

International Commission for



the Northwest Atlantic Fisheries

Serial No. 3543
(D.c.3)

ICNAF Res.Doc. 75/61

ANNUAL MEETING - JUNE 1975

Considerations on squid (*Loligo* and *Illex*) population dynamics and recommendations for rational exploitation

by

David Au

National Marine Fisheries Service
Northeast Fisheries Center
Woods Hole, Massachusetts 02543

Abstract

Yield per recruit analysis on squid (*Loligo* and *Illex*) in Subareas 5 and 6 indicate a 55% and 65% exploitation ratio (F/Z) on the respective species would maximize yield. The parameters used were estimated from growth and longevity information. A nearly proportional relationship between stock and recruitment is further proposed. This relationship requires that short-lived species with high natural mortality such as squid, be fished moderately.

Introduction

Squid are rapid growing, productive animals whose life span is typically short, often one year. The concept of a productive annual crop that should be harvested at high exploitation levels therefore has justification. In 1973 the ICNAF Assessments Subcommittee recommended a Total Allowable Catch (TAC) for squid (*Loligo pealei* and *Illex illecebrosus*) from Subareas 5 and 6 off the northeastern United States of between 50,000 and 80,000 MT (ICNAF Redbook, 1973, Part 1). A TAC of 71,000 MT was established for 1974 and 1975 by ICNAF. The recommendations were based largely upon the analysis by Ikeda *et al.* (1973) of the offshore winter fishery (primarily *Loligo*) in which an exploitation rate of 80% was considered acceptable. This rate will be reexamined here, considering the life history of the species and, in particular, considering the type of stock-recruitment relationships that should hold for squid.

Life span and natural mortality

Estimates of mortality rate Z can be obtained from information on the population structure of the stock. Thus information on the mean length of the exploited stock and mean length at recruitment, combined with the von Bertalanffy parameters, can give an estimate of Z (Beverton and Holt, 1957, p. 41). Similarly, the mean age of the exploited stock can be used to estimate Z. These methods depend upon an accurate aging procedure, lacking for squid, or require following the length frequencies of a squid year class throughout its fishable life to obtain the annual mean length. A further difficulty is that small differences in mean length or age are generated by a large range in Z because of the short life span of the squid. Thus these methods are subject to large errors. A more direct approach would be to use the life span alone to estimate mortality, *i.e.*, to use physiological information rather than population measurements.

It is not at present possible to age squid, but comparing growth rate estimates of *Loligo* (Summers, 1971) and *Illex* (Squires, 1967) with the largest observed sizes suggests that some *Loligo* males (>40 cm in spring) may live 3 years and some *Illex* (>30 cm) to 1.5 years. However, the majority of individuals in each species probably live not more than one year, a physiological life expectancy associated with spawning. Post spawning mortality was an assumption basic to the growth schemes proposed by these authors. Where such mortalities are known they are usually associated with rapid maturing, short lived species of animals. Post-spawning mortalities have been observed in *Loligo opalescens* off California (McGowan, 1954; Fields, 1965) and in *Todarodes pacificus* (Mamabe and Shimizu, 1966) the common Japanese squid related to *Illex* (both of the family Ommastrephidae). Thus information on spawning age provides estimates of the life expectancy or mean life span, T, of these species.

The life expectancy of *Loligo pealei* must be about 1-1.5 years. The majority of individuals spawn at 12 months, although a significant number may spawn at 17-19 months (Summers, 1971). However he felt that the latter constituted less than 25% of the breeding stock. Examination of length frequencies (Tibbetts, 1975; Ikeda *et al.*, 1973; Paulmier, 1974; commercial sample data reported to ICNAF) indicates few squid live beyond 18 months and probably most die after spawning at 12 months.

Similarly, *Illex illecebrosus* is expected to live only to 1 year at which time spawning occurs (Squires, 1967), although length frequencies (Tibbetts, 1975; Paulmier, 1974; commercial sample data reported to ICNAF) indicate that some may live to 1.5 years. There is no evidence of mature squid surviving a spawning season as in *Loligo pealei*, so mean T for *Illex*, considering other forms of natural mortality, should be even less than that of *Loligo*.

The actual seasonal distribution of natural mortality is of course unknown, although presumably it is heaviest during the spawning period. If the true survival curve is such that the life expectancy always remains at 12 months, *i.e.* the age at first spawning, then the squid population can be approximately represented by an effective population characterized by a constant natural mortality rate M that also generates a 12-month life expectancy. Then with survival exponential

$$Z = M = \frac{1}{T}$$

in the unexploited state (Allen, 1971). M so calculated would be an effective natural mortality rate during the life span. In both *Loligo* and *Illex*, T is probably <12 months, the expected age at spawning. Then effective

$$M = \frac{1}{<12} > 1.00.$$

Note that other short-lived species, *e.g.* capelin, smelt, and certain minnows (Beverton and Holt, 1959) generally have M estimated larger than 1.00. For purposes of this discussion M between 1.00 and 1.50 will be considered with M <1.25 applied to *Loligo* and M >1.25 applied to *Illex*. Note that M = 1.25 corresponds to a mean life expectancy of 9.6 months while M = 1.50 corresponds to 8 months.

Growth Rates

Growth and maturation of both *Loligo* (Summers, 1971) and *Illex* (Squires, 1967) is rapid (Fig. 1), maturity being reached in one year. *Illex* grows about twice as fast as *Loligo*. Note that *Loligo* males grow larger than females whereas the opposite is true for *Illex*.

Loligo growth declines very slowly with age with no indication of an approach to asymptotic length. A von Bertalanffy curve fit to the growth data by Summers gives L_{∞} values of 65.6 and 44.9 cm for males and females respectively with corresponding K values of .330 and .452, describing growth curves with very slight downward curvature. Such L_{∞} 's are much larger than the largest observed *Loligo* and so cannot be interpreted as asymptotic length. Therefore to obtain biologically meaningful growth parameters for *Loligo* L_{∞} was set at the largest mean sizes of each sex, at 34-36 months for males and 24 months for females. The growth parameters so obtained are thus effective values that reflect the biological features of *Loligo* growth even though the predictive value of the growth equation is lessened.

The growth curves for *Illex* were fit, using the procedures given by Gulland (1969), to the calculated lengths given by Squires for Newfoundland squid. *Illex* growth in SA 5 and 6 may differ but presently there are no published growth curves for this area. The following von Bertalanffy growth parameters were obtained:

	Sex	L_{∞}	K/year
<i>Loligo</i>	M	45	.606
	F	27	1.235
<i>Illex</i>	M	30.05	2.491
	F	32.27	2.442

The mean value, sexes combined, of the developmental rate parameter, K, is .920 for *Loligo* and 2.46 for *Illex*.

Production/Biomass Ratio

Assuming exponential survival and von Bertalanffy growth, the ratio of production per mean biomass, P/B, is equal to M (Allen, 1971) in the unexploited state, so that this ratio should be greater than 1.00 in both species. If M between 1.00 and 1.25 for *Loligo* and between 1.25 and 1.50 for *Illex* is accepted, then P/B ratios should lie between the same values for the respective species. Because M used here is the effective natural mortality during the life span, whereas the actual M during the exploited stage, when the squid are older on average, may be less, these P/B ratios may be considered too high. But the P/B ratio during the exploited stage may also be estimated from the average weight gain in that period, i.e. $P/B = g$, the instantaneous rate of weight growth, $= \ln \frac{W_t}{W_0}$ (see also Allen, 1971). With *Loligo* the mean length of the ascending portion of graphs of length-frequency from the fishery (see Ikeda *et al.*, 1973; Tibbetts, 1975) is about 8 cm, or 5 months of age, an estimate of mean recruitment size. At one year of age mean length has increased to 17 cm, the weight increasing from 19.7 to 112.6 g (length-weight conversion given by Ikeda *et al.*, 1973). Then $P/B = g = 1.74$ during the 7 months. For *Illex* Squires (1967) reports a sixfold increase in weight, from 54 to 324 g between May and October in the Newfoundland fishery. This corresponds to a P/B ratio of 1.79 for those 5 months. It thus appears that P/B is quite high in both species. If these ratios or growth rates held throughout the life span and survival continued at constant exponential rate, it would mean that the estimates of M given above are too low. But there is no need for further speculation on this point until more is known about the seasonal distribution of mortality. The proportion of this production that can be harvested on a sustained basis depends both upon the nature of exploitation and upon the minimum stock size necessary for continued and adequate recruitment.

Exploitation rates

The exploitation rate to obtain maximum yields from this production can be estimated using the FAO yield tables (Beverton and Holt, 1966). Entry into these tables requires estimates of the M/K ratio and c, the age at entry to the exploited stage, measured as a fraction of the species' potential growth.

The M/K ratio is obtained as follows, using the parameter values discussed above:

Species	M	K	M/K
<i>Loligo</i>	1.00-1.25	.920	1.09-1.36
<i>Illex</i>	1.25-1.50	2.46	0.51-0.61

The parameter c is normally estimated by the ratio l_c/L_{∞} where l_c is the mean length at entry to the exploited stage. For both species, however, it is presumed that post-spawning mortality precludes significant further growth toward L_{∞} . Therefore in this analysis L_{MAX} is substituted for L_{∞} to obtain a more realistic estimate of the fraction of potential growth reached at age of entry to the fishery. L_{MAX} is taken as the mean size, sexes combined, of 18-month *Loligo* and of 12-month *Illex*, these being the highest values to mean life expectancy that might be encountered. The length at entry to the fishery, l_c is taken at 8 cm for *Loligo* (previous section). For *Illex* it is seasonal availability rather than mesh selection that governs l_c . In SA 5 and 6 the mean length of the main group of *Illex* first appearing in the spring is between 10 and 20 cm, similar to the 14 cm described by Squires (1967). Fourteen cm was therefore taken as l_c for *Illex*. The values of c are then calculated as:

Species	l_c	L_{MAX}	c
<i>Loligo</i>	8 cm	23.5 cm (18 mo.)	.340
<i>Illex</i>	14 cm	28.5 cm (12 mo.)	.491

64

The following statistics are thus obtained from the yield tables using for each species M/K and c increments that span the estimated values:

Species	c	M/K	E_{max}	Relative stock size at E_{MSY}
<i>Loligo</i>	.34	1.0	.55	.241
		1.50	.55	.232
<i>Illex</i>	.50	0.5	.65	.216
		1.0	.65	.201

Thus for *Loligo* $E_{MAX} = \frac{F}{Z}$ = the exploitation ratio that maximizes yield/recruit, is

estimated at 55%, the stock size being reduced to 23-24% of the unfished level. *Illex* should be fished harder since it becomes available to the fishery relatively late in its growth history, the estimate of E_{MAX} being 65% with the mean stock size reduced to 22-22% of initial level.

E is also a measure of the ecotrophic coefficient, the proportion of prey production taken by a predator (Dickie, 1972). In this case, it is the proportion of prey production taken by an additional predator, man. Then on a sustained basis maximum yield is $E \times \text{Production} = E \times MB_0$ where MB_0 is the production estimate of the unexploited biomass B_0 (since M estimates production/biomass). Taking the values of E calculated above, the following proportion of initial biomass might be obtainable at the MSY level:

Species	E_{MAX}	Production	Yield
<i>Loligo</i>	.55	$(1-1.25)B_0$	$(.55-.69)B_0$
<i>Illex</i>	.65	$(1.25-1.50)B_0$	$(.81-.98)B_0$

This calculation assumes that production is not impaired by the reduced population size resulting from exploitation. Note that the method is essentially the same as used by Alverson and Pereyra (1969) who used a similar relationship derived by a slightly different argument. These results suggest that a very high proportion of the initial mean biomass can be taken as yield, obviously a result of the very rapid growth of these squid.

The above calculations on sustained yield all further assume that the recruitment level is unimpaired by exploitation. It was calculated above that at MSY fishing levels *Loligo* would be reduced to 23-24% and *Illex* to 20-22% of initial abundance. For both species then a pertinent question would be whether impaired recruitment could be expected.

Stock-recruitment relationships

The kind of stock-recruitment relationship applicable to these squid may be deduced from considerations of their biology. Their fecundity is relatively low, 3500-6000 eggs in *Loligo pealei* (Summers, 1971) and perhaps a general level of 10,000 eggs in *Illex* (M. Lipinski, Sea Fisheries Institute, Gdynia; pers. comm.). Ommastrephids generally have a higher fecundity than Loliginids. Zujew and Nesis (1971) have given a range of 70,000 to 150,000 eggs for the related *Todarodes pacificus*. Obviously, the rapid maturation rate is of the greatest importance to squid reproductive potential. The earliness of the age at maturity has long been recognized as being one of the most important parameters governing the rate of increase in animal populations (Cole, 1954). A further consequence of their short life span is that the overlap between generations, hence intraspecific competition, is minimized. These features point to an opportunistic type species, characterized by high turnover rate and production/biomass ratios, and with short life histories and relatively simple population structure. Such species have been termed "r-strategists" (MacArthur and Wilson, 1967) because their populations are characterized by high relative rates of increase (r) with little density dependent regulation. Ecosystems tend to evolve with such productive species being of paramount importance in the food web (Odum, 1967). Because the rate of reproductive increase is strongly dependent upon the numbers of mature individuals and their rapid turnover, rather than fecundity, such species tend to show geometric increase when conditions are suitable, and their stock-recruitment relation would tend to be proportional, i.e. recruits should increase gradually with stock size such that the stock-recruitment curve is only slightly convex downward. This is in contrast to the domed stock-recruitment curves of Ricker (1954) or the horizontal type curves, showing constant recruitment over most stock densities, of Beverton and Holt (1957). Domed curves are most easily understood as resulting from strong, negative interaction between adult stock and larvae, juveniles, or even with the reproductive process itself, at higher stock densities. The abbreviated age structure of squid would suggest that this density dependent mechanism is relatively unimportant. Independence between recruitment and parent stock, as in the standard yield per recruit model, results from increased density dependent mortality among larvae and pre-recruits, which could be mediated through qualitative changes in stock structure in long-lined species. The less important this mechanism, the more dependent is recruitment

on parental stock size (Beverton and Holt, 1957, p. 51). Cushing (1971) has argued that the domed Ricker curves are characteristic of fish species with high fecundity, generally greater than 100,000 eggs, that is correlated with density-dependent population control (see also Murphy, 1968), and that species with lower fecundity have a gradually increasing, non-domed, stock-recruitment curve. More fundamentally, it is the rate of reproductive increase that is involved, for which maturation rate is most important. Thus those species with lower fecundity but rapid maturation have sacrificed some population stability for increased reproductive potential, and their stock-recruitment curve would tend toward a proportional relationship. Similar relationships between stock, recruitment, and surplus production as a function of the reproductive potential of species have been discussed by Pianka (1972) who shows that opportunistic species would tend to have symmetrical yield-biomass curves. Thus the stock-recruitment relationship applicable to squid should be the non-domed type of the Ricker family of curves or the slightly convex type of the one parameter form of the Beverton-Holt, asymptotic curve (Ricker, 1958, p. 269).

A corollary to these arguments is that species with slightly convex, stock-recruitment curves are relatively strongly influenced by their abiotic environment. This effect is evident in the Newfoundland *Illex* fishery (Squires, 1957) and is well known in the Japanese *Todarodes* fishery (reviewed by Clarke, 1966). Similarly, abundance indexes of *Loligo pealei* from the US Fall Groundfish Survey in Subareas 5 and 6 show large annual variations (Tibbetts, 1975; Serchuk and Rathjen, 1974).

Exploitation curves with stock recruitment effects

To explore the effects of recruitment changes on yield, and hence upon the recommended exploitation level, the yield functions previously used will be modified by appropriate stock-recruitment relationships. For this purpose the Ricker one-parameter form of the recruitment function of Beverton and Holt will be used. It was argued above that the domed stock-recruitment curves were not to be expected for squid, so the model to be used here describes curves ranging from a near direct relationship between progeny and parent stocks to complete independence. It was further argued that the latter condition of constant recruitment over a wide range of stock abundance was not to be expected in squid. The relationship by Ricker (1958) is:

$$R = \frac{W}{1+A(W-1)}$$

where W and R are parent and progeny stock abundances respectively, in terms of replacement level (equilibrium abundance of unfished stock), and A is a parameter varying between 0 and 1 that determines the shape of each individual curve. As A approaches 1 the curve described approaches the constant recruitment curve. Theoretically A is proportional to density dependent mortality so that the model demonstrates how the increasing importance of this form of mortality changes the curves from the direct to the zero (horizontal) relationship between recruitment and parental stock size. When A is less than 0.8 or 0.9, the curves are very similar to the gradually rising stock-recruitment curves of Ricker (1954) with parameter values at ≤ 1 . In this paper W and R in the model will be replaced by B_t and B_{t+1} , the mean biomass of the parent and progeny generations respectively. B_t is obtainable from the FAO yield tables (Beverton and Holt, 1966) as a relative stock size index at any level of exploitation, and B_{t+1} will be determined by the stock-recruitment function. Now in this model B_t and B_{t+1} are in the same units such that at replacement level $B_t = B_{t+1}$. But since the biomass of the model population is assumed to be changing only by the effects of fishing mortality and recruitment, the decrease in B_{t+1} is an index of recruitment level, varying from 1 at zero exploitation to zero at 100% exploitation. Then the relative yield per recruit function from the FAO tables, multiplied by this index, gives a new index of relative yield with stock recruitment effects incorporated.

Figure 2 shows the recruitment function for various levels of stock size and for different values of the parameter A , and Figures 3 and 4 show the resulting recruitment-adjusted, yield-biomass curves for the range of M/K ratios appropriate to *Loligo* and *Illex*. The lower half of these latter figures show the relationship between mean stock size and exploitation ratio, E . This last relationship is derived from the constant recruitment case so that when considering the curves characterized by parameter $A < .8$, *i.e.*, those corresponding to reduced recruitment by the expected stock-recruitment relationship, it must be remembered that a given mean stock size will have resulted from a lesser exploitation level than indicated in the figures. Therefore the exploitation-biomass relationship presented should be considered as maximal for any relative stock size.

Finally, it should be noted when the parameter A equals 1.0, recruitment level becomes constant. Therefore, the uppermost curves ($A = 1$) in each M/K family in Figures 3 and 4 correspond to the standard yield/recruit function directly obtainable from the FAO tables.

As is to be expected, theoretical yield levels decline sharply at higher effort levels when stock-recruitment effects are considered as has been shown by Beverton and Holt (1957, p. 330-370). The general result is to make the yield-biomass curves more symmetrical. This effect becomes more significant with yield-biomass curves that are strongly asymmetrical because of high M/K ratios.

Inspection of Figures 3 and 4 again show that for the constant recruitment case ($A = 1.0$) exploitation for maximum yield should be 55% for *Loligo* and 65% for *Illex* as previously discussed. But when stock recruitment effects are incorporated ($.2 < A < .8$), the exploitation levels to maximize yield should be no more than 40% for *Loligo* and 50% for *Illex*.

Returning to the earlier estimate of yield from production and using these recruitment-adjusted exploitation rates we obtain:

Species	Adjusted E_{MAX}	Production	Yield
<i>Loligo</i>	.40	$(1-1.25)B_0$	$(.40-.50)B_0$
<i>Illex</i>	.50	$(1.25-1.50)B_0$	$(.62-.75)B_0$

where B_0 is the initial, unexploited biomass. Ikeda *et al.* (1973) used the area-density method to calculate the numbers of squid on the winter fishing grounds each year between 1968 and 1972. The mean for this period was 650×10^6 squid, and their 1970-71 value, 642×10^6 squid, was estimated to be 50% of an approximate 100,000 MT biomass. These squid would be mostly *Loligo*, so that by the relationship of yield to biomass given above, approximately 50,000 MT or 50% could be harvested on a sustained basis.

The relationship given for *Illex* cannot be used for estimating sustainable yields until more is known of the degree to which availability governs the seasonal abundance of this squid. Until then assessments in terms of stock biomass will be difficult because seasonal availability is probably most important in the *Illex* fishery.

Discussion

The degree to which these results hold depends upon the robustness of the model. The estimates of natural mortality are very preliminary as are the growth rate parameters. The ecology of these animals is relatively little known and significant variations in life history patterns may be expected in different regions as a consequence of their rapid biological turnover. However, the results are in fact quite robust.

Thus for *Loligo* the appropriate M/K ratios may be as low as 0.5 (for mean life span of 1.5 years and $K = 1.3$) or as high as 4.0 (mean life span of 0.5 years and $K = 0.5$). These extreme ratios are unlikely because M and K are parameters that tend to vary together in the same direction. However, if the M/K ratio is < 1.0 , the optimal exploitation level would be relatively low so that stock-recruitment effects should not be of concern. On the other hand if the M/K ratios are high, the yield biomass curves rapidly become asymmetrical, but still with stock-recruitment effects incorporated, optimal exploitation levels remain near 50% (see Figure 5 for M/K ratios of 3.0 and 4.0).

In *Illex* both M and K are probably more precise because the population is more uniformly aged. But what if length at 50% availability to the fishery were 20 cm instead of 14 cm so that $c = 0.70$? The following table shows that for M/K = 1.0 and 2.0 (for extremely asymmetrical yield-biomass curves) that the recommended exploitation ratios would still be close to 50%.

c	M/K	E_{MAX}	E_{MAX} with stock-recruitment effect
.70	1.0	.70	.55
.70	2.0	1.00	.60

Summary

The population parameters of both *Loligo* and *Illex* have been estimated using information on growth rates and longevity. Yield per recruit analysis then showed that optimal exploitation ratios should be about 55% for *Loligo* and 65% for *Illex*, considerably lower than the 80% previously recommended. In general the growth rates of squid are so rapid that to allow for increased population growth through a reduced exploitation rate is good fishing strategy. When appropriate stock-recruitment effects are taken into account, the exploitation ratios should be even lower, down to 40 and 50% respectively. It is often suggested that productive species such as squid should be exploited heavily on a sustained basis. But it is precisely for such species that recruitment can be expected to fall proportionately with stock size. Furthermore such species are normally of great importance in the community food web so that any heavy exploitation may be detrimental to other species stocks.

Literature Cited

- Allen, K. R. 1971. Relation between production and biomass. J. Fish. Res. Bd. Canada, 28(10): 1573-1581.
- Alverson, D. L. and W. T. Pereyra. 1969. Demersal fish explorations in the northeastern Pacific Ocean--an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. J. Fish. Res. Bd. Canada, 26(8): 1985-2001.
- Beverton, R. J. H. and S. J. Holt. 1957. On the dynamics of exploited fish populations. U. K. Min. Agr. and Fish., Fish. Invest. Ser. 2, Vol. 19, 533 pp.
- _____. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Ciba Fdn. Colloq. Ageing, Vol. 5, pp. 142-180 (eds. G. E. W. Wolstenholme and M. O'Conner).
- _____. 1966. Manual of methods for fish stock assessment, Part II--Tables of yield functions. FAO Fish. Tech. Paper No. 38. 67 pp.
- Clarke, M. R. 1966. A review of the systematics and ecology of oceanic squids. Adv. Mar. Biol. 4:91-300.
- Cole, L. C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29(2): 103-137.
- Cushing, D. H. 1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. Int. Explor. Mer., 33(3): 340-362.
- Dickie, L. M. 1972. Food chains and fish production. ICNAF Spec. Publ. No. 8, Symposium on Environmental Conditions in N.W. Atlantic, 1960-1869. P. 201-219.
- Fields, W. G. 1965. The structure, development, food relations, reproduction, and life history of squid *Loligo opalescens* Berry. Calif. Fish Game Bull. No. 13, 108 pp.
- Hamabe, M. and T. Shimizu. 1966. Ecological studies on the common squid *Todarodes pacificus* Steenstrup mainly in the southwestern waters of the Japan Sea. Bull. Japan Sea Reg. Fish. Res. Lab., 16: 13-55.
- ICNAF 1973 Redbook Part I. Intern. Comm. N. Atl. Fisheries
- Ikeda, I., and F. Nagasaki. 1973. Stock assessment of common American squid in ICNAF Subarea 5 and Statistical Area 6. ICNAF Res. Doc. 73/62, 8 pp.
- Gulland, J. A. 1969. Manual of methods for fish stock assessment, Part I. Fish population analyses. FAO manuals in Fish. Sci. No. 4, 154 p.
- MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N. J. 203 pp.
- McGowan, J. A. 1954. Observations on the sexual behavior and spawning of the squid, *Loligo opalescens*, at La Jolla, California. Calif. Fish. Game, 40: 47-54.
- Murphy, G. I. 1968. Pattern in life history and environment. Am. Nat. 102:391-403.
- Odum, E. P. 1969. The strategy of ecosystem development. Science, 164:262-270.
- Paulmier, G. 1974. Preliminary observations on commercial squids (*Loligo pealei* LeSeur and *Illex illecebrosus* LeSeur) on Georges Bank-R/V *Cryos* cruise, Sept.-Oct. 1973. ICNAF Res. Doc. 74/50. 14 pp.
- Ricker, W. E. 1954. Stock and recruitment. J. Fish. Res. Bd. Canada 11(5):559-623.
- _____. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Bd. Canada (119). 300 pp.
- Serchuk, F. M. and W. F. Rathjen. 1974. Aspects of the distribution and abundance of the long finned squid, *Loligo pealei*, between Cape Hatteras and Georges Bank. Mar. Fish. Rev. 36(1):10-17.
- Squires, H. J. 1967. Growth and hypothetical age of the Newfoundland bait squid *Illex illecebrosus* *illecebrosus*. J. Fish. Res. Bd. Canada, 24(6):1209-1217.
- Summers, W. C. 1971. Age and growth of *Loligo pealei*, a population study of the common Atlantic Coast squid. Biol. Bull. 141:189-201.

- Tibbetts, A. M. 1975. Squid fisheries (*Loligo pealei* and *Illex illecebrosus*) off the Northeast United States, ICNAF Subarea 5 and Statistical Area 6. ICNAF Res. Doc. 75/ .
- Zujew, G. W. and K. N. Nesis, 1971. Kalmary. Biologia i promysiel. Izd. "Pisozewaja Promyszlennost" Moscow, 360 pp.

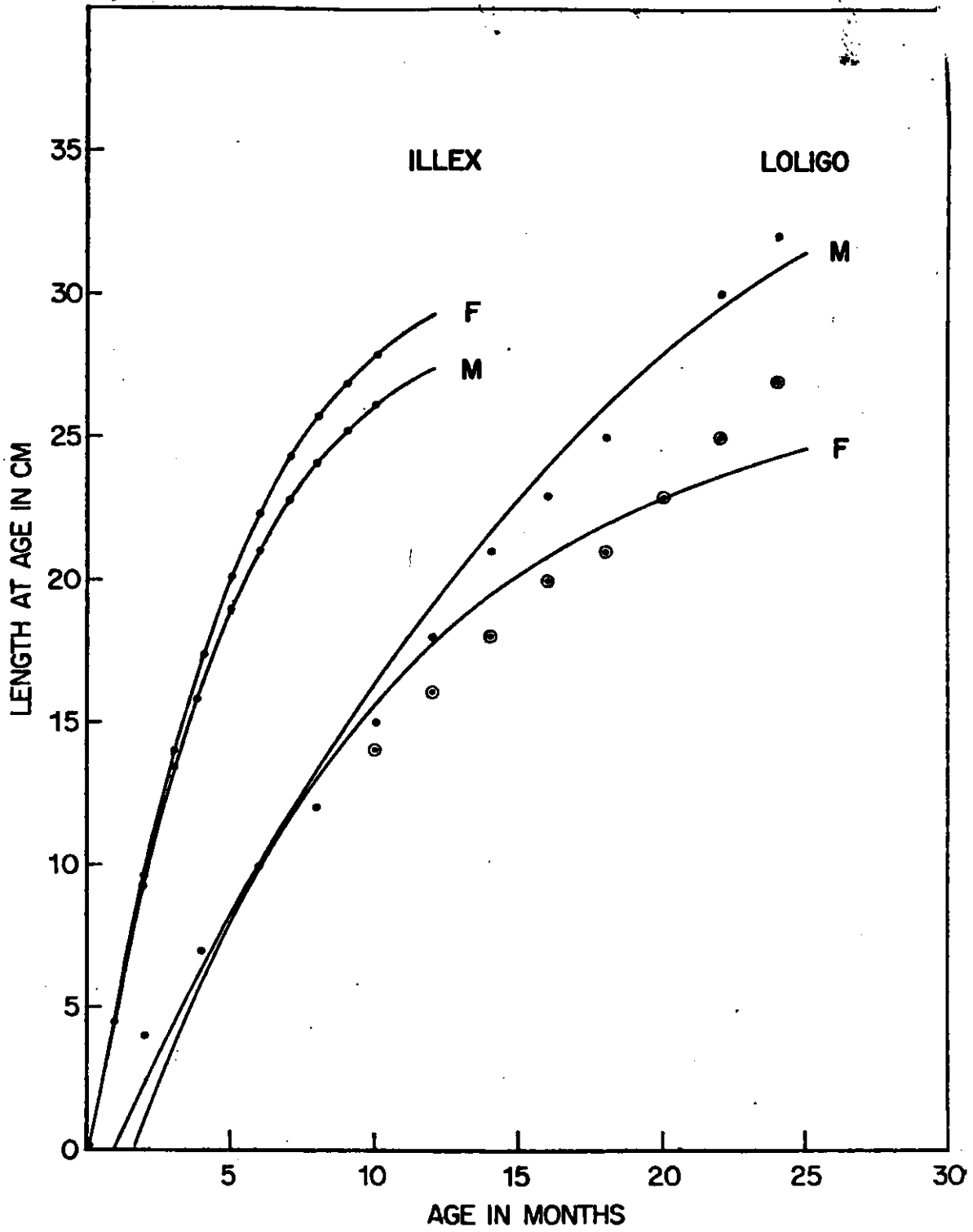


Fig. 1. Growth of *Loligo* (data from Summers, 1971) and *Illex* (from Squires, 1967).

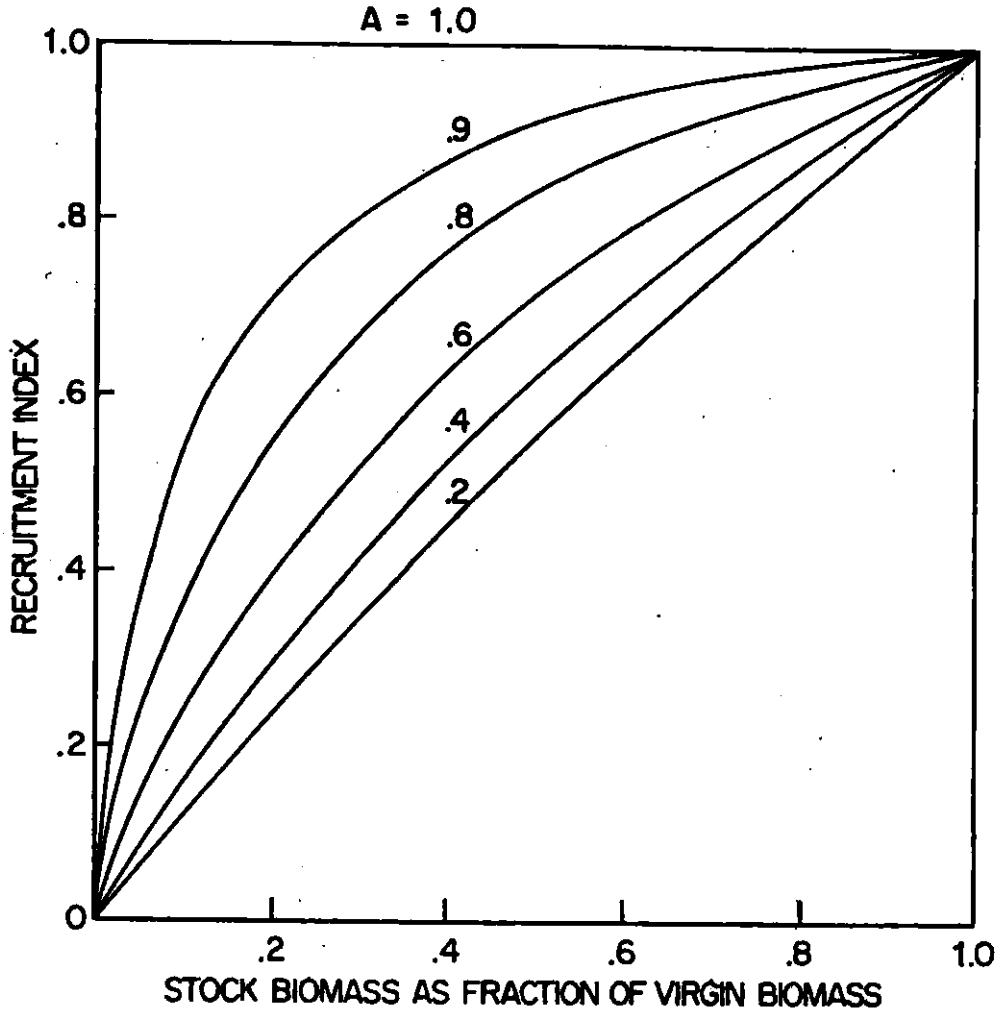


Fig. 2. Relationship of recruitment (R) to stock biomass (B) of the form $R = \frac{B}{1+A(B-1)}$ for different values of A.

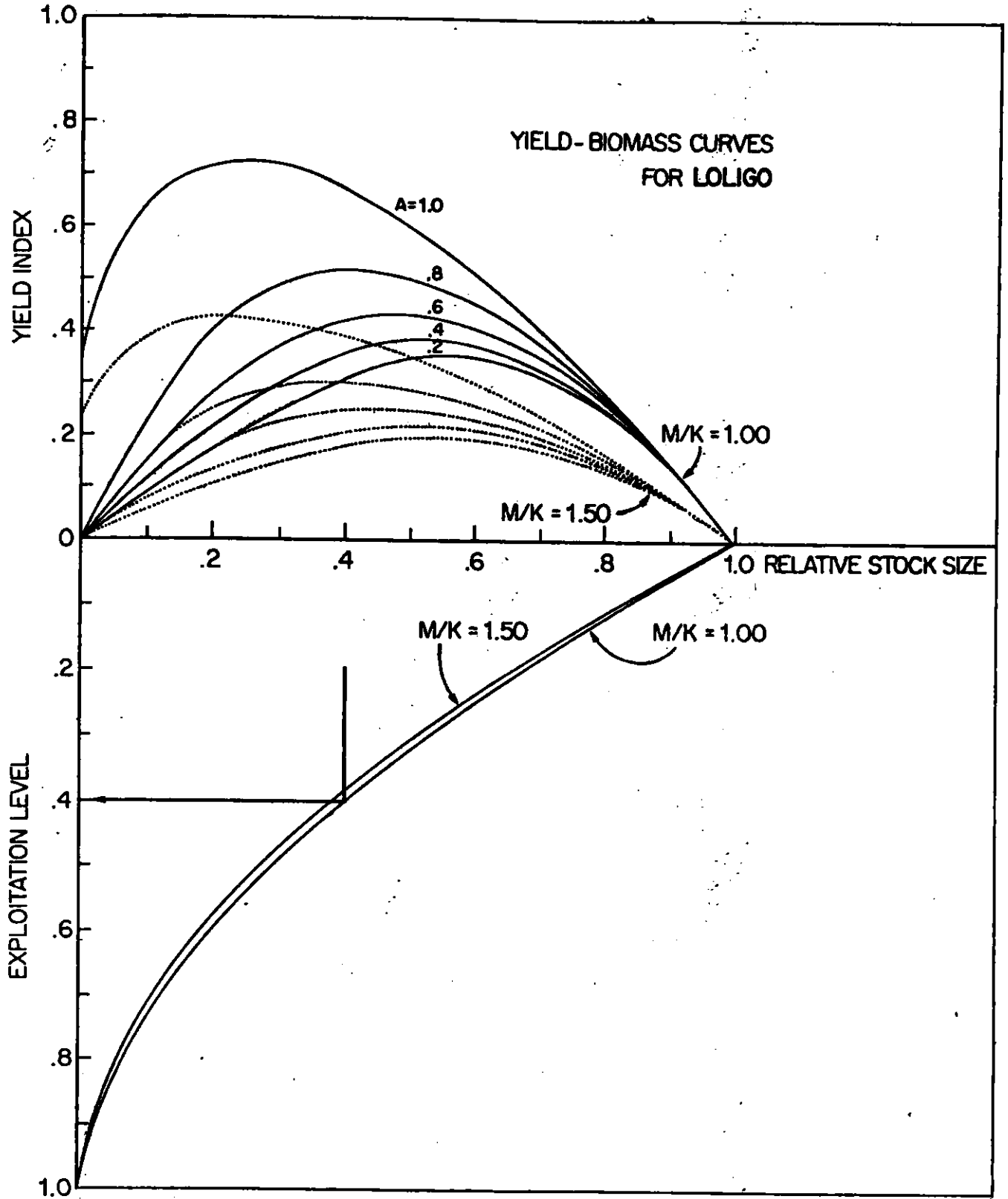


Fig. 3. Yield-biomass and exploitation curves for *Loligo*.

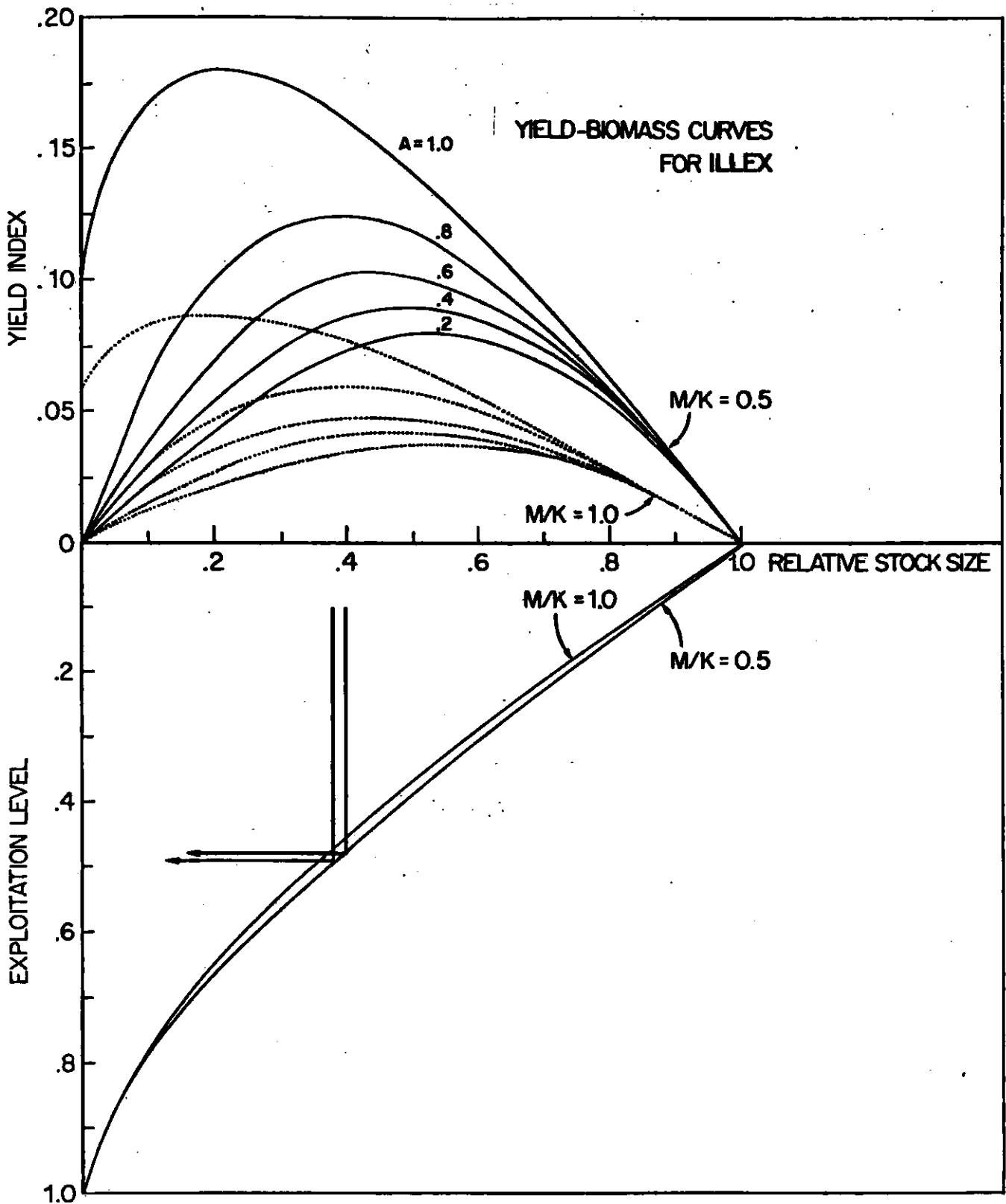


Fig. 4. Yield-biomass and exploitation curves for *Illex*.

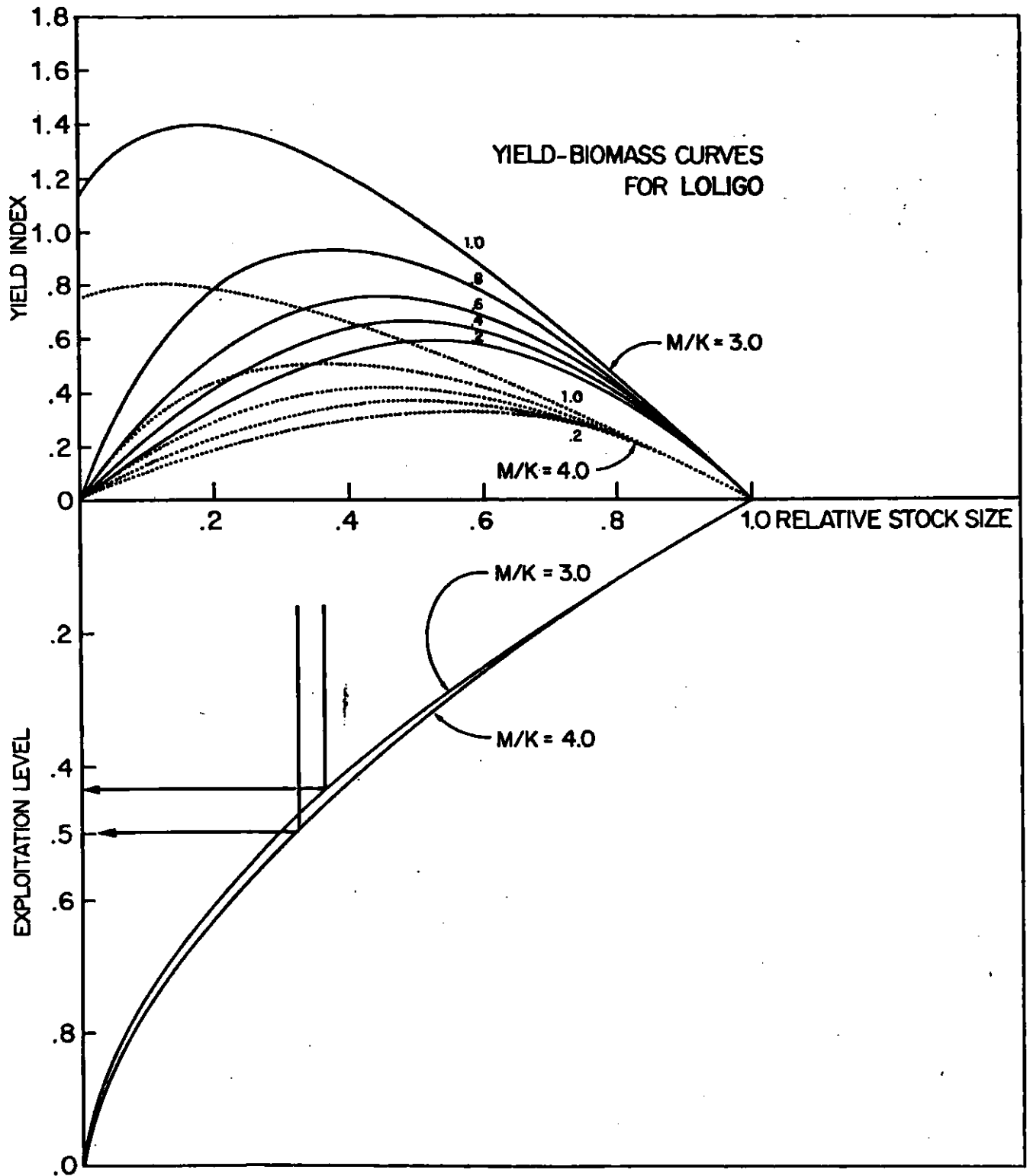


Fig. 5. Examples of extreme yield-biomass and exploitation curves for *Loligo*.

