

Chapter 12

Impact of fishing on life histories

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Abstract: Artificial selection pressures imposed by fisheries can impact population structure in the short term and drive evolution of life-history traits in the long term. In exploited squid populations the short life span and lack of mating between generations is likely to intensify the effects of artificial selection. Selection on size, age and maturity status can occur through the physical characteristics of the gear or by non-random fishing effects. In squids of the genus *Illex* there is considerable variation in overall growth rate, the size at which sexual maturation commences, the rate at which maturation proceeds and the size at which full maturation is reached. Although there are no data on heritability of fitness traits in squid it is unlikely that additive genetic variance in growth rate would be less than in fish, where life-history parameters have been shown to be susceptible to selective breeding. Model studies indicate that there is a large potential for selective effects to occur in exploited squid populations. The fishery can greatly influence the population structure and reproductive potential of a particular cohort. Analyses of life-history functions can be used to investigate how changes in mortality rate can affect the age of maturation. The temporally restricted effects of exploitation within a season may have important consequences for the evolutionary responses of a species. Suitable long-term data sets for squid fisheries should be examined for evidence of the selective effects of fishing on life-history traits.

1 Introduction

Intensive exploitation by commercial fisheries of cephalopods such as *Illex* can be expected to impact on the structure of populations in the short term and on life-history traits on an evolutionary time-scale. All fisheries are, to a greater or lesser extent, selective in terms of the size, age, sexual maturity and, in some instances, the sex of the catch (Law 1991). In the short term, selectivity at high rates of exploitation can radically alter the age/size structure and breeding structure of exploited populations. In the long term, mortality caused by harvesting may act as an artificial selection process, in the evolutionary sense, and drive evolution of life-history traits of the exploited stocks in unintended, and possibly undesirable, directions.

If a fishery catches more fast-growing individuals than slow growers, because they are the first to become large enough to be caught, then a disproportionate number of slow growers will survive to breed. Over a number of generations this will lead to a gradual change in the heritable component of growth and a consequent reduction in the average growth rate. Similarly if some individuals in an exploited population reach sexual maturity before they become large enough to be caught they will have a higher probability of contributing to the gene pool of the next generation. Over time this would lead to a reduction of the average size at which sexual maturity is attained. Given the correlation between body size and fecundity in cephalopods this will have the inevitable consequence of a reduction in fecundity at maturity.

The various *Illex* species have a short generation time of one year. Each squid matures once and dies after a single spawning and consequently there is little or no temporal overlap between cohorts. It is therefore unlikely that any significant number of matings takes place between squid generations from different years. The short life span and lack of mating between generations in *Illex* is likely to speed up the effects of artificial selection in heavily exploited populations (Hatanaka *et al.* 1993). Because each squid breeds once and dies, the problems of studying changes in growth rate and size at maturity over a number of generations should be relatively simple as there are no overlapping generations in the populations and this simplifies analysis of the data.

The greatest problem in studying the selective effects of fishing at the genetic level lies in distinguishing the compensatory response of the plastic phenotype from genetic change. Because increased mortality is generally compensated by increased growth rate and survival as a result of density-dependent effects, genetic effects may be masked. There are, therefore, few convincing data for intra-population selection in the fisheries literature, although there are strong theoretical grounds for concluding that the process is important (Kirpichnikov 1981).

2 Mechanisms of selection

Selection by a fishery occurs in two ways. Firstly, there can be differential escape of the squid once they have come into contact with the fishing gear. Secondly, there are selective effects which are related to the life cycle and behaviour of the squid and the fishing patterns adopted by the fishing fleet.

Throughout the Atlantic region the major fisheries for the various *Illex* species are pursued by trawlers, using bottom or pelagic trawls, or by jiggers which attract the squid towards the vessel with incandescent fishing lights and catch them by jigs on lines operated by automatic machines.

For trawl nets it can be assumed that the size composition of the population entering the net is the same as in the close vicinity of the gear. Selection then occurs as the meshes of the net retain larger squid and allow the smaller specimens to escape. Different codend mesh sizes have characteristic selection curves depending on species but for practical purposes a net can be defined in terms of a single mean selection length (Gulland 1983). This is the mean length at which squid start to be retained by the net. The principles are the same for drift nets, which have been found to selectively increase fishing mortality of large, sexually mature, females in the North Pacific fishery for *Ommastrephes bartrami* (Murata 1990).

Jigs consist of a plastic body with two rows of barbless hooks at the lower end. Jig bodies used for catching *Illex* range in length from 48 to 72 mm and are made of hard or soft plastic of various colours or of clear plastic. Some are luminescent. They are classified according to the length of the hooks. The smaller, 11-mm variety, has two rings of 16 hooks each. The larger, 16-mm variety has two rings of 14 hooks each. The size of the jig depends on the size of the targeted species (Long and Rathjen 1980). The jig size used by a fishery at any time is chosen to optimize the catch rate by selecting the most abundant size range of squid in the population. The size of jig thus exerts a selective effect on the mean size of the catch and so age, sex and maturity.

Where the physical characteristics of the gear are not responsible for selectivity then non-random fishing activities on squid concentrations and non-random distributions of squid of different size, age and maturity will ensure selection. In the case of squid being exploited on the feeding grounds prior to migration to the spawning ground, selection will occur in the case where commencement of the spawning migration is related to maturity. Squid which mature early in the season and migrate out of the fishery sooner would have a higher probability of surviving to spawn than those that mature late. It is of fundamental importance in analysing the potential for fisheries selection on squid stocks to have good information on the migration and spawning patterns of the species concerned.

It should be emphasized that, although in fisheries science selectivity by the fishery focuses on the phenotype preferentially removed by the gear, in considering the evolutionary consequences of artificial selection by a fishery, the genotype that escapes the gear and survives to reproduce is the focus. Furthermore, squid escaping the fishery may interbreed at the spawning grounds with others that have migrated there from areas outside the fishery and so have not been subject to its selection pressures. The effects of migrations in diluting the effects of selection are therefore potentially important.

The extent to which fisheries selection will bring about genetic change in populations will depend on the intensity of selection, the heritability of the traits being selected and the association between the various traits under selection.

3 Evolution of life history

In order to understand the way in which artificial selection, imposed by a fishery, may affect squid life histories, it is worth considering the mechanisms by which natural selection causes life histories to evolve.

An organism's life history is defined by its rate of growth, an age-specific rate of reproduction and an age-specific probability of death (Law 1979). Throughout the life of species with indeterminate growth there is a shifting allocation of energy and nutrient resources between somatic growth, reproduction and maintenance. The lifetime form of this shifting pattern is the result of natural selection which, in most circumstances, will tend to drive the allocation pattern, within certain constraints, towards an optimum solution that maximizes the lifetime rate of reproduction, and hence Darwinian fitness, by trading off the risk of mortality associated with reproduction, against fecundity. Populations consist of groups of individuals differing genetically from each other in their rate of reproduction and risk of death. The assemblage of genotypes in an unexploited population reflects the natural selective forces which have been brought to bear over time, modified by the effects of migration, mutations and random genetic drift.

Fecundity and the number of times an organism reproduces in its lifetime are thus determined by natural selection and they are primarily determined by the relative survival of adults and offspring. Where survival of offspring is relatively high, natural selection will favour high fecundity whereas poor survival of offspring will favour more restrained egg production. Where adult mortality exceeds juvenile mortality the organism should reproduce only once in a lifetime (semelparity). Where juvenile mortality exceeds adult mortality the organism should reproduce more than once in a lifetime (iteroparity) (Stearns 1976).

Most cephalopods, and especially the squids including *Illex*, are semelparous, the known exceptions being the nautiloids (Ward 1987) and some octopodids (Mangold 1983, Rodaniche 1984). The case of multiple spawning in the ommastrephid squid *Stenoteuthis oualaniensis* from the tropical Pacific (Harman *et al.* 1989) is apparently an example of semelparity in which egg release is intermittent. This may be widespread in species including *Illex* spp. (Laptikhovskiy and Nigmatullin 1993). It would appear that in the semelparous squids, including *Illex*, high growth rates result in reduced juvenile mortality because of the reduced time that they remain small and vulnerable to predation (Calow 1987). However, we shall see that although *Illex* has become constrained in the number of reproductive events per lifetime, within species there is variation in the allocation of resources to somatic and reproductive growth and the size at which individuals attain maturity.

4 Variability in life-cycle parameters in *Illex*

Following a period of heavy exploitation, a population of a species such as *Illex* will start to reflect the artificial selection pressures brought to bear since the start of culling and this will be expressed in the genotype. The phenotype response may appear as a shift in the lifetime allocation of resources towards a new optimum. The intensity of the response will be modified by the intensity of selection pressure, the degree of heritable variability in the traits under selection, and population genetic parameters such as migration patterns.

There is considerable phenotypic variability in a number of life-cycle parameters in *Illex* (Rodhouse and Hatfield 1990, 1992, Hatfield *et al.* 1992, Coelho and O'Dor 1993). *Illex argentinus* grows to full sexual maturity in the space of one year. Early growth is entirely somatic, followed by a shift towards reproductive growth which is gradual at first, with an increasing allocation of resources to gonad production as sexual maturity approaches. Overall growth rate, the size at which sexual maturation commences, the rate at which maturation proceeds and the size at which full sexual maturity is reached all show a high level of variability. There is thus potentially a considerable amount of raw material for artificial selection and exploitation-driven evolution in the squids of this genus.

The response to artificial selection imposed by exploitation, measured as the selection differential, will depend on the intensity of selection, the heritability of the traits selected (the extent of additive genetic variation) and the presence of non-additive variation.

There is no information at the present on heritability of fitness traits in squid or other cephalopod species but with recent advances in the husbandry of cephalopods (Hanlon 1987, Forsythe *et al.* 1991) the data needed to assess heritability of growth and other traits are likely to become available in the future. There is, however, a considerable amount of information in the literature on heritability of fitness traits in fishes bred in captivity (Gjedrem 1983) which shows that virtually all life-history parameters are susceptible to selective breeding. There is no reason to suppose that additive genetic variance of growth parameters in the squids is any less than in fishes.

Equally there are no data for cephalopods on the extent of non-additive variability in fitness traits such as the correlation of growth rate or fecundity with heterozygosity. In bivalve molluscs individual heterozygosity has been shown to be correlated with rate of growth (Zouros *et al.* 1980, Koehn and Gaffney 1984), fecundity (Rodhouse *et al.* 1986) and aspects of the physiological energetics of growth (Koehn and Shumway 1982, Garton *et al.* 1984, Rodhouse and Gaffney 1984). Correlation between individual heterozygosity and a variety of growth-rate parameters has also been observed in a number of other organisms including plants, pigs, sheep, humans, salamanders and polychaetes. This suggests that there is probably a universal relationship which at least partly arises from the reduced cost of enzyme synthesis in multiple locus heterozygotes (Koehn 1991). Non-additive genetic variance is not subject to the same selection processes as additive variance so the effects of selection on life-cycle parameters are modified by its presence.

5 Evidence for artificial selection effects on life histories

Measuring selection and response to selection in exploited populations of aquatic organisms is a difficult task (Nelson and Soulé 1987). Detection of selection is confounded by the natural, environmentally driven variability in life-history traits in wild populations and also by the effect of exploitation itself which, in reducing population density, is liable to influence those life-history traits which are density dependent. For instance, culling may increase overall growth rate by reducing intra-specific competition for the food resource. The compensatory response of a plastic phenotype may thus mask any underlying response of the genotype to selection. There are, however, three studies, one in the laboratory and two based on field data, that demonstrate selection effects.

In the laboratory, selective culling regimes on populations consisting of standard mixtures of clones of the water-flea, *Daphnia magna*, have produced genetic differences in life histories after 150 days (Edley and Law 1988). Clones selected by culling large-sized individuals grew more slowly through the small size classes, delaying the age at which they became vulnerable to harvesting. Also reproduction was redistributed to size classes that were not culled so that after experimentally culling small sizes, the clones that predominated were those that made their major reproductive contribution at a larger size. After culling larger sizes, clones in which there was a substantial reproductive contribution at a smaller size predominated. Culling could thus cause evolution of growth rates and the age/size-dependent distribution of reproduction in a population and as a consequence a potential reduction in yield.

A systematic study of genetic selection by fisheries for the five salmon species of western Canada was carried out by Ricker (1981). This study is particularly relevant in the context of fisheries selection in *Illex* because the salmon species were all semelparous. The salmon are caught by gill nets or by trolling. Gear selectivity is a feature of both methods of capture. Gill nets select by virtue of their mesh size whilst trolls select by exploiting for a longer period those fish that reach the legal or catchable size first. In all five species of salmon the size of fish caught has decreased and this reflects a size decrease within the different populations. The greatest decreases were observed in coho and pink salmon and these could be attributed almost entirely to a cumulative genetic effect caused by the selective removal of larger than average size fish.

A decline in growth rate and condition following exploitation by a gillnet fishery has also been reported for the iteroparous whitefish, *Coregonus clupeaformis* (Handford *et al.* 1977). This was suggested to be the result of selection for slower growing fish which mature later but at a smaller size.

Ricker (1981) pointed out that semelparity simplifies the problems of detecting changes in growth rate and age-at-maturity in exploited populations and that it is difficult to confirm genetic changes in populations of iteroparous species even though there may be shifts in catches towards smaller sizes and ages. Shifts in catches towards smaller size and age can result from the well-established phenomenon of "fishing up" (Baranov 1918 cited in Ryman and Utter 1987), in which older, larger classes are preferentially removed. There are a number of other studies of iteroparous species (Gwahaba 1973, Borisov 1978, Favro *et al.* 1979) that demonstrate possible selective effects of fishing but the evidence is circumstantial and the possibility cannot be discounted that the observed effects are due to the "fishing up" phenomenon.

Given the difficulties of detecting the effects of selection in natural populations of iteroparous fishes, the modelling approach provides alternative means of tackling the problem of identifying a response to selection. Law and Grey (1989) modelled the effects of selection on life-history traits in *Gadus morhua* and showed that evolution driven by harvesting selection will generally result in a decrease in yield.

6 Selection on non-additive genetic variance

The presence of non-additive genetic variance such as heterozygosity effects might act to reduce the impact of artificial selection on the evolution of life-cycle parameters. But fishing pressure may also have an effect on this aspect of non-additive variance as it will tend to reduce genetic diversity within populations and thus reduce overall levels of heterozygosity. Such an effect has been observed in the New Zealand orange roughy (*Hoplostethus atlanticus*) fishery where the virgin biomass was reduced by about 70 percent over six years of exploitation (Smith *et al.* 1991). This was accompanied by significant decreases in the number of heterozygous loci present in samples from each of three fishing grounds. In extreme cases this process could lead to rare alleles being driven to extinction or near extinction.

In the southwest Atlantic *I. argentinus* is characterized by low levels of genetic diversity reflected by low heterozygosities per locus. Within the species' geographical range there is marked population differentiation, indicated by significant differences in allele frequency among samples collected within a single fishing season (February-May) (Carvalho *et al.* 1992). Exploitation at high levels could potentially reduce genetic diversity in *Illex* populations in the southwest Atlantic. Although the species is fast-moving and widespread, localized diminution in numbers in relation to a specific spawning area could reduce subpopulations to levels at which they suffer so-called "population bottlenecks". This has occurred in exploited species elsewhere (Bonnell and Selander 1974) although in very different circumstances. Population bottlenecks reduce genetic diversity to the level present among the small numbers of survivors when severe over-exploitation occurs.

7 Evidence for change in population structure in exploited squid populations

There have been no systematic studies on the effects of fishery selection on the life-cycle parameters of squid populations. There are, however, some records of shifts in the structure of exploited squid populations that provide some circumstantial evidence that fishing pressure may be responsible for change in *Illex illecebrosus* and *Todarodes pacificus*.

7.1 *Illex illecebrosus*

In this species growth rates estimated from population data from the northwest Atlantic are variable (Squires 1957), as are growth and feeding rates in the laboratory (O'Dor 1983). Size distributions of natural populations vary markedly from year to year (Coelho 1986) and analysis of a 20-year data set collected over 200 of latitude off the east coast of North America suggested there was a mixing of cohorts generating complex population structure, which arose in part from an overall protracted spawning period (Coelho and O'Dor 1993). Several seasonal spawning groups could be identified from length frequency data and there was clear geographic variability in the fishery that was especially pronounced in the most northern area (Coelho *et al.* 1994).

The *I. illecebrosus* in the northern area, which were subjected to intensive fishing pressure, were characterized by a short peak of spawning in the south, during winter, and heavy feeding, during summer, in the north. This winter-spawning group had the shortest life span and the lowest degree of mixing between generations. These features, of what is apparently the least plastic part of the population, are likely to have enhanced the effects of artificial selection by fishing on the winter component. Following a period of high fishing pressure a decrease of the winter-spawning component, while other components became predominant in the catches, preceded a virtual collapse of the *I. illecebrosus* Canadian fishery (O'Dor and Coelho 1993).

There are strong links between the environment and variation in the squid-population dynamics which affect the fishery. Catch levels in the Newfoundland fishery were directly related to the abundance of the winter-spawning component in all areas. An analysis of relationships between catch and biological characteristics of the *I. illecebrosus* population during a period of heavy fishing (1979–1981) showed that surface temperature and month of the year explain significant proportions of the total variance in catch (Coelho and Rosenberg 1984). Sexual maturity in the population develops during the season so that as the animals grow and mature some are being fished while others may have left the area through emigration.

When maturity data are available, mean size at maturity can be calculated from the percentage of mature (stages 3 and 4) squid by fitting sigmoid curves and estimating the mantle length at 50 percent (ML50%) maturity on the sigmoid distributions (Coelho 1986). During the period of low exploitation (1967 to 1976) of *I. illecebrosus* inshore at Newfoundland, when catches varied between a minimum of 9 and a maximum of 11 000 metric tonnes, the ML50% varied between 225 and 235 mm. Conversely, during the period of high exploitation (1977 to 1981), with catches varying between 18 000 and 88 000 metric tonnes, the ML50% was greater (245–255 mm) but the population had variable proportions of larger immature squid. The time of migration was assessed from the departure dates available from the Newfoundland inshore waters. It is notable that during the early period of low exploitation, the spawning migration was earlier than in the later period. Departure and arrival dates seem to be related (Dupouy and Minet 1982), as do catch and departure dates, and Coelho (1986) has noted a positive correlation between years of high catches and years of late departure from inshore Newfoundland waters.

Variability in maturation of *I. illecebrosus* from different geographic areas and the presence of intermixed cohorts in a complex population structure, have been interpreted to be the consequence of limited tolerance to temperature extremes for spawning, and related dependence on oceanic current regimes for

transport of young and spawners. However, it is apparent from the available data (Coelho and O'Dor 1993) that considerable variation in maturation rate exists even when the population structure is least complex, as in the northern area of the distribution of *I. illecebrosus*. Investigation of the short- and long-term effects of fishing on the biological characteristics of *I. illecebrosus* seems feasible only in the northern part of its range because it is here that the fishery is most dependent on a single population component. This component has a short peak of winter spawning, so maturity and length data have more consistent modes throughout the range of distribution than the rest of the population (Coelho and O'Dor 1993).

The selective effect of fishing is assumed to have most impact on the proportion of the population with largest body size and advanced state of maturity. Over a number of years and at heavy fishing pressure, the squid will be smaller and have an overall decreased reproductive potential. Size-at-maturity, numbers of mature squid which survive and migration time must all be critical to the reproductive potential of an *I. illecebrosus* population. The possible effects of fishing on these features are worth special consideration, at least to the most prominent, winter component of the population (Coelho *et al.* 1994). Maturity of the population would have to be examined, as well as size, in any future study of the effects of fishery selection. The value of the data would depend on the consistency of the methods used to assess maturity, a suitably long period of sampling and sufficient coverage of the geographical area. These data are fundamental to understanding the population dynamics of species with long migratory routes, such as *I. illecebrosus*, and where there is a lack of precise age information.

7.2 *Todarodes pacificus*

The Japanese fishery for *Todarodes pacificus* changed from an artisanal to an industrial operation in the early 1960s. During this latter phase there has been a more or less steady increase in fishing effort and decline in catch rates (Murata 1990). Over the same period the start of the fishing season for the various stocks and peak catch rates have tended to become earlier in the year. Although not available in the English language, there are reports of changes in biological features and stock structure of *Todarodes pacificus* (Kasahara 1982; Sasaki 1987 cited in Takayanagi 1993).

A detailed study of changes in growth and maturity in relation to stock size has been carried out by Takayanagi (1993) on data collected in the Tsugaru Strait between 1965 and 1989. This time period was divided in two: 1965–1975 was considered as a time of high squid abundance, 1976–1989 was considered as a time of low abundance. The study was confined to males and in the latter period of low abundance the squid were shown to be smaller, at least in the early part of the season, and the proportion of mature males was higher.

8 Modelling the selective effects of fishing on the population dynamics of ommastrephid squids

The semelparous aspect of most ommastrephid squid discussed above means that harvesting has a direct impact on the spawning stock characteristics. The effects of the selection are not distributed over a range of year classes, which could buffer the selection effects of a given year. A range of models have been developed that include various aspects of squid population dynamics, but only very recently has there been any attempt to consider the evolutionary consequences of harvesting. The rate of any response to selection depends on a range of factors such as the selection differential, heritability of traits and degree of additive genetic variance. The immediate response of fishery managers to calls to consider evolutionary aspects will be to question whether the induced changes are likely to be important in assessing the sustainability of the fishery.

9 Squid population dynamics

To examine part of this question we need first to consider the potential selective effects within a squid fishery. The model analyses carried out by Murphy *et al.* (1994) on *I. argentinus* investigated the within season selective effects of fishing on the characteristics of the spawning stock. The semelparous life history allows such harvesting effects to be examined directly. The model the authors developed utilized current thinking on the migration of *I. argentinus*, assuming that it was connected to the maturation of adults on feeding grounds in shelf waters around the Falkland (Malvinas) Islands. Thus, it was assumed that the squid are exploited by the fishery on the feeding grounds and, on reaching maturity, migrate out of the area moving towards the spawning areas. The model considered a cohort that is fished for a seven-month season from the time it migrates into the feeding grounds at an early phase of the sexual maturation process. Following recruitment the squid grow and mature simultaneously and numbers are reduced by natural mortality, fishing mortality, and emigration from the feeding ground on attaining full sexual maturity. The maturation rate was described by a simple fitted function linking percentage maturity to the time of the season in the fishery data. These processes generate a size-selective effect within the fishery based on the rate of maturation. The effects of variation in the rate of maturity and the timing of harvesting were then examined.

The analyses of Murphy *et al.* (1994) indicate that data from the fishery support the general results produced by the model. In particular, the data on maturity stages of males and females and their ratios in the catches correspond to the earlier maturation of the males than the females with a simultaneous earlier migration by males. Data from outside the fishery indicate that there is a more widespread migration pattern in this species (Arkhipkin 1993). Changes in the maturation rate have a large effect on the population structure of the adult squid that survive the fishery and emigrate to become part of the spawning stock. This affects both the mean length and the variance in the length distribution of the spawning stock. Thus a larger number of much smaller squid survive with early maturation and migration, while fewer larger squid form the reproducing stock when maturation is delayed. The pattern of harvesting within a season can also have marked effects on the population structure of the spawning stock, with early season harvesting having a similar effect to early maturation. These changes also affect the yield from the fishery, with earlier maturation generally producing lower yield while earlier exploitation produces higher yield for the maturation times observed in the fishery. So the variation observed in the maturation rates and the harvesting

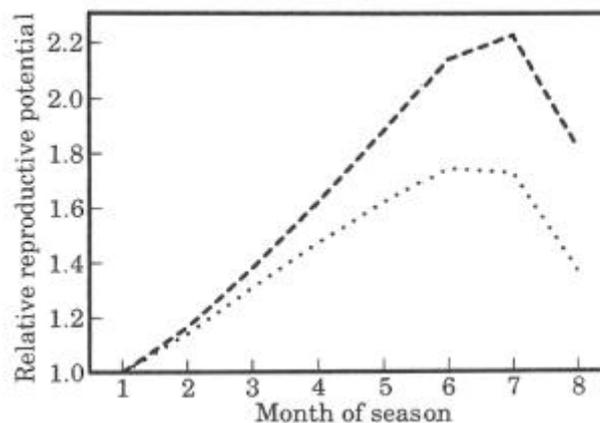


Figure 12.1. Changes in the relative reproductive potential of model *Illex* cohort with different months of 50% maturation; female (dotted line); male (broken line); see Murphy *et al.* (1994) for details.

pattern can generate significant effects on the characteristics of the spawning population. These effects result in large changes in the reproductive potential of the spawning stock. Empirical relationships for deriving the fecundity of *Illex* were utilized, with the model, to investigate these effects. Generally, later maturation results in greater reproductive potential, but this peaks with very late maturation (Fig. 12.1). Increased mortality late in the season generates smaller squid, reduces the overall reproductive potential of the population and will selectively favour those squid that matured earlier in the season. Clearly, the overall reproductive potential at the end of the season is a result of a trade-off of both growth and maturation functions against survival. The study did not consider variation in growth or make any links between growth and maturation rates. To consider the potential effects in the longer term of such selective effects we need to consider the life-history evolution.

10 The optimisation of life-history functions

We can get some idea of how the harvesting effects may influence the squid population by analysing the life-history functions of the squid. This has been done for *Illex* by Murphy and Rodhouse (*unpubl. data*), who examined the trade-off between the functions relating changes in fecundity and survival with time, and considered the long-term consequences of harvesting. Here we review some of the key aspects of their study. They derived an expression for fecundity (f_t) as a function of time (t):

$$f_t = \theta (\alpha + \beta t)^\varphi \quad (1)$$

where,

$$\theta = \mu\sigma\gamma^\eta \text{ and}$$

$$\varphi = \delta\eta,$$

α is the estimated mantle length at the start of the fishing season,

β is the rate of growth,

γ , μ and σ are constants, and

δ and η are, respectively, the allometric coefficients relating body and ovary mass to mantle length.

So for positive real values for all the parameters of equation 1, fecundity increases exponentially with time.

The survival function was also determined for the period of harvesting. Assuming natural and fishing mortalities occur at constant rates, the survival (8) at any time t is given by:

$$S_t = e^{-(F+M)t} \quad (2)$$

where,

M and F are respectively the instantaneous rates of natural and fishing mortality, and

Z is the total mortality rate ($Z = F+M$).

For semelparous species exploited over a major period of their life history, where any asymptotic growth effects occur late in the season, an appropriate measure of the fitness of any combination of life-history traits is the lifetime reproductive potential, R_o (Roff 1992). This is simply the product of the survival and fecundity functions, assuming that all animals in a cohort mature at the same time, t .

$$R_o = f_t S_t \quad (3)$$

Using equations 1 and 2 this gives:

$$Ro = e^{-Zt} [\theta (\alpha + \beta t)^\varphi] \quad (4)$$

This function can be optimized by calculating the rate of change of the lifetime reproductive potential to obtain the roots where

$$dRo/dt = 0$$

The only root we are interested in is where

$$\beta\varphi - Z(\alpha + \beta t) = 0 \quad \text{or}$$

$$t_{opt} = \beta\varphi - \alpha Z / \beta Z \quad (5)$$

The fitness function, **Ro**, therefore shows a single peak at age t_{opt} . Examination of this equation (5) shows that an increased total mortality rate (**Z**) during the fishing season will result in an earlier optimum time of maturation. A larger size at first recruitment (α) will also result in an earlier optimum time of maturation. Thus, the selection would also favour a more rapid growth rate before the fishery opens. The effect of changing the growth rate (β) within the season is dependent on the relative magnitudes of the parameters. Figure 12.2 shows the change in form of the reproductive potential-maturation time relationship with changing total mortality rate. The optimum maturation age decreases with increased mortality rate, but the reproductive potential at this optimum is also reduced.

The above analysis assumed that the growth was adequately represented by the linear relationship derived by Rodhouse and Hatfield (1990) based on data from the fishery. It is likely that later in the season there is some reduction in growth rate. Such a reduction would lead to the lifetime reproductive potential showing an earlier peak than that shown in Fig. 12.2 so the maturation optima would also be earlier.

This simple analysis illustrates the way in which harvesting can change the optimum time for maturation. In reality the harvesting is not carried out at a constant rate (Murphy *et al.* 1994). The fishing effort is concentrated into a restricted period and most of the catches are obtained during that period. Murphy and Rodhouse (*unpubl. data*) have examined the consequences of such temporally restricted harvesting by including a time-varying function for fishing mortality. The form of the resultant curve for the lifetime reproductive potential is shown in Fig. 12.2. There are a number of important effects. The curve now shows two optima – one early and one late. The reproductive potential of the early peak is greater than for the later. By numerical analysis of this function it can be shown that the two optima are separated by a critical maturation time below which the evolutionary pressure is towards the earlier optimum, while above it the selection is towards later maturation. The potential rate of evolution is much greater towards the early optimum than to the later. The analysis raises a number of important questions. The more obvious ones relate to the growth function for the squid and its form late in the season. Obtaining estimates on the magnitude of the additive genetic variance is problematic. The model results indicate that in the medium term the population variance may be maintained at a high level in the face of selection because of the occurrence of two optima. Further complex issues are raised relating to the degree to which changes in growth rate prior to the start of fishing occur and change the form of the lifetime reproductive potential function. The ability of an organism to be able to adapt in the way suggested by the analysis will depend on a range of other factors such as matching the timing of spawning to localized production peaks and particular oceanographic regimes. The possible density-dependent effects of changes in growth and survival rates due at reduced population levels will affect the rate of genetic responses. One intriguing aspect of the analysis is the

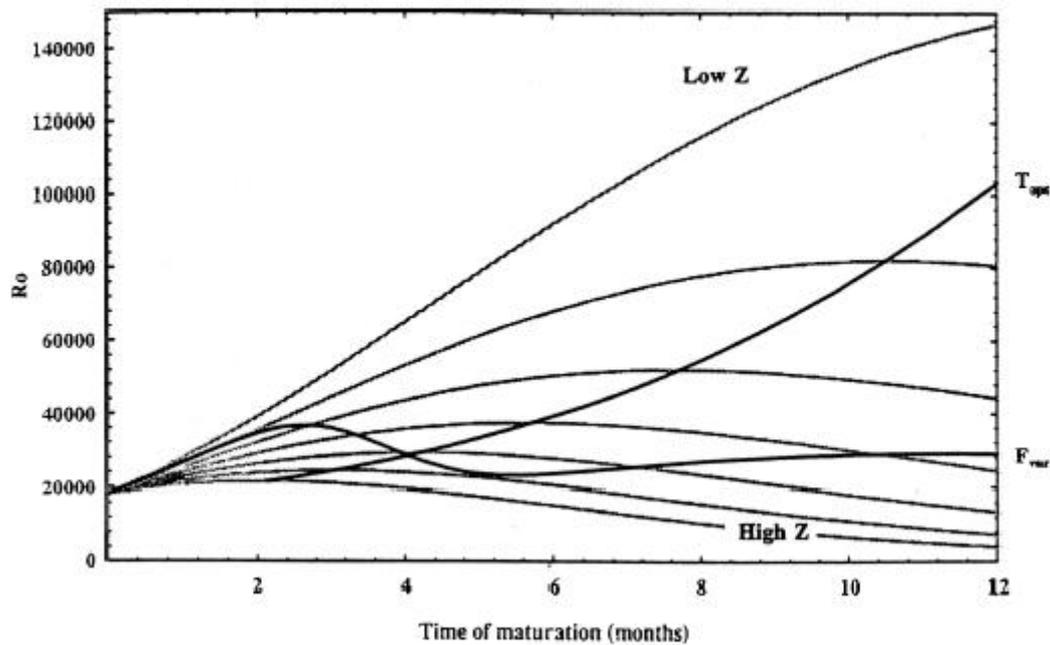


Figure 11.2. Curves showing the changing form of the lifetime reproductive potential function for changing values of constant total mortality (Z) (grey lines); the position of the optimum maturation time is shown by the black line marked T_{opt} . The form the lifetime reproductive potential function with fishing mortality varying with time is shown by the black line marked F_{var}

indication that separation of groups of squid may occur relatively rapidly because of the timing of peak mortalities. Thus, the population may be responding very rapidly to changes in the timing of mortalities. The occurrence of more than one brood per year in some species of squid may therefore be a natural consequence of the relatively rapid evolution in this system. Such effects may occur in unexploited populations where the temporally restricted mortalities are due to predation. The assessment of the rate at which such evolution may occur in exploited populations requires a much greater understanding of the genetic effects of selection and the level of heritability of life-history traits and external constraints on the life-history functions. The analyses carried out so far, however, do indicate that such evolutionary effects are likely to occur in squid fisheries and they are likely to be rapid enough and of such significance as to alter fundamentally the basis on which management assumptions are based.

11 Glossary

Additive genetic variance: the additive effect of alleles within and among loci which gives rise to the resemblance between parents and their offspring

Fitness: the average contribution of one allele or genotype to the next generation or to succeeding generations, compared with that of other alleles or genotypes

- Heritability: the proportion of the variance among individuals in a trait that is attributable to differences in genotype
- Intensity of selection: the selection differential divided by the phenotypic variance of the stock in respect to the character selected
- Response to selection: the difference in size between the unselected stock and the progeny of the selected parents
- Selection: non-random differential survival or reproduction of classes of phenotypically different entities
- Selection differential: the difference between the average size of parents and that of the stock from which they were selected

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