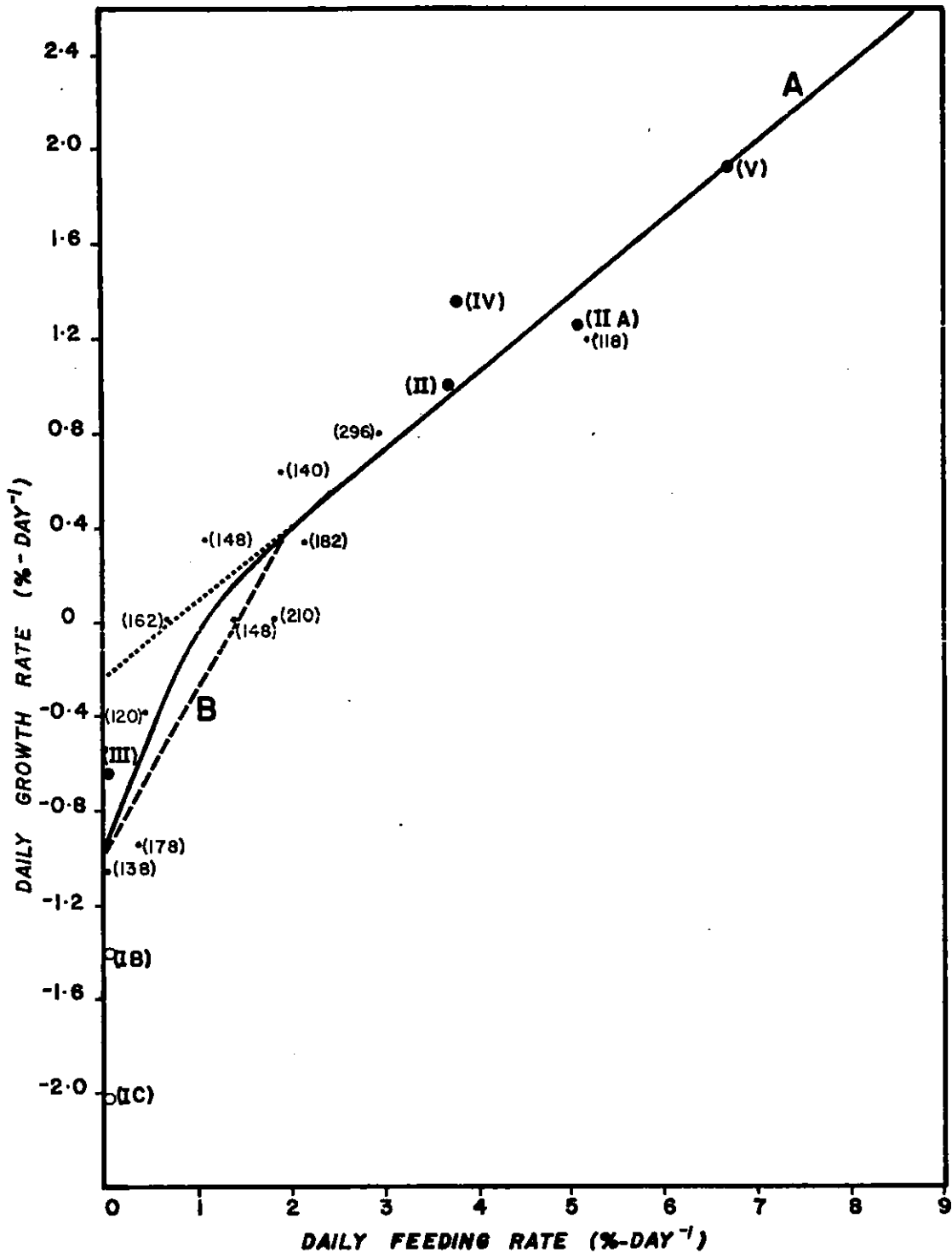| Experiment	Dates	Temperature °C mean (range)	DFR (%)	DGR (%)	Food conversion rate (%)	Conversion efficiency (%)	Mean weights initial-final (g)
IA	19/7-1/8	8.4 (7.0-8.8)	*	*	-	-	-
IB	19/7-29/7	8.4 (7.0-8.8)	0	-1.4	-	-	-
IC	29/7-5/8	13.5	0	-2.0	-	-	-
II	1/8-7/8	9.7 (8.7-11.0)	3.6	1.1	29%	42%	152-166
IIA	1/8-7/8	9.7 (8.7-11.0)	5.1	1.3	25%	33%	152-166
III	8/8-10/8	9.6 (9.3-9.8)	0	-0.6	-	-	166-165
IV	11/8-24/8	10.3 (9.1-12.5)	3.8	1.4	36%	51%	165-201
V	25/8-7/9	15.5 (13.0-17.0)	6.7	1.9	29%	35%	201-264

Fig. 1. Daily growth rates of squid feeding at various rates. Large filled circles are
the results of the indicated population experiments (see Table 1); small filled
circles are individual animals from Experiment IA with initial weight in grams in
parentheses; open circles are the average values for starved individuals in
Experiment I. Line A is the regression for all experiments which showed no weight
loss (DGR = 0.33DFR - 0.24; r^2 = 0.88). Line B is the regression for all
experiments at 10.0 ± 0.5°C which showed no weight gain (DRG = 0.66DFR - 0.95;
r^2 = 0.64). The solid line approximates the overall relationship between DGR and DFI
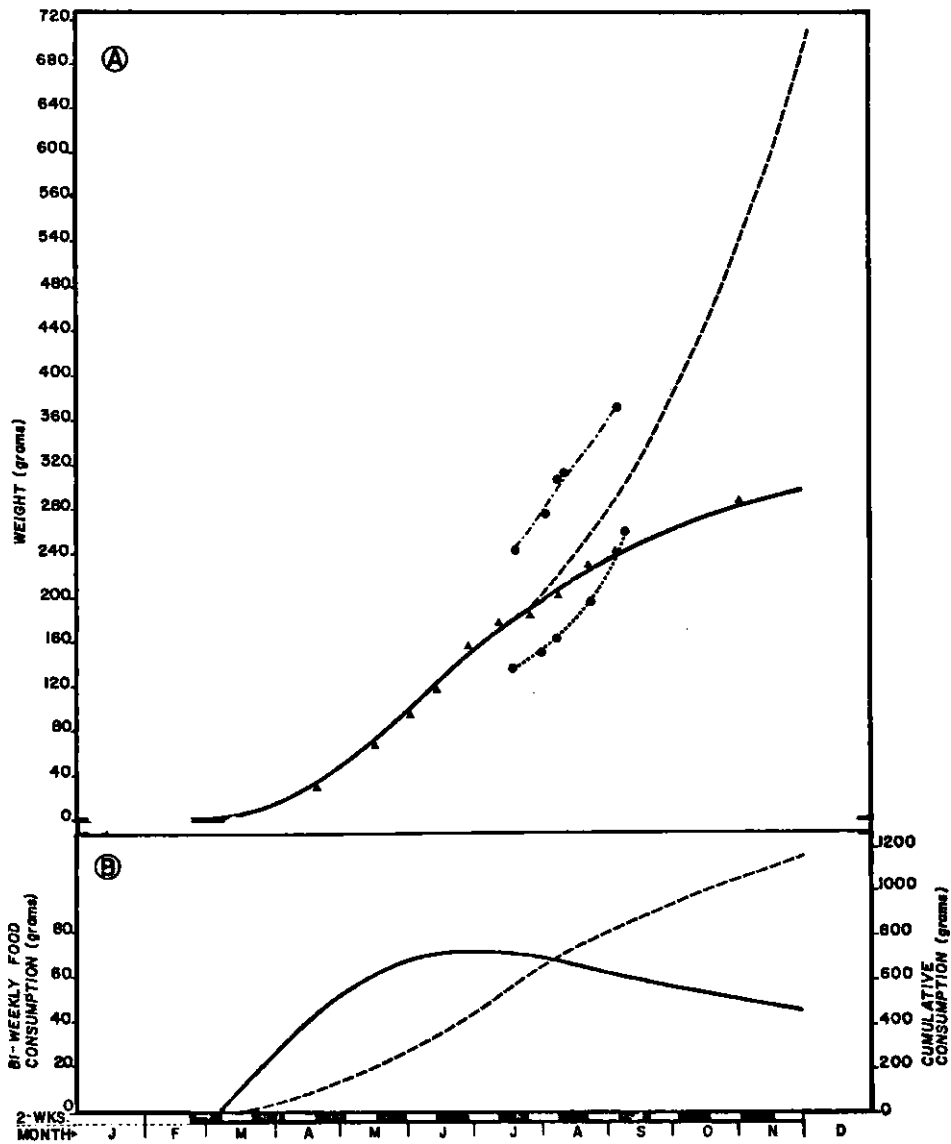
Fig. 2A. Seasonal weight changes in captive and wild squid. The solid line is a von
Bertalanffy curve fit to mean weights (triangles) of female squid caught in 1977
(Amaratunga et al., 1978). The dotted lines indicate changes in mean weight of
captive animals in 1978 (....) and in the weight of the longest lived tagged
individual (—·—·—·). The dashed line shows the expected individual weights of
the 1977 population if feeding and growth had continued at the mid-June rate which
is similar to the rate maintained by captive squid fed ad libitum.

B. Biweekly (solid line) and cumulative (dashed line) food consumption for an average
squid estimated from growth rates of the 1977 population using the feeding rate -
growth rate relationship from Fig. 1. Note: These estimates are for food
consumed and do not include waste. The values for food removed from the environ-
ment would be about 25% greater.

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