Chapter 11

Squid life-history strategies

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Abstract: This chapter briefly examines and contrasts current views of the links between life-history strategies and recruitment processes in fish with the pattern emerging for squid. The general perspective is that the roles of space and time are reversed in the two groups. That this is particularly true of the wide-ranging commercial ommastrephids is emphasized by a comparison with the less extreme strategies of loliginids, which are more localized, not fully semelparous, and probably longer lived. Fish stocks store genetic diversity and stabilize recruitment through numerous co-existing year classes that have survived under a wide range of potentially limiting conditions as larvae. Annual squid stocks can only achieve such diversity and stabilization by having microcohorts spawned throughout the year and being dispersed widely in space to find microhabitats with equivalent variability. The population dynamics and the tactics used appear quite complex, possibly including kinship, school cohesion and cannibalism.

1 Introduction

In their review Fogarty *et al.* (1991) concluded that "Recruitment variability is inextricably linked with the life-history strategy of many exploited marine fish and invertebrate populations." In a subsequent exchange, Mullen (1992) argued that "forecasting recruitment is not essential for management", and Fogarty (1992) concurred that the storage mechanisms (Chesson 1984) provided by delayed maturation and iteroparity did ensure population stability of most commercial fishes, so long as a "robust age structure" was maintained. Multiple year classes provide a reserve of both reproductive potential and genetic variability. Risk-spreading strategies like this evolve because they reduce the chances of population collapse and extinction, which equates in the long term to increased geometric mean fitness (Ward and Dixon 1984). But what about squids; as annuals, they are the marine equivalent of weeds. Risk-spreading can occur in several dimensions including time, space and phenotype. Survival in fluctuating environments requires the production of genetically and phenotypically diverse offspring, which appears to be the best short-term rationale for sexual reproduction (Maynard Smith 1979), the single most important generator of diversity. With their nearly semelparous reproductive patterns, do squid compensate for the lack of temporal risk-spreading by increasing spatial and genetic diversity? Can recruitment variability be reduced or predicted through a better understanding of the risk-spreading strategies of squids? "The role of environmental variability in the maintenance of genetic diversity (Chesson 1985) and the possible effects of harvesting on the genetic structure of exploited populations must be understood to assess fully the implications of different harvesting strategies" (Fogarty 1992). Do squid compensate for the lack of a robust age structure, and if so, what can we learn from the contrasts between squid life-history strategies and those of their more commercially valuable competitors?

In general, marine life-history strategies flood the environment with many orders of magnitude more small larvae than could ever be supported as adults, such that recruitment represents a minute fraction of production. Hjort (1914) hypothesized that these enormous losses reflected either (1) mismatches between the time of larval occurrence and temporally patchy food production, leading to starvation (match/mismatch, Cushing 1975) or (2) removal from retention areas by spatially variable currents (member/vagrant; Sinclair 1988). Although both proposed mechanisms no doubt playa role, the latter hypothesis is particularly attractive because it also accounts for the development of distinct populations that form the basis of fisheries and are the units of management. The genetic differentiation between populations indicates some degree of reproductive isolation, but there are really no good quantitative data for evaluating recruitment dynamics. If a population is large, gene flow from adjacent populations may be low, based simply on probability, but if populations are severely reduced, chance matings between populations could contribute dramatically to recruitment.

Given the large geographic scale of the physical systems in which ommastrephid squids move and the migrations of which they are capable, we must consider carefully what a population is. Mayr (1942) defines biological species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups". The implication is that absolute barriers to gene flow define species, while gene flow between populations is merely restricted. For fishes these barriers are primarily

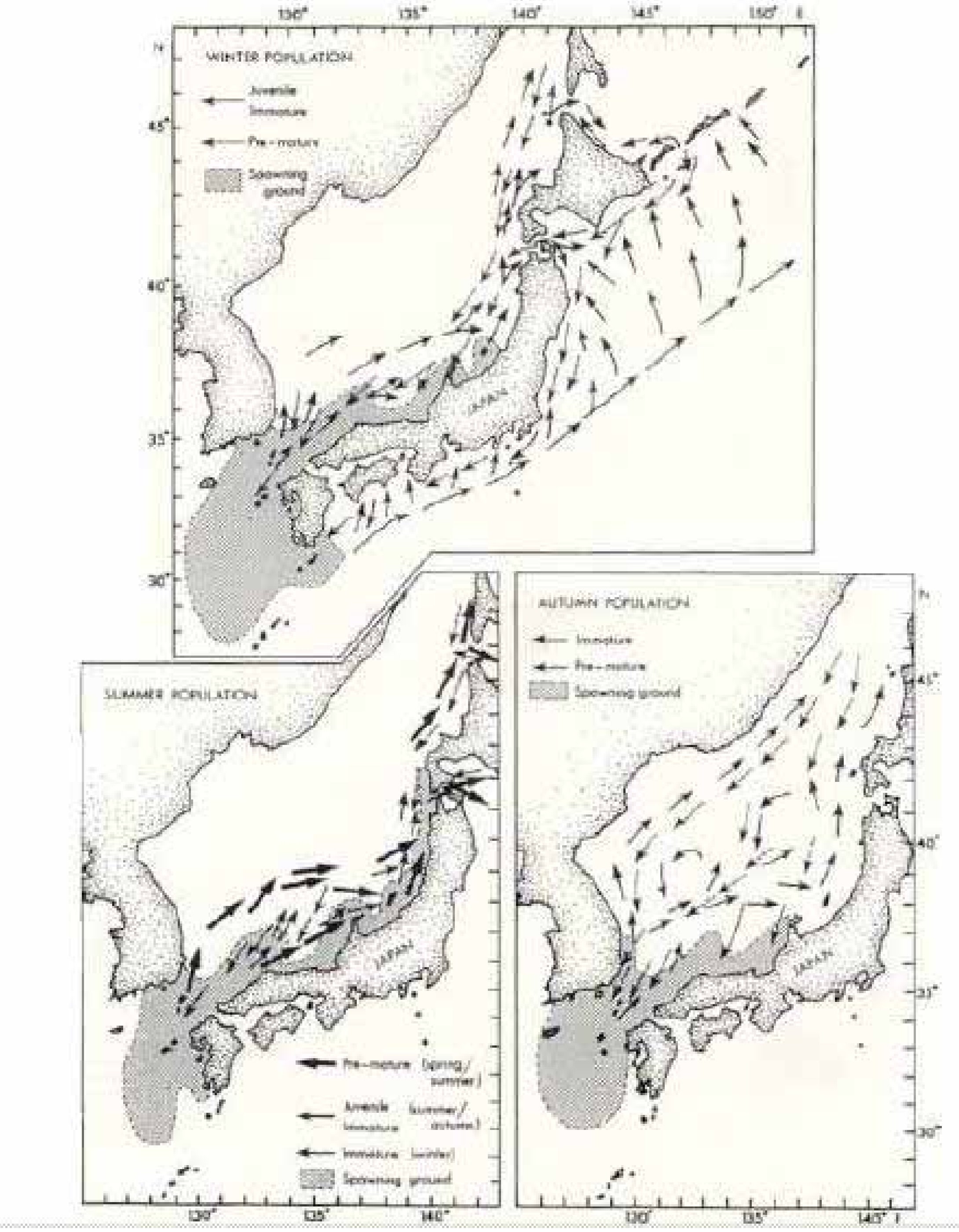

Figure 11.1. Spawning areas (shaded) and migration routes of the three populations of *Todarodes pacificus* in the waters around Japan based on extensive tag-recapture studies (Hatanaka *et al.* 1985 with permission NAFO)

spatial and based largely on the stability of oceanographic structures that provide suitable spawning grounds (Sinclair 1988). Some squids seem to use such large oceanographic features as spawning grounds (e.g. western boundary currents) that populations must subdivide this resource on a temporal basis, producing seasonal spawning groups (Fig. 11.1, Hatanaka *et al.* 1985). There is as yet no direct evidence for genetic isolation between these temporal "populations", but fisheries for these spawning groups appear to collapse and recover independently (Ogawa and Sasaki 1988, Nakata 1993). The limited evidence for high genetic variability between squid collected in the same place at different times (*see Chapter 10*) may reflect reproductive isolation of schools. So far, however, it fails to distinguish between behavioural and temporal isolation.

The typical life cycle of a modern coleoid cephalopod is short by most standards (Calow 1987, Heller 1990). One to two years is usual, but life spans as short as six months in small tropical squids (Jackson 1990) contrast with estimates of up to five years in high latitudes (Jarre *et al.* 1991). The typical female reproductive pattern for squids appears to be production of several batches of eggs late in life over a spawning period ranging from days to months (Harman *et al.* 1989). Males mature earlier and may live longer; anomalously large male loliginids appear to spawn in their second year, although there is no direct evidence that they are multi-year spawners (Mangold 1987). This lack of evidence that spawning ever recurs in a second year is often described using the term "semelparity" (O'Dor and Webber 1986, Calow 1987) and contrasted with almost universal iteroparity among fish that compete with squids. Although the big-bang mass spawnings and mass mortalities classically associated with squid (Lane 1957, Fields 1965) are not universal, and the term semelparous is not fully appropriate (Kirkendall and Stenseth 1985), the coleoid pattern is quite distinct from that of fishes and of the only surviving primitive ectocochleate cephalopod, *Nautilus*, which requires several years to mature and then spawns annually for a decade or more (Landman and Cochran 1987).

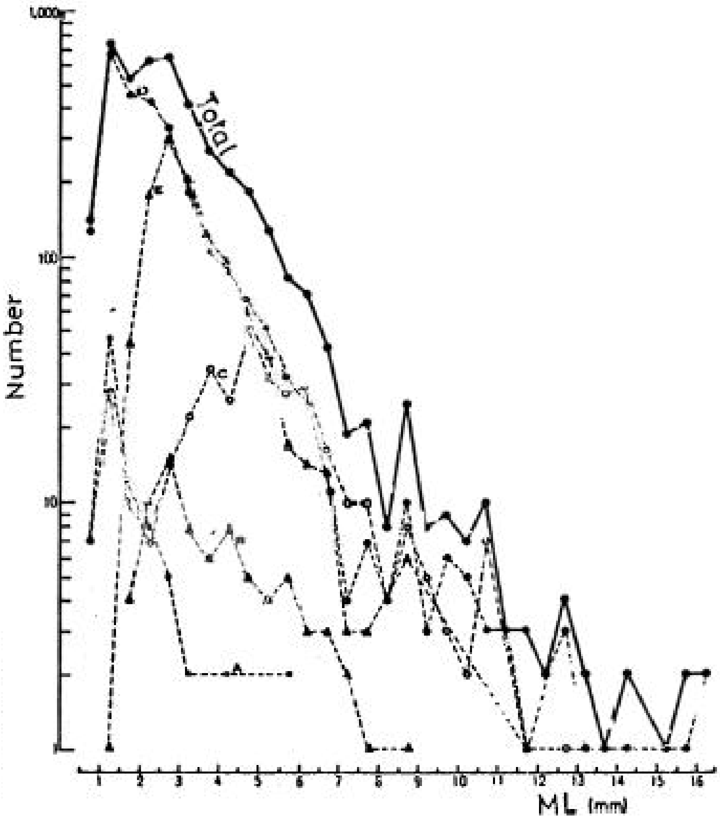

Figure 11.2. Paralarval abundance by mantle length class for *Todarodes pacificus* in February-March in the East China Sea; total values are summed from various gear types (A-E). (From Okutani & Watanabe 1983)

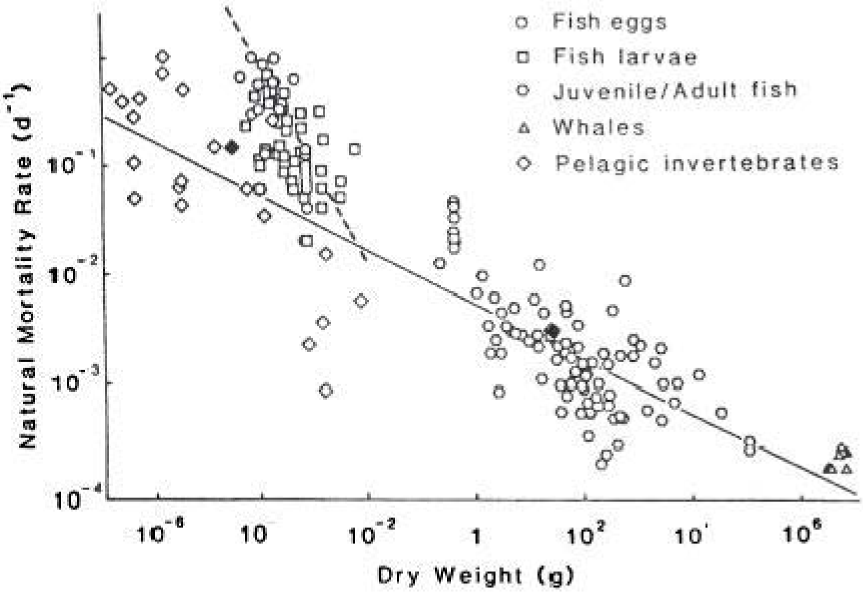

Figure 11.3. Instantaneous daily natural mortality rates vs. dry weights of marine organisms (McGurk 1986) with the added filled diamond for paralarval *Todarodes pacificus* from Fig. 11.2; the adult *Illex illecebrosus* value from the original is also filled solid. Solid line is the Peterson & Wroblewski (1984) model ($M = O.OO256W^{-O.25}$); dashed line is the much steeper regression ($M = 0.00022W^{-O.85}$) for fish eggs and larvae.

The contrast in life cycles and, therefore, life-history strategies, between squids and both their ancestors and major competitors, is among the most interesting features of the group (O'Dor and Webber 1986). It raises questions about the role of squid in the marine ecosystem, their recruitment processes and appropriate management strategies. Why are these large, mobile, complex, learning organisms unable to survive for a second spawning season? Is there some constraint that prevents them from spreading their reproductive effort over time to stabilize their recruitment? In other groups, high standing biomass in multiple cohorts serves as a reserve of reproductive potential (Fogarty *et al.* 1991); what is the alternate strategy for squids?

A recent review of mammals found that live-fast, die-young life histories were correlated with high levels of natural mortality and suggested that evolution of such traits could be explained by age-specific cost/benefit relationships (Promislow and Harvey 1990). Does this hold for squids as well? They certainly have the high metabolic/growth rates and the small numerous offspring associated with this strategy (Calow 1987). Calow has argued against the concept of programmed-senescence because no selective advantage was obvious, but perhaps such age-specific cost/benefits provide a rationale. Jackson (1994) pointed out that the view that young squid grow rapidly to "speed them through" a vulnerable juvenile period is not really supported by statolith ring counts which show that squids spend a much higher proportion of their life histories as juveniles than most organisms.

What little we know about juvenile mortality in squids, suggests that while they are certainly at much higher risk than mammals, they are about average for marine plankton and much less vulnerable than fish. Figure 11.2 summarizes paralarval abundance for the winter population of *Todarodes pacificus* (Okutani and Watanabe 1983), which was used to estimate a daily mortality rate ofo.23d-l for squid from 1.5 to 7.5 mm ML. Figure 11.3 shows that this value and one other for *Illex illecebrosus* fall quite close to a widely used relationship for weight-dependent mortality in marine species. Since it is clear that the *T. pacificus* paralarvae are being rapidly removed from the East China Sea by the Kuroshio Current, even this mortality is probably an overestimate because it does not distinguish mortality from emigration or dispersal.

McGurk (1986) argued that the greatly elevated mortalities of fish eggs and larvae result from predators taking advantage of their patchy distribution. Perhaps both the scale of associations among young squids and their individual physiologies are important in determining their life-history characteristics. Individuals in small schools are able to hide among their conspecifics (kin?) to reduce individual risks on the small scale, but patches that are too big attract big predators which treat the patches as fIlterable prey. Net avoidance by small squid appears quite common (Okutani and Watanabe 1983, Wormuth and Roper 1983), suggesting that jet propulsion may be particularly effective for avoiding capture by filter feeders. Thus, squid paralarval and juvenile mortalities may be low compared to fishes so that cost/benefit ratios favour a short adult period and semelparity.

Given our limited knowledge of squids and squid fisheries, expecting answers to all these complex questions is premature, but perhaps the critical infonnation needed to answer the questions can be identified. New techniques for reconstructing individual growth histories from statolith and gladius (pen) growth lines promise to provide details about the life histories of surviving squids that are available for few other organisms (Arkhipkin and Bizikov 1991, Perez and O'Dor 1993, Perez *et al.* 1996, *see Chapter 8*). The social structure of squid schools appears to make it possible to extrapolate infonnation about individuals that did not survive from the records of those that did. In Fig. 11.4, for example, the tight correlation between daily growth increments on the gladii for 50 individual squids of both sexes suggests that the members of this school have experienced the same feeding regime and environmental conditions throughout the 60-day interval examined (Perez 1995). Combining these techniques with genetic analysis of school structure (*see Chapter 10*) gives us tremendously powerful tools for understanding population dynamics and the factors that shape life-history strategies.

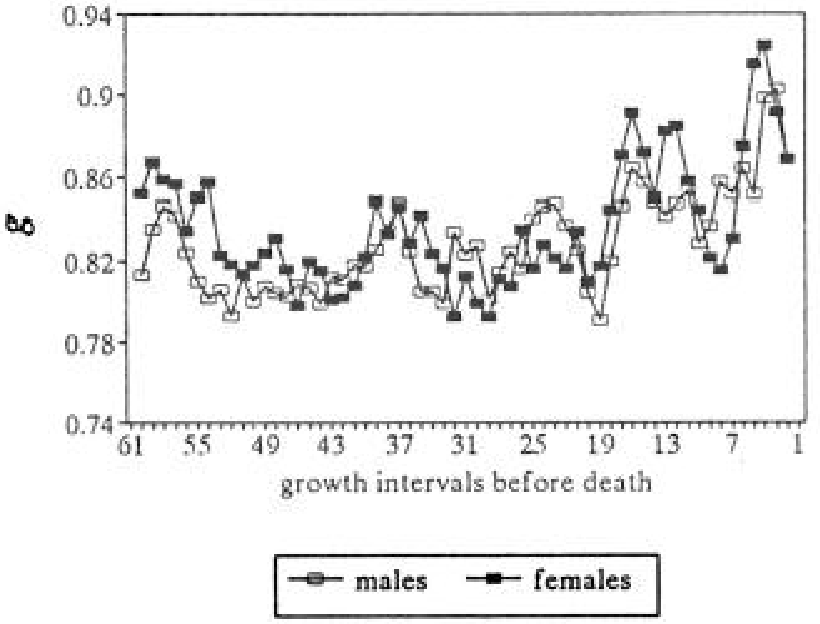

Figure 11.4. Mean daily gladius growth increments as a percentage of total gladius length (g) for 60 days (growth intervals) in 50 *Illex illecebrosus* caught in a single short trawl set at 45°N, 61°W on 24 July, 1989; average mantle length is 164 mm; average weight is 70 g. (J.A.A. Perez *unpubl. data*)

2. Squid vs. fish, space vs. time

The ultimate long-term strategy of any species must be to avoid having a generation fail to reproduce. Reproductive units must not become so rare that they fail to reproduce themselves – **under all conceivable sets of environmental circumstances!** Genetic diversity and phenotypic plasticity are hedges against environmental variability. Mobile species also avoid the risks of local environmental catastrophes by spreading their offspring but this risks dilution to the extent that mating fails to occur (Rankin *et al.* 1985). Reproductive units must be capable of surviving and growing large enough to find a mate and produce viable offspring. Primary production in the ocean is generally nutrient-limited, so that high production levels only occur as a result of physical mixing events which are driven by nearly unpredictable fluid dynamic processes (either atmospheric or oceanic). This means that the success of individuals typically depends on finding "patches" of production that are more or less randomly distributed in time and space. Life-history strategies of marine organisms are, in part, determined by the particular food resource targeted and the degree of uncertainty associated with it.

Patchiness means that marine organisms must have energy reserves which allow them to either wait for new patches to appear or move from patch to patch (McGurk 1986). Sessile animals have no option but to store reserves and wait for the next patch to come to them; mobile ones have to make a choice. This choice is really a dilemma; maintain large reserves and sacrifice mobility or maximize mobility and carry no baggage – the "gonzo" option[1]. On this patchiness-survival spectrum fish are generally conservative; they carry large fat reserves and, with highly efficient undulatory locomotion, they can afford the compromise. Jet propulsion, as practised by squid, is very effective, allowing rapid acceleration for attack or escape, but it is comparatively inefficient (O'Dor and Webber 1991). The logical extension of a feeding strategy that stores all available resources and maximizes efficiency is to overwinter and have an iteroparous life-history strategy. The ultimate gonzo life-history strategy is semelparity, but even squid have to make some compromises and hold back from full semelparity (Harman *et al.* 1989).

As pointed out above, species need reserves of genetic diversity for long-term survival, just as individuals need reserves of energy. In iteroparous fishes these reserves are temporal; annual cohorts live out their lives in a series of parallel "universes", each feeding on a different segment of the food size-spectrum until they reach maturity. Then, size distinctions begin to blur as investment in gametes decreases somatic growth rates. Older cohorts begin to compete for the same food resources, but they also represent a common resource to the natural ecosystem and the fishery. Thus, occasional highly successful year classes can be a tremendous reserve of genetic diversity that helps to conserve the species and stabilize fisheries (Fogarty *et al.* 1991).

Fish, as individuals, store energy in fat and, as species, store genes in time, but squids appear to do neither. One end of the patchiness-survival spectrum is as efficient as possible, stores everything, lives forever and reproduces when there is no risk. The other end consumes everything available, grows as fast as possible, and pours it all into a terminal reproductive event at the first sign of risk. Obviously neither extreme is a viable option, but, if we consider fish to be on the conservative right, then it seems clear that squid are well to the left of center in each category. Still, survival requires some compromise strategy that works in both the short and long term. Based largely on observations of *I. illecebrosus* (Coelho *et al.* 1994), this chapter suggests that spatial distribution is the key to both; intra-school cannibalism provides an energy reserve without a locomotor penalty and geographical spreading provides a genetic reserve without. inter-generational competition. To illustrate the advantages and disadvantages of life histories evolved along the time and space axes, brief, overstated and oversimplified examples are outlined below.

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[1] The term 'gonzo' was originally applied to a style of no-holds-barred journalism pioneered by Hunter S. Thompson, but was generalized to a no-limits life style by the Muppets character, Gonzo.

3 Time

Long-term species survival in a variable environment requires maintenance of genetic variability. However, the number and biomass of offspring produced by local populations may be maximized by genetic specializations (adaptations) that arise under a particular subset of conditions. Thus, assurance of long-term, global survival is at odds with short-term, local optimization which determines whether genes that allow survival under unusual conditions will be eliminated or retained. A compromise solution, common in marine fish, is to produce very large numbers of small offspring from mass spawnings, assisted by behavioural mechanisms such as schooling and migrations which ensure a degree of genetic mixing. In particularly productive years large numbers of offspring survive. Despite relaxed selection in highly productive years, there will presumably be a partially selected subset of genes suited for survival under the particular conditions that led to high productivity.

As an oversimplified example, consider a high mean temperature selecting for "hot" genes that yield faster growth, increased gamete production and eventually higher fitness at high temperatures. At maturity this large cohort begins to contribute disproportionately more to the gene pool of the stock. If mean temperatures remain high (e.g. the greenhouse effect), its offspring would have high survival rates and lead eventually to another high recruitment year. If mean temperatures drop again (short-term oscillation), survival would be low, but there will be some survivors because in iteroparous fishes the less numerous spawners that survived in earlier low temperature years will still be contributing their "cold" genes to the pool. Genetic mixing in mass spawnings, which include offspring from previous years, prevent hot genes from being fixed in the population. Such a temporally mixed reproductive strategy prevents big mistakes and should cope well with gradual climatic changes, but it will likely result in reduced recruitment during short-term climatic oscillations. It makes the best of bad years, but not of good years.

This strategy also provides, each year, large numbers of larvae capable of taking advantage of much or all of the production at the small end of the food size-spectrum. However, limited growth potential prevents an increase in the number of consumers higher on the spectrum, and total consumption is limited by the growth and storage capacity of existing adults. The amount of spawn in the subsequent year is limited by the stored energy and nutrients. Thus, the maximum production of offspring biomass is, at best, a linear function of adult biomass and cannot reflect the full variability of primary production.

4 Space

If we accept that squid lack the efficiency to compete directly with pelagic fishes because of the inherent limits of jet propulsion at the sizes and speeds required, as argued in O'Dor and Webber (1986), can we define an alternate life-history strategy that allows them to compete on the basis of inefficiency (i.e. the capacity for almost unlimited consumption and growth)? The same criteria for long- and short-term survival must apply, and there should presumably be limited overlap in resource requirements. An alternative, allowing selection for and retention of both "hot" and "cold" genes, is to disperse the larvae widely. Imagine the dispersion resulting from a half-kilogram *I. illecebrosus* female in the Florida Straits releasing five egg masses containing 100 000 eggs each on successive days in or near the Gulf Stream to be dispersed as indicated in Fig. 11.5.

Some of the widely dispersed offspring will encounter high temperatures, others low. Selection will favour hot genes in some areas and cold genes in others, or, if production is high and there are no limitations on food, perhaps most will survive. Remember that the chief virtue of jet propulsion is fast acceleration, so predation on squid may not be high. The offspring feed voraciously, absorbing protein and growing rapidly, but wasting much of the lipid they consume because it is more slowly digested and would interfere with rapid throughput (O'Dor *et al.* 1984, Boucher-Rodoni *et al.* 1987). From an energetic perspective this seems an inefficient waste of carbon and available energy, but from a locomotor or reproductive perspective only nitrogen for muscle or gametes really matters. This is, after all the gonzo strategy “grab it all now, there is no tomorrow" (or at least no next year).

There is limited evidence that some squid schools form early. are cohesive (Brown and Lima 1994) and involve kinship. In even the most productive years the rapidly increasing biomass in these schools must eventually become food-limited and some individuals do better than others. Fish larvae survive until they burn up all their energy. but in adult *Illex* schools in captivity. the smaller. weaker and less aggressive individuals begin to be cannibalized after three days without food (O’Dor 1983). The young, with even higher metabolic rates, seem unlikely to give their colleagues any more time. Cannibalism, even among siblings as discussed below. results in biologically sound, rapid selection of the fittest individuals under prevailing conditions at a given place and time (Polis 1981). In addition to the advantage of selection, cannibalism allows much of the nitrogen accumulated by young squid at the low end of the food size-spectrum to be retained by the species (and the school). Most of the carbon collected by larval fish is ultimately wasted by starving or weakened nonsurvivors, and most of the nitrogen benefits their predators, perhaps increasing the predators ability to eat fish larvae. It should be better to benefit a comptetitor with a predictable appetite and shared genes than a predator with neither. What better way to improve fitness while dying than to feed a relative?

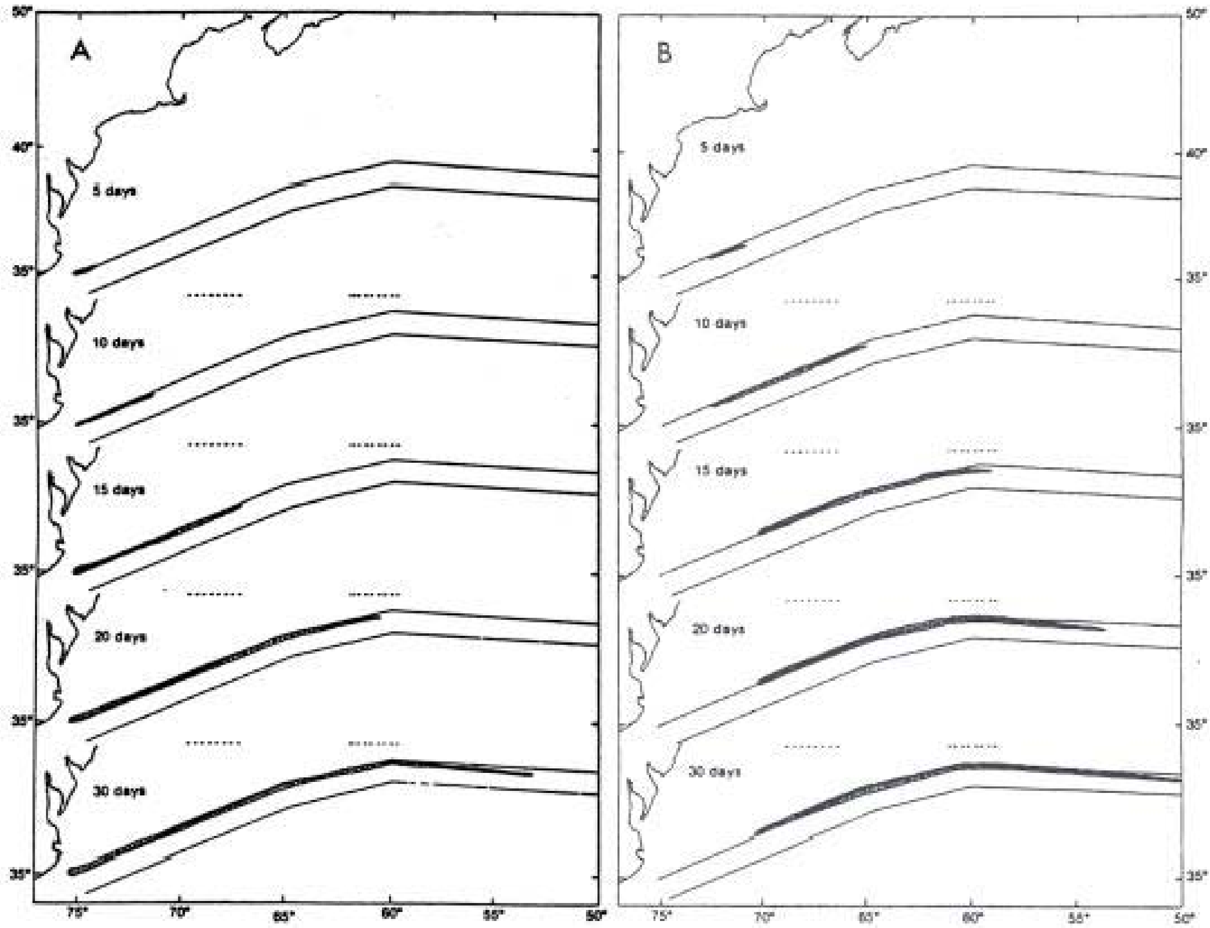


Figure 11.5. Schematic illustration of patch location and size at 5, 10, 15, 20 and 30 days after point source.-release of larvae: (A) at the edge of the shear zone of the Gulf Stream and (8) 12 km inside the shear zone (Trites 1983 with permission NAFO)

Table 11.1. Life cycle and genetic strategy differences between myopsid and oegopsid squids

	Loligo	*Illex*
Sexual dimorphism	male > female	female > male
Gene pool	panmixia	micro-differentiation
Maximum age (months)	18–24?	12
Cannibalism	male on male	female on male
Male/female at spawning	> 0.6	< 0.4?
Spermatheca	yes	no
Matings	multiple	??
Mating time	minutes–hours	seconds
Egg cases	10^2–10^3	10^1–10^2?
Fecundity	10^4–10^5	10^5–10^6
Egg length (mm)	2.8	0.9
Spawning	benthic grounds	midwater drifting
Time/egg case	minutes	15 s
Spawning range	100 km	??
Schooling starts	15 mm ML	??
Migrations	100s km	1 000s km

Energy from a primary production event – a "bloom" – moves up through the trophic levels over a period of weeks to months. Voracious feeding and rapid growth allow squid to grow at about the same rate as energy moves up through the food size-spectrum, so that a school or microcohort (Caddy 1991) could actually track a peak of production through time. The initial biomass of schools (assuming adequate egg production) will reflect the magnitude of the production event, and the surviving cannibals will continue to use all the collectively assimilated nitrogen to consume fixed carbon. The squid will compete with fishes from various year classes with varying degrees of effectiveness as they grow. Fish in a particular size class only get one chance at a production peak as it passes through their part of the size-spectrum, but the total squid biomass at the end of the season should reflect the maximum number of cannibals that could be sustained at the most limiting point on the food size-spectrum despite other causes of mortality.

As schools of squid approach sexual maturity they migrate back to spawning areas (Arkhipkin 1993). Selection continues as cannibalism partially fuels the migration, but the final mix of genes will reflect the survivorship in schools from a range of localities and conditions. The spawning biomass and gene frequency will reflect the integrated conditions over the geographic range in the **current** year. This strategy should allow squids to take up any excess production in an ecosystem (i.e. displace longer-lived species following a collapse), while retaining genetic variability and allowing faster changes in gene frequency to track changes in climate or biological conditions. The annual peak biomass of such a population could increase to reflect any level of productivity, limited only by the egg production of spawners over the entire range. The downside is that it might take many generations (years) for stocks to build up after a widespread failure or widespread overfishing. Nonetheless, a population that ranges over a diversity of habitats while maintaining some gene flow is both less likely to collapse and has a greater ability to show recruitment fluctuations.

5 Squid vs. squid

The broad-brush comparison above can be refined by considering squid species at the same end of the spectrum and in similar current systems, but with differing life-history strategies. *Illex illecebrosus* still exemplifies the extreme, as contrasted with a typical, more fish-like, *Loligo* in Table 1. Recent studies resulting from increased commercial interest in the *Loligo vulgaris* population off South Africa have made it one of the world's best characterized squid (Augustyn *et al.* 1992, 1994), and the parallels between the warm Agulas Current and the Gulf Stream are convenient. In fact, as Fig. 11.6 shows, this loliginid appears to be occupying a niche that might suit an ommastrephid. But the smaller scale of this pseudo-western boundary current and its less variable traits may allow for a less extreme life-history strategy. Although the warm current carries paralarvae out to feeding grounds, the back-eddy that aids the adult return to the spawning grounds never drops below 14°C, so that there are no thermal limitations on spawning areas. The key differences between loliginids and ommastrephids that determine life-history strategies are benthic spawning and less athletic swimming of loliginids (O'Dor and Webber 1991).

Specific benthic spawning sites in bays along a coastal migratory route, used year after year, should be easier to locate in a migration of hundreds of kilometres than ever-moving frontal zones in a migration of thousands of kilometres. The higher chance of finding a good site and the lower chance of being exposed to poor conditions at that site must increase survival probability such that fewer, larger eggs yield adequate survival. Waves of thousands of individuals mate near, and add to, enormous masses of eggs in gel" fingers" attached to the bottom. Multiple matings are well documented and spawning masses involve many individuals; there is, in fact, a complex, site-specific, lek-like mating competition (Sauer *et al.* 1997). Recent tagging studies (W.H.H. Sauer, *Rhodes University, Grahamstown, South Africa, unpubl. data*) show that squid (particularly males) that spawn in one bay show up at other spawning grounds up to 100 km along

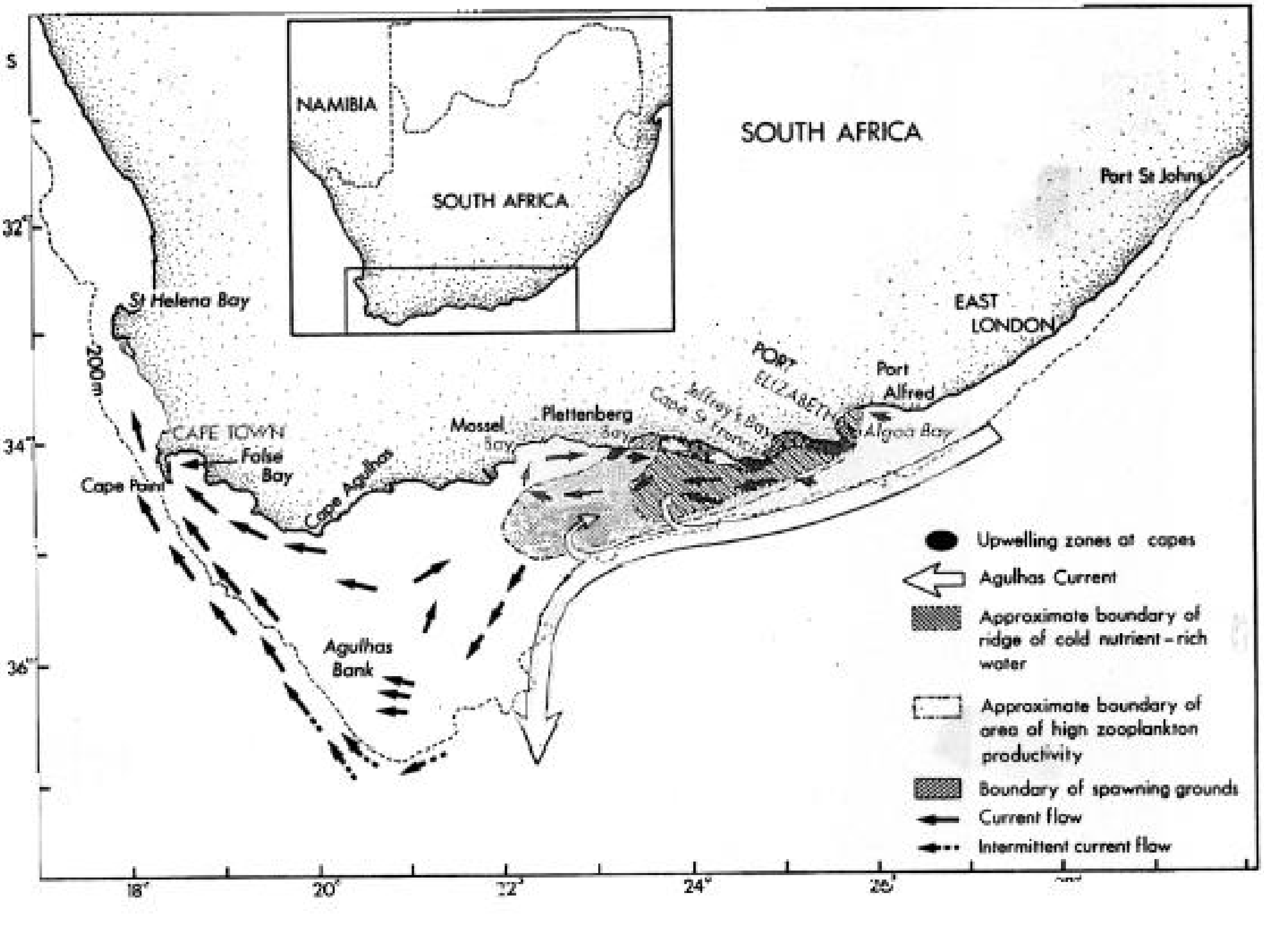


Figure 11.6. The current system in the Agulas Bank region in relation to the spawning and nursery grounds for *Loligo vulgaris* (Augustyn *et al.* 1992 with permission *South African J. Mar. Sci.*)

shore. If the smaller females make smaller migratory loops and males survive longer while continuing to move, it contributes to both spatial and temporal mixing in the population. There may even be overlap between generations. Hatchlings from these masses are thought to move offshore, perhaps carried by an intermediate mixed layer generated by nearshore mixing (*see Chapter 6*), until they intersect with the Agulas Current, which carries them to feeding grounds. Laboratory evidence (Yang *et al.* 1983) indicates that loliginids do not begin schooling until they are about 15 mm ML. All of these features of the life cycle contribute to the panmixia in loliginids seen in the limited studies to date (*see Chapter 10*); there is little temporal or spatial isolation possible.

Contrast this with the emerging picture of population dynamics of *Illex* outlined in earlier chapters. Although the life cycle is also a circle in space -out on one current, back with a little help from another – the circle is bigger and the pace faster. The need to release eggs in inflated gel "balloons", which take only seconds to produce, arises because jet propulsion is disabled and the spawners sink if it takes longer (O'Dor and Balch 1985). These balloons immediately begin to drift in the current. Mating is less ritualized and fertilization also takes only seconds, perhaps because of the risk of being cannibalized (O'Dor 1983). Males certainly mate more than once in the laboratory (O'Dor *et al.* 1980, *see Chapter 5*), and females probably do as well, although males sometimes represent as little as 10% of the inshore population and availability may limit fertility in some situations. Continuous sampling in one place over the spring and summer yields squid of slowly increasing size, but of relatively constant age (Rodhouse and Hatfield 1990, Dawe and Beck 1992, Uozumi and Shiba 1993). Genetic studies suggest (Carvalho *et al.* 1992) that stable schools of common age and genetic composition may be moving rapidly around the current loop. Seasonally increasing temperatures increase growth and maturation rates (Dawe and Beck 1992).

How could such schools form? Schools of adult squid moving south in the cooler, less saline currents along the continental shelf must eventually intersect with the Gulf Stream south of Cape Hatteras if they move alongshore, or perhaps with slope water sooner if they are further out near the continental slope. As Bakun and Csirke (*see Chapter 6*) show, egg balloons released in the Gulf Stream will sink to an isopycnic point in the Gulf Stream, but even balloons inflated with cooler, less saline water near the interface are likely to be entrained in the downwelling zone and become isopycnic as they equilibrate in temperature but fail to equilibrate in salinity. Calculations show that differential equilibration would guarantee adequate time at high enough temperature to produce hatching in slope water (O’Dor and Balch 1985), and Trites (1983) showed that there is a strip of water along the shelf break over 1 000 km long where suitable development temperatures are available all year round.

As the frontal zones, which would be very prominent physical cues for spawning in an otherwise homogenous water mass, are themselves in rapid motion, egg balloons are most likely to drift off individually. An isolated egg balloon could produce up to 100 000 siblings and/or half siblings, and if survival in some balloons were high these might constitute a school. We know that some *Loligo* do not begin to school until they reach 15 mm ML, but *Illex* may start much earlier. It has also been suggested that the balloon itself, which becomes inhabited by plankton, may provide both food and a stable habitat for hatchlings (O'Dor 1983) that could hold them together until they become compulsory schoolers (Mather and O'Dor 1984). Thus, the schools travelling the circuit might also be families. Even if the hatchlings disperse from the balloon, as has been recently suggested for *T. pacificus* egg balloons (Bower and Sakurai 1996), they may still be sufficiently isolated from other squid to reform into a school. *Illex* hatchlings are basically designed to swim up against a downwelling current (O'Dor *et al.* 1986), so that the frontal zone could provide a perfect concentrator for squids where food, in the form of plankton too small to resist the flow, would constantly rain down like "manna from heaven" (Franks 1992).

How might this affect life-history strategy, population structure and recruitment? In classical terms, *Illex* would appear to be r-selected (MacArthur and Wilson 1967, Boletzky 1981), with semelparous adults sending large numbers of young off into an unpredictable environment, but, to the extent that each egg balloon represents a pre-programmed package of parental care and familial cannibalistic competition, the opposite is true. These are K-selection features. The classical expectation would be to have a spawning group of 4 000 randomly selected individuals (male and female) produce 1 000 000 000 randomly dispersed offspring, of which 4 000 survive. If, however, these offspring are in packages of 100 000 and the risk is primarily where the package goes, rather than survival of the individual, the situation is quite different. The focus of the life history shifts to the adults; it would be where and when the parents spawn that determined survival, not what the hatchlings do. Juvenile and adult cannibalism provides the arena for selection among individuals later in life. A school that was particularly successful for a couple of generations might produce an enormous population creating the kind of genetic bottle-neck that could produce the "races" seen in *Illex argentinus.* In many ways a school created by a genetically homogeneous egg balloon is almost like a seasonally generated parthenogenetic clone (Ward and Dixon 1984), if it doesn't interbreed with other schools on some mass spawning ground. These balloons also resemble colony ships; they carry in them everything necessary to found a new and independent population.

The colonization analogy can be taken further and is consistent with the genetic diversity at the species level. The relatively high minimum (13°C) and optimum (20–26°C) temperatures for egg development (Balch *et al.* 1985) make it clear that *Illex* is a sub-tropical species that exploits but cannot really survive in temperate waters. *Illex coindetii* is moderately successful in tropical waters, but rarely so successful as to form a major fishery. The big omrnastrephid populations are mobile and move through high productivity areas at times of maximum production; thus success is coupled to large current systems spanning both tropical and temperate zones (Coelho 1985, Hatanaka *et al.* 1985, O’Dor 1992, O’Dor and Coelho 1993). Success means getting on a current loop at the right time and moving around it at the right speed so that production in various locations is matched to the demands of the school at all times **and** arriving back at the same spot to start the next lifecycle loop. To the extent that the currents are stable and such animal features as growth rates, swimming speeds, temperature preferences and maturation are genetically controlled, populations should become "tuned" to take advantage of environmental features such as spring and fall blooms. The mechanism certainly exists for rapidly increasing the numbers of successful genotypes.

Wynne-Edwards (1993) discusses a number of examples of similar situations in marine as well as terrestrial ecosystems and argues that they meet Wright's (1931) criteria for unit gene-pools. He holds such local units to be the rational basis for group selection in evolution, allowing rapid fixation of local adaptations. Although the evidence is still sketchy, this view does seem consistent with the patterns seen among ommastrephids to date. Clearly "local units", originally used for territorial species, is the wrong term for migratory squid. Perhaps in view of the key role Japanese tag and recapture studies (Nagasawa *et al.* 1993) have played in recognizing squid population structure, the term "*uchi*" should be adopted; it means in-group and has familial overtones without being totally familial (and is derived from the word for octopus pot). This is an important point because local units must amalgamate and interbreed with adjacent units when tough times cause population collapses. For migratory *uchi*, the risks of a highly tuned population being wiped out by any one of many critical environmental changes at points on the loop is high. These multiple risks mean that barriers to interbreeding between surviving individuals in spawning areas must remain low to maintain the high genetic variability needed to colonize the full range of habitats. This tension between adaptation through inbreeding and survival through interbreeding may explain how marked population differentiation can arise with low overall levels of genetic variability at the species and genus level, as outlined above.

Before considering the mechanisms for colonizing a piece of a space-time continuum, consider how the *Loligo* situation differs from that for *Illex*. Most *Loligo* species and/or populations appear to occupy a volume of space where they can survive at any life stage. In the Agulas Bank region spawning appears to occur all year round on the inshore sites (Augustyn *et al.* 1992), although hatching shows seasonal peaks that probably result from temperature-varying development rates, as described by Voight (1992). The full extent of potential spawning sites is not known, but the inshore sites clearly account for niuch of the recruitment. Thus spawning is fixed in space but not in time. This appears to produce a population that is relatively genetically homogeneous and, probably, well adapted to the entire range of conditions it experiences. Loliginids seem unable to colonize areas with more variable conditions. This is illustrated by the lack of permanent populations in the Benguela upwelling area, despite continuous low-level introductions by water movements (*L. vulgaris*, Roberts and Sauer 1994), and in Newfoundland waters where occasional vagrants show up (*L. pealei*, Dawe *et al.* 1990). There is also accumulating evidence (*see Chapter 10*) that, despite a high degree of homogeneity within populations, loliginids show cryptic speciation between populations with relatively limited geographical isolation. The picture seems to be one of small populations with limited gene flow allowing adaptation to particular local conditions and a potential for rapid speciation. The complex mating behaviours of the loliginids may play an important role in this isolation.

6 Space ∝ time

Distributing offspring geographically from a common spawning area has temporal consequences. The wider the distribution the longer the distribution time and the longer the return time. This has several possible effects:

1) If squid from different regions return to the spawning areas at different times, it may restrict gene flow.
2) It may reduce fertility, given the evidence that sexually dimorphic small males avoid schooling with larger and therefore potentially cannibalistic females (O'Dor 1983). The importance of these factors may vary with the efficiency of sperm storage mechanisms, which are quite variable between genera. Some squid appear to be able to mate weeks or even months before spawning occurs (e.g. *T. pacificus*, Ikeda *et al.* 1993), while others have only a few days (Hamabe *et al.* 1974, O'Dor 1983).
3) Spawning times may become dissociated from productivity peaks as a result of increasing travel time. This may be offset by the fact that larger squid travel faster (O'Dor 1988).

The ultimate law of biology seems to be, "Whatever works works." Genes that produce animals that successfully reproduce in an environment continue to exist in that environment, while those that don't eventually disappear. Of course, any change in the environment may alter what works, so too much local adaptation can be as bad as none. As we learn more about squid life cycles from statolith ageing, the pattern emerging appears to show hatching spread over nearly the entire year but with peaks at times associated with high productivity in a particular system. This could reflect many generations of selection of individuals with the right combination of growth parameters and timing cues to optimize reproductive success. It could also reflect differential survival if eggs are produced at a constant rate but few survive in periods of low production. Whether selection can act on such characters probably depends on the repeatability of such factors as timing of production peaks and rates of distribution by currents. It may be possible to distinguish between these two processes by measuring daily growth rates from gladii (Perez and O'Dor 1994). If growth rates are low in times of low production, it suggests that mortality is high (food limiting, cannibalism high) and egg production constant. If growth rates remain high in times of low production, it implies that spawning is sufficiently well-timed to match egg production to the timing of primary production cycles.

Statolith results from both *I. illecebrosus* and *I. argentinus*, cited above, show that the. later hatching occurs in winter, the larger the squid will be on the feeding grounds in summer; an effect attributed to increased feeding and growth on essentially unlimited food supplies at higher temperatures. However, gladius analysis suggests that this trend reverses as the season progresses. Juvenile *I. illecebrosus* caught in June and August, after the peak of the spring bloom, show much lower growth rates than similar-sized squid (c. 40 mm ML) caught in April (Fig. 11.7; Perez 1995). Although more data are required to account for complex environmental factors, as discussed below, this evidence supports the model of continuous egg production followed by high selection. Prior to the bloom growth is only limited by temperature, but it likely becomes food-limited after the bloom peaks.

Figure 11.7. Seasonal variation in juvenile squid growth rates; mean size-specific variation of gladius growth increments (GInc) for 60 *Illex illecebrosus* juveniles collected in the indicated months of 1989 near 42°N, 61°W (From Perez 1995 with permission)

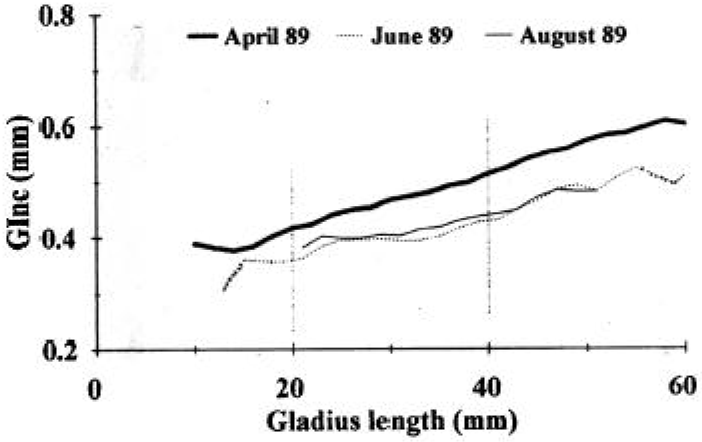
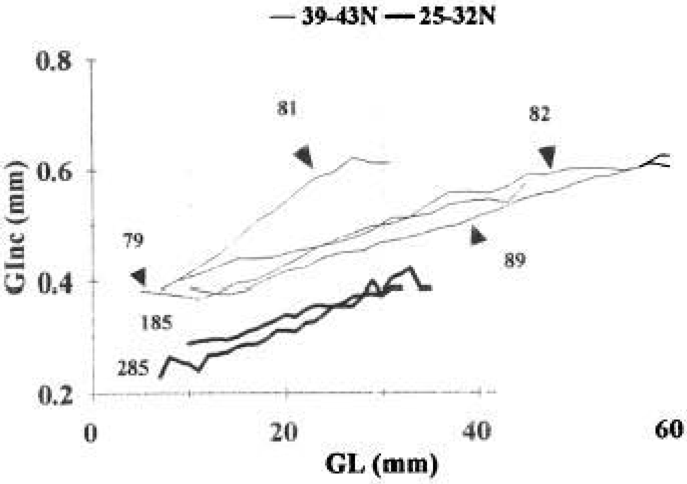


Figure 11.8. Latitudinal variation in juvenile squid growth rates;mean size-specific variation of gladius growth increments (GInc) for 60 *Illex illecebrosus* juveniles collected in the winters of the indicated years grouped by latitude (From Perez 1995 with permission)



There may be varying degrees of selection acting on different segments of a population. A selection scenario for squid stocks of large size in large, powerful current systems has been discussed by O'Dor and Coelho (1993). Maximum growth occurs only when feeding is maximized and routine metabolism is minimized. Optimum temperatures decrease as squids grow (O'Dor and Wells 1987), so that large boundary current systems provide both a highly productive environment and an environment where appropriate temperatures are available at all life stages. Because swimming speed and cost of transport scale with size (O'Dor 1988, 1995, O'Dor and Coelho 1993), near maximal growth is required for adults to swim fast enough to successfully complete spawning migrations on time in such systems. Increased fecundity and greater success at cannibalism would add their selective forces to that of increased migratory range. Together these would provide a powerful selection for large size, but such a specialized sub-population would be vulnerable. The longer the migration the narrower the window when a particular *uchi* can spawn successfully without extensive interbreeding with other components which have been less rigorously selected for these particular characters.

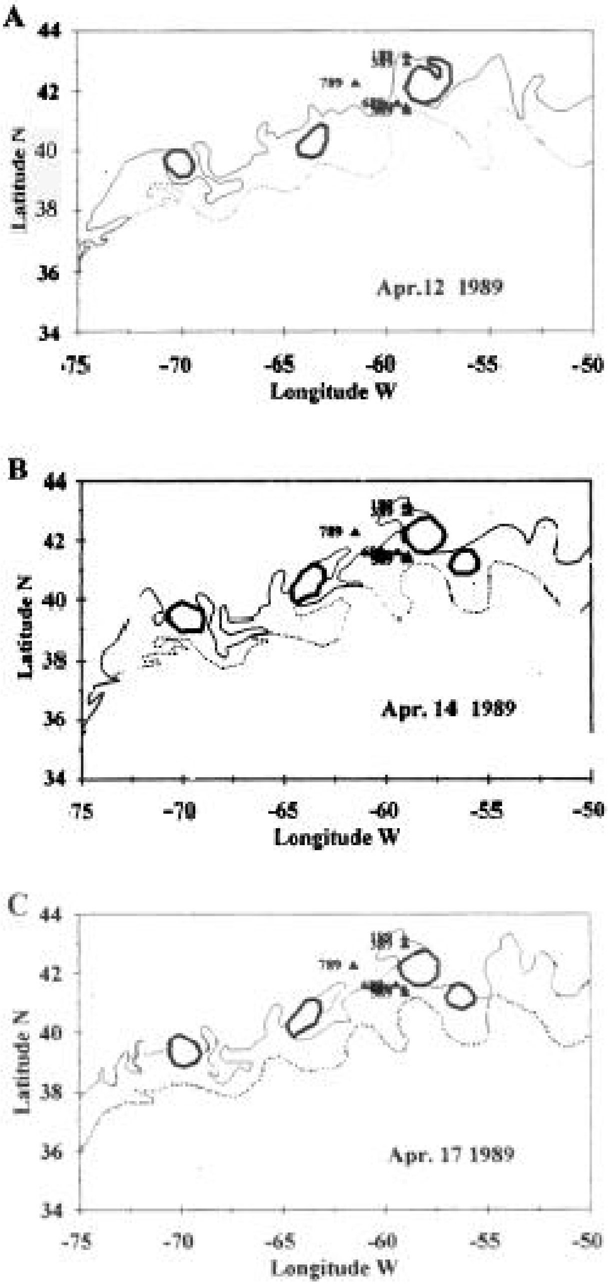


Figure 11.9. Where baby squid come from; satellite images of the dynamic changes in the northern boundary of the Gulf Stream (dotted line), the shelf/slope front (solid line) and the warm-core rings (thick line) during a sampling period in April, 1989; samples used for gladius growth-rate analysis (See Fig. 11.10), indicated by triangles, ranged from 189 (89/04/12) to 789 (89/04/17). (From Perez 1995 with permission)

Again, the limited new data from detailed analyses of temporal characters of populations support this view. Statolith analysis of *I. illecebrosus* collected in Newfoundland from July through November show that well over 90 percent of squid sampled had hatched in a 90-day window between mid-February and mid-May (Dawe and Beck 1992). Only well-fed large squid can complete the loop to this northern limit of the range. In contrast autumn-spawned squid collected in southern waters showed the lowest growth rates of any *Illex* gladii ever analysed (Fig. 11.8; Perez 1995). The latitudinal trend is compromised by questions of annual and seasonal variation as well as the inability to distinguish among the juveniles of the *Illex* species in southern waters, but this is really the point. Are special seasonal characters being selected for in these stocks?

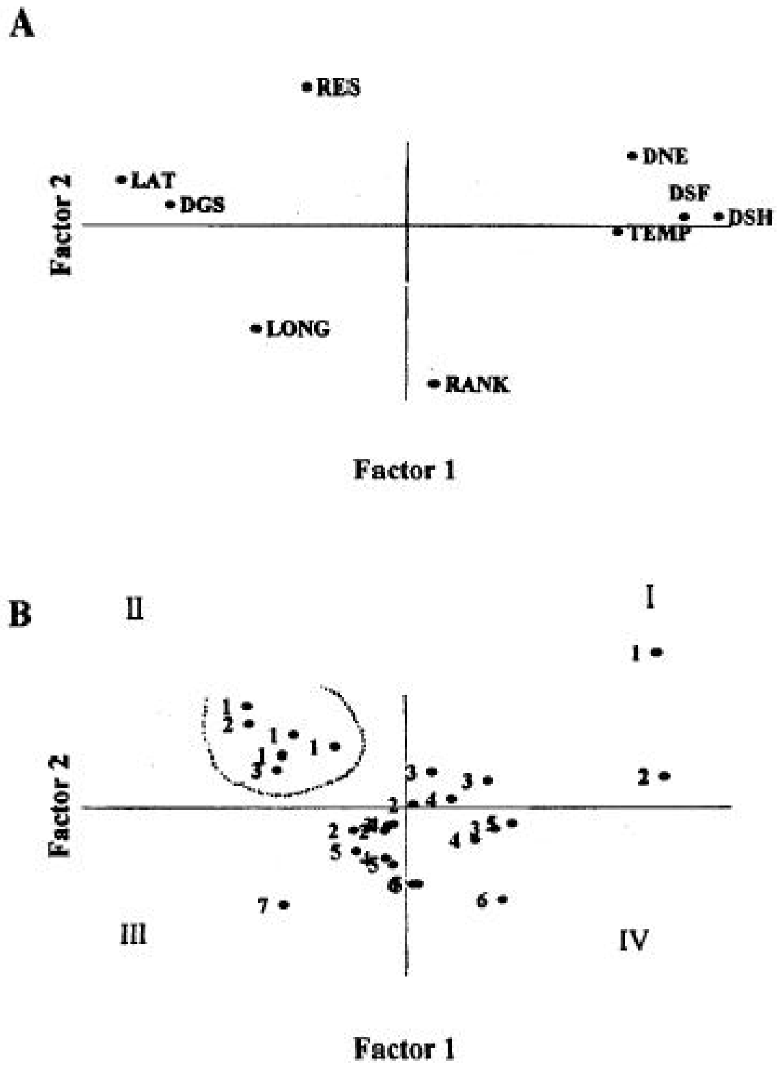


Figure 11.10. Spatial representation of geographic, environmental and growth variables (A) and of samples (B), scored by the first two factors in a principal component analysis (PCA); the horizontal axis (Factor 1) explains 46 percent of the variance and the vertical axis (Factor 2), 20%. In panel B, samples are labelled by their ranks within each of five surveys. The dotted line encloses a cluster of samples showing superior growth. The components employed were: TEMP, surface temperature; LAT, decimal latitude; LONG, decimal longitude; DSH, distance from shelfbreak; DGS, distance from Gulf Stream boundary; DSF, distance from shelf/slope front; DNE, distance from nearest eddy (ring); RANK, growth rank within a survey; RES, residuals of the regression of recent growth index on initial gladius length. (From Perez 1995 with permission)

Because squid are nearly semelparous, disruption of such delicately 'balanced life cycles by physical events can result in virtual annihilation of stocks. The recovery from such events probably requires that populations of squid of large body size "re-evolve" from the smaller, more stable populations of small-sized squid (the southern autumn stock mentioned above, for example) that operate in a different "time-loop". If this process requires a fairly consistent time, it could account for abundance "cycles". There may even be inherent biological instabilities that cause collapses in the absence of human exploitation or physical events, as seen in insects (Baltensweller 1984). For example, generations of progtessively larger squid may regularly overextend their migratory loop and suffer partial collapses.

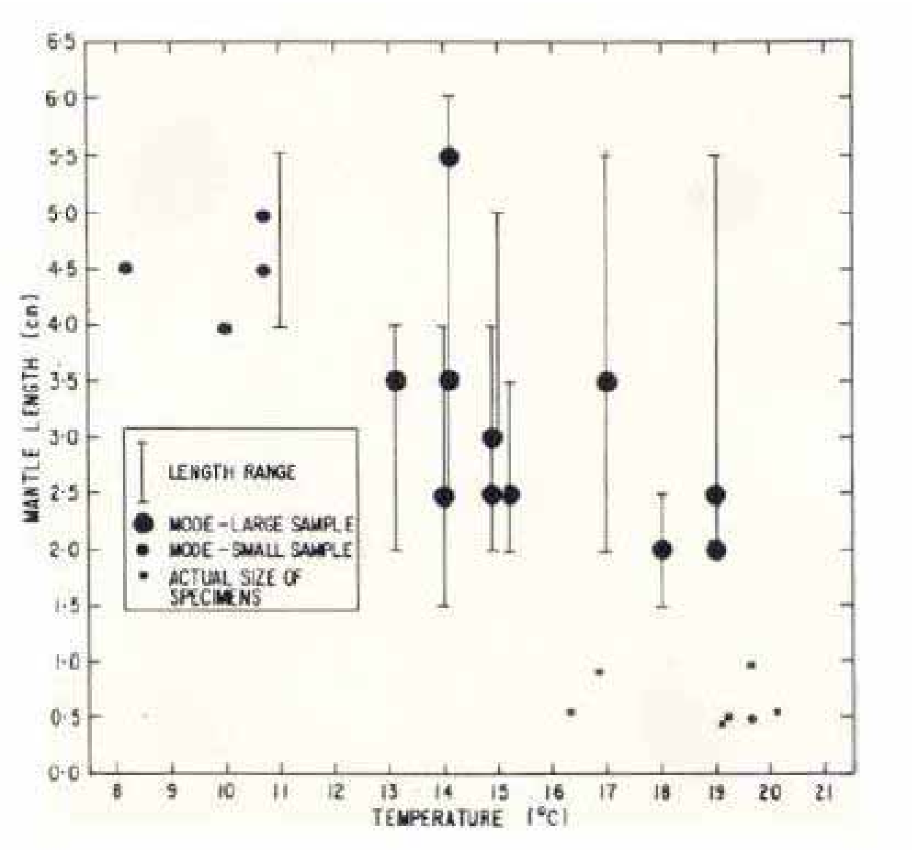


Figure 11.11. Mantle lengths of *Illex illecebrosus* juveniles in samples collected from water of various temperatures along the northern edge of the Gulf Stream (37–41°N, 61–67°W), 4–22 February, 1982 (From Dawe *et al.* 1982 with permission NAFO)

7 Tracking temperature through time and space

If squid life-history strategies focus on juveniles being delivered to areas of high productivity under optimal growth conditions, their association with the boundaries of large current systems is certainly appropriate, but these locations are so dynamic that staying in the right place likely requires more than luck. Figure 11.9 illustrates the dynamics of the Gulf Stream edge, shelf/slope front and warm-core rings in relation to a series of juvenile *I. illecebrosus* samples taken over five days in April, 1989. Perez (1995) analysed recent growth rates from the last 15 gladius increments in 26 samples from similar series in five different years to identify what conditions paralarvae should be seeking. The results are summarized in the principal components analysis (PCA) in Fig. 11.10. Except for one sample taken at the edge of a ring, the fastest growing squid were those taken in the coolest water, furthest from the Gulf Stream and furthest north. Figure 11.11 summarizes data from 60 stations along the northern edge of the Gulf Stream in 1982, originally used simply as evidence that the Stream was the source of *I. illecebrosus* paralarvae. Observations by Perez (1995) suggest that movement out of the Stream into more productive waters was also the cause of the increased growth rate.

Another interpretation of Fig. 11.11 is that paralarvae avoid cooler water until they reach larger sizes, or perhaps even actively seek cooler waters where they can optimize growth (O'Dor and Wells 1987) as they become larger. This could be an important factor in recruitment and a powerful selection pressure for producing specially adapted microcohorts. For example, adult squid that migrate too far north, stay too long or are too small to swim far enough south for winter spawning might intersecthe Gulf Stream north of Cape Hatteras. Egg balloons released there have a high probability of travelling beyond continental influence before reaching the appropriate size/temperature combination to exit the Stream. Such vagrants might contribute to a mid-Atlantic ridge population as discussed in Chapter 1, but will never operate on the same long/large/cool loop as their parental microcohort or *uchi*. Conversely, autumn-spawned paralarvae that chose to leave the Gulf Stream early at warmer temperatures re-establish a pattern of slow growth which keeps them in a short/small/warm loop.

8 Conclusions

This chapter is rather broad in scope, attempting to shed some light on recruitment patterns by relating the differences between the life-history strategies of squids and fishes to differences in their reproductive strategies, ecological roles, behaviours, physiologies and, finally, their genetics. Although the information available for these comparisons is still scant, "the effect of genetic differences among individuals and the linkage between selection pressure under different environmental regimes is critical" (quoting again from Fogarty *et al.* 1991). From a fisheries perspective recruitment is quantitative, but from a population perspective it is also qualitative. All genes are not of equal value in all environments.

Different organisms have different ways of dealing with environmental variability. Large mammals optimize their physiologies within narrow limits and then stabilize the environment. Many poikilotherms maintain alternate genes producing enzymes that can acclimatize them in the short-term (Clarke 1993). Bacteria rapidly evolve new forms, such as the new antibiotic-resistant forms currently in the news. Many animals seem even to carry extra blueprints to develop alternative life-history styles that include different morphs, depending on the conditions they initially experience (Bruton 1989).

There is some recent evidence for different morphs in squid (Nesis 1993), but only DNA or culture studies can determine whether these represent multiple options for the same individuals or diverse metapopulations in different habitat zones. Overall, the latter seems more probable. There are only a few hundred species of cephalopods, compared to tens of thousands of fishes. In general, cephalopod species are widely dispersed and opportunities for gene flow between populations seem particularly large among oceanic squids. Fishes have high standing biomass made up largely of old animals, while cephalopods have high production focused on the young of the year. These cephalopod trends are all consistent with life-history strategies producing rapid genetic adaptations, at rates more like insects than vertebrates.

Summarizing, the selection of the fastest growing juveniles in a particular environmental regime through cannibalism each year would produce a rapid genetic shift in response to changing conditions. Interbreeding between widely dispersed populations would stabilize this process if populations began to decline, but genetic changes would not be slowed if the same environmental changes were occurring over the entire range. Thus, organismal change could keep pace with both rapid global environmental change and with opportunities for colonization. Trends toward interbreeding between annual cohorts would stabilize the population, but reduce its flexibility. If squid were iteroparous it would restrict the rapid responses to changes in environmental production or competition that characterizes this life-history strategy. As The Hustler might have said, "Genepool is like nine-ball, **what** you leave behind is more important than how often you score."

A practical consequence of this pattern of population dynamics and life-history strategy is recognition that conservative management of stocks will not be possible without reasonably detailed information about individual microcohorts. Simple tests of pre-season abundance (Kawahara *et al.* 1993) will not be adequate unless the fishery is prepared to move with a large microcohort. Stationary fisheries should probably monitor stocks acoustically (*see Chapter 9*) or estimate catch-per-unit-effort continuously to avoid destroying individual stock units as they pass by.

Acknowledgements

I thank Janet Voight and several chapter authors for their comments on this chapter and their attempts to keep me in check.

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