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CAN UNDERSTANDING SQUID LIFE-HISTORY STRATEGIES AND RECRUITMENT IMPROVE MANAGEMENT?

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Current views of the links between life-history strategies and recruitment processes in fish are contrasted with the pattern emerging for squid. A general perspective is that the roles of space and time are reversed in the two groups, suggesting that management strategies also should differ. The space/time reversal appears to be more marked in the wide-ranging commercial ommastrephids than in the loliginids, which are more localized and have less extreme strategies. Fish have large energy reserves and efficient lifestyles, allowing stocks to produce numerous co-existing year-classes; as larvae surviving a wide range of potentially limiting conditions in different years, they store genetic diversity and stabilize recruitment in time. Squid are primarily annual species, so stocks can only achieve such diversity and stabilization by spawning microcohorts throughout the year to disperse widely in space into equally variable microhabitats. This behaviour would link recruitment more tightly to environmental variability. The population dynamics and the tactics used appear quite complex, possibly including kinship, school cohesion and cannibalism.

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," but, in a subsequent exchange, Mullen (1992) argued that "forecasting recruitment is not essential for management". Fogarty (1992) concurred that, so long as a "robust age structure" was maintained, the storage mechanisms (Chesson 1984) provided by delayed maturation and iteroparity did ensure population stability of most commercial fish. In fish, multiple year-classes provide a reserve of both reproductive potential and genetic variability. Such risk-spreading strategies as 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).

However, what about squid? As short-lived annuals (Jackson 1994), most squid are the marine equivalent of weeds and cannot have a "robust age structure". Do they require a special kind of management? 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, genetic and phenotypic diversity? Can recruitment variability be predicted through a better understanding of the risk-spreading strategies of squid? According to Fogarty (1992), "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." Do squid somehow compensate for the lack of a robust age structure? If so, what can be learned from the contrasts between squid life-history strategies and those of their more commercially massive and 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, numerically, recruitment represents a minute fraction of production. Hjort (1914) hypothesized that these enormous losses could reflect:

(i) mismatches between the time of larval occurrence and temporally patchy food production, leading to starvation (match/mismatch; Cushing 1975), or
(ii) removal from retention areas by spatially variable currents (member/vagrant; Sinclair 1988).

Although several mechanisms no doubt play a role, the second hypothesis is particularly attractive because it also accounts for the development of distinct populations which 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

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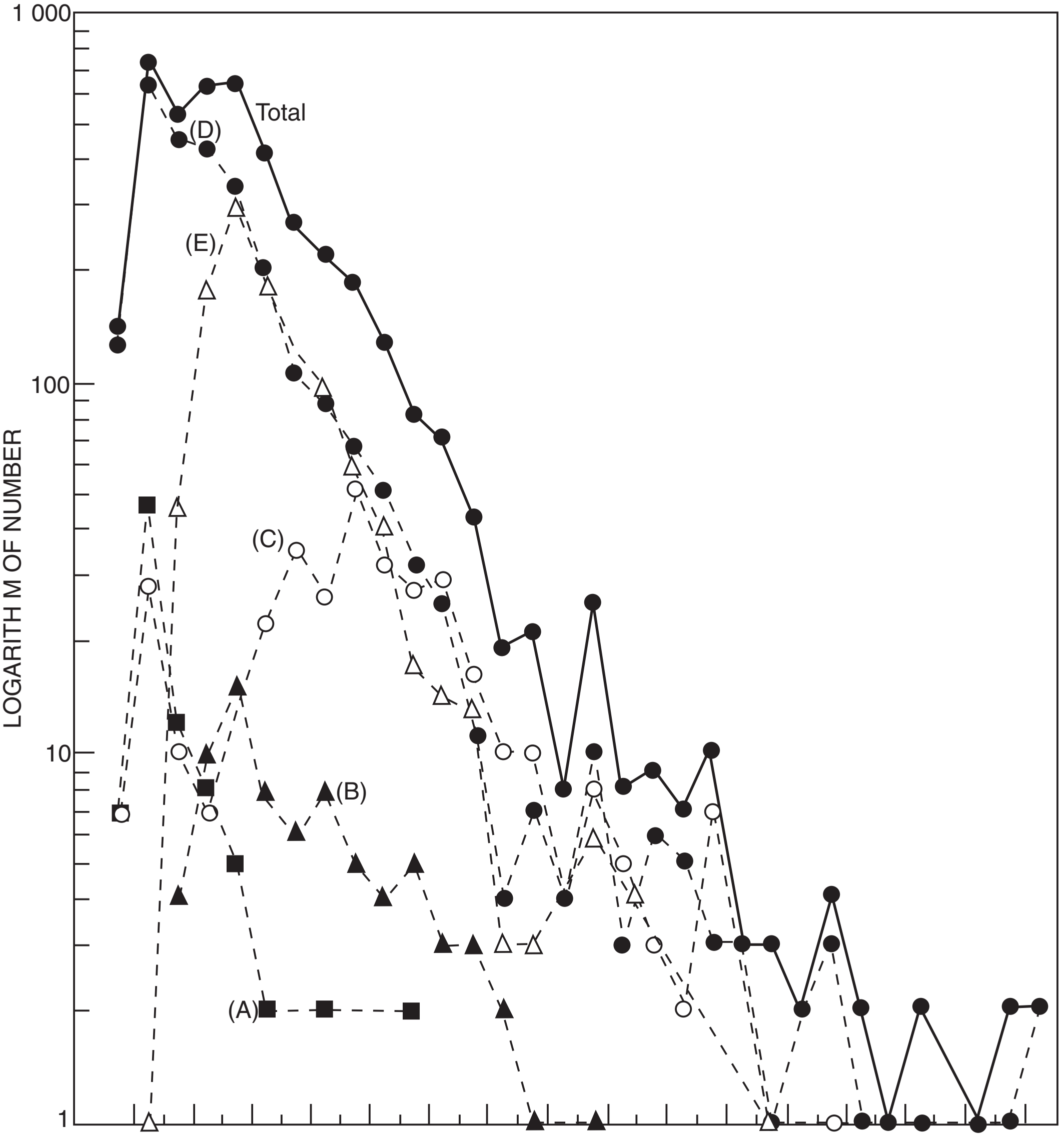

Fig. 1: Larval abundance by mantle length class for *Todarodes pacificus* in February/March in the East China Sea. Total values (filled circles) are summed from various gear types A – E (after Okutani and Watanabe 1983)

between populations could contribute dramatically to recruitment.

Given the large geographic scale of the physical systems in which many squid move and the migrations of which they are capable, it must be considered carefully what a population is. Mayr (1942) defined 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, whereas gene-flow between populations is merely restricted. For fish these barriers are primarily spatial and based largely on the stability of oceanographic structures that provide suitable spawning grounds (Sinclair 1988). Some squid seem to use very large oceanographic features as spawning grounds (e.g. western boundary currents) so that populations must subdivide the resource on a temporal basis, producing seasonal spawning groups (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 (Carvalho *et al.* 1992) may reflect reproductive isolation of schools. However, so far, it fails to distinguish whether these isolated schools reflect hatching times or selective behaviour.

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 lifespans may range from a few months in small tropical squid (Jackson 1990) to several years in cold water and high latitudes (Jarre *et al.* 1991, Wood *et al.* 1998). The typical female reproductive pattern for squid 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 evidence that they spawn in multiple years (Mangold 1987). This lack of evidence that spawning ever recurs in a second year is often contrasted with almost universal iteroparity among fish that compete with squid, using the term "semelparity" (O'Dor and Webber 1986, Calow 1987). Although the big-bang mass spawnings and mass mortalities classically associated with squid (Lane 1960, Fields 1965) are uncommon, and the term semelparous is not fully appropriate (Kirkendall and Stenseth 1985), the coleoid pattern is quite distinct from that of fish 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).

This contrast in life cycles and, therefore, life-history strategies between squid 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 fish and many 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 squid?

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 (e.g. high survivorship among protected young versus high predation on exposed adults, Promislow and Harvey 1990). Does this hold for squid as well? They certainly have the high metabolic/growth rates and the small numerous offspring associated with this strategy (Calow 1987). Calow (1987) argued against the concept of programmed senescence (Wodinsky 1977, O'Dor and Wells 1978), 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 (Calow 1987) is not really supported by statolith ring counts, which show that squid spend a much higher proportion of their life history as juveniles than most organisms.

What little we know about juvenile mortality in squid 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 1 summarizes larval abundance for the winter population of *Todarodes pacificus* (Okutani and Watanabe 1983), which was used to estimate a daily mortality rate of $0.23 \cdot \text{day}^{-1}$ for squid from 1.5 to 7.5 mm mantle length *ML*. Figure 2 shows that this value and one other for *Illex illecebrosus* fall quite close to a widely used relationship for mass-dependent mortality in marine species. It is clear that the *T. pacificus* paralarvae are being removed rapidly from the East China Sea by the Kuroshio Current, so this mortality value is an overestimate because it does not distinguish mortality from emigration or dispersal, but it is still below the values for fish larvae.

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 association among young squid (Sauer *et al.* 1992) and their individual physiologies are important in determining their life-history characteristics. The benefits of schooling are complex, because individuals in small schools are able to hide among their conspecifics (see below) to reduce individual risks on the small scale, whereas patches that are too big may attract big predators which treat the patches as filterable prey (McGurk 1986). Net-avoidance by

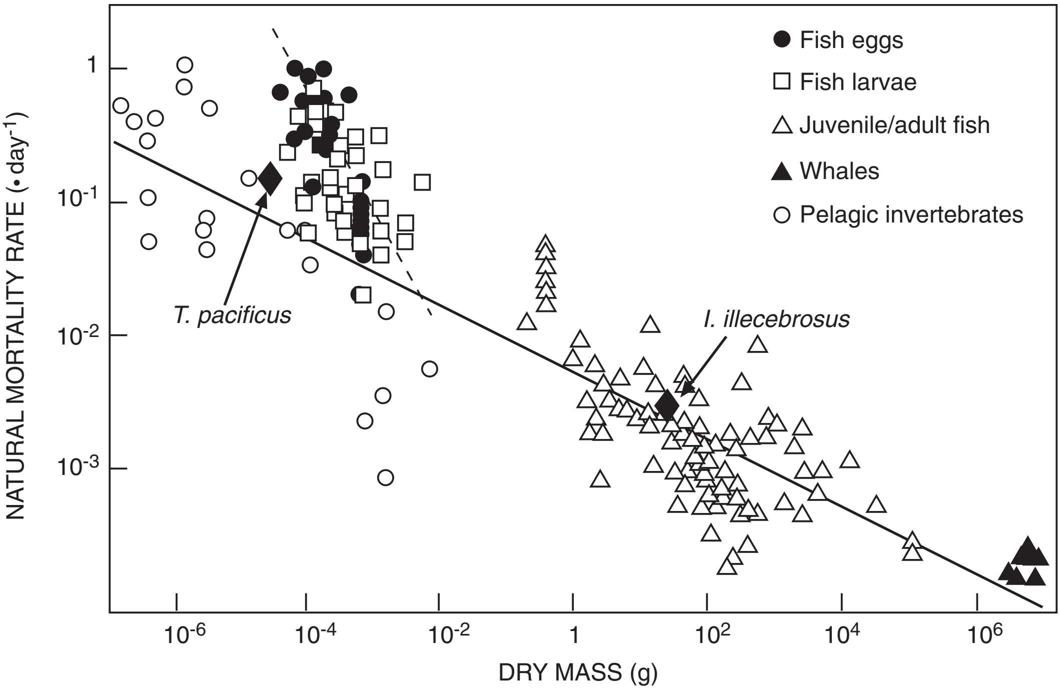

Fig. 2: Instantaneous daily natural mortality rates plotted against dry mass of marine organisms (McGurk 1986), with the relationship for *Todarodes pacificus* from Fig. 1 (*Illex illecebrosus* value also shown). Solid line is the Peterson and Wroblewski (1984) model, where $M = 0.00256W^{-0.25}$; dashed line is the much steeper regression ($M = 0.00022W^{-0.85}$) for fish eggs and larvae

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. Much remains to be learned, but mortalities of squid paralarvae and juveniles may be low compared to those of fish, so that cost/benefit ratios favour a short adult period and semelparity.

Given current limited knowledge of squid and squid fisheries, expecting answers to all these complex questions is premature, but it is perhaps possible to identify the critical information needed to answer some questions. New techniques for reconstructing individual growth histories from statolith and gladius growth lines promise to provide details about the life histories of surviving squid that are available for few other organisms (Arkhipkin and Bizikov 1991, Perez and O'Dor 1992, 1994, 1998, Perez *et al.* 1996, Hughes *et al.* 1997). The social structure of squid schools appears to make it possible to extrapolate information about individuals that did not survive from the records of those that did. In Figure 3, for example, the tight correlation between gladii daily growth increments (as a percentage of gladius length) among 50 individual squid 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 (Carvalho *et al.* 1992) could provide tremendously powerful tools for understanding population dynamics and the factors that shape life-history strategies.

SQUID v. FISH, SPACE v. TIME

The ultimate long-term strategy of any species must 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, phenotypic plasticity and life-cycle strategies are hedges against environmental variability. Mobile species

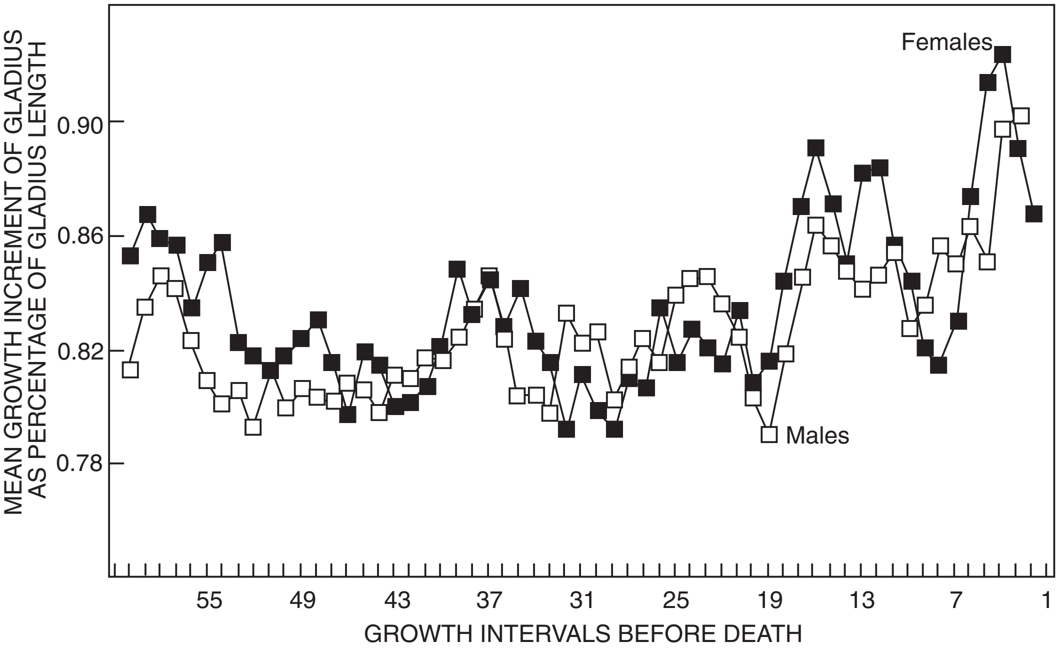

Fig. 3: Mean gladius growth increments for 60 intervals before death. Intervals are assumed to be days, based on comparisons with statoliths. Means are for a total of 50 *Illex illecebrosus* caught in a single short trawl set at 45°N, 61°W on 24 July 1989 (average *ML* 164 mm, average mass 70 g). Note the general correspondence in trends between the sexes, indicating similar feeding and growth patterns throughout the school (see Perez and O'Dor 1998 for further details)

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 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 levels of production 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 which are chaotically 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 of encountering the resource.

Patchiness of food 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 to 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. (This term was coined to describe Hunter S. Thompson's no-holds-barred style of journalism, but became the name of a Muppet character with a no-limits life style.) On this patchiness-survival spectrum, fish are generally conservative; they accumulate and then carry large fat reserves, and, with highly efficient undulatory locomotion, they can afford the compromise. Jet propulsion, as practiced 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 to have an iteroparous life-history strategy. The ultimate gonzo life-history strategy is semelparity, but even squid 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 for short-term survival. In iteroparous fish 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 which 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 squid 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 converts it all into gametes for a terminal reproductive event at the first sign of risk. Obviously neither extreme is a viable option, but if fish are considered to be on the conservative right, then it seems clear that squid are well to the left of centre in each category. Still, species survival requires some less extreme, compromise strategy that works in both the short- and the long-term. Observations of *I. illecebrosus* (Coelho *et al.* 1994) suggest that spatial distribution is the key on both time-scales; intraschool cannibalism provides an energy reserve without a locomotor penalty, and the combination of geographical spreading with life-cycle flexibility provides a genetic reserve without intergenerational 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.

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. Therefore, 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 migration 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 greater fitness at high temperature. 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), the offspring would have good rates of survival which lead eventually to another strong recruitment. If mean temperatures drop again (short-term oscillation), survival would be poor, but there will be some survivors because, in iteroparous fish, the less numerous spawners that survived in earlier years where temperature was low 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 is conservative and makes the best of bad years, but not of good years because the response to bad times is swift but that to good times is slow.

This strategy also provides large numbers of larvae each year, capable of taking advantage of most of the production at the small end of the food size-spectrum. However, low 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 quantity of spawn in the subsequent year is limited by the stored energy and nutrients. Therefore, the maximum offspring biomass is, at best, a linear function of adult biomass and cannot reflect the full variability of primary production.

Space

If it is accepted that squid lack the efficiency to compete directly for limited resources with pelagic fish because of the inherent limits of jet propulsion at the sizes and speeds required, as argued in O'Dor and Webber (1986), can an alternative life-history strategy be defined 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-kilogramme *I. illecebrosus* female in the Florida Strait releasing five egg 'balloons' (see below) containing 100 000 eggs each on successive days in or near the Gulf Stream to be dispersed as estimated by Trites (1983). In less than three weeks, balloons and paralarvae could enter the mixing zone along the northern edge of the Stream at any point over a range of 2 000 km.

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 great. 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. Even in the most productive years, the rapidly increasing biomass in these schools must eventually become food-limited and some individuals will 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 faster metabolic rates seem indisposed 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 non-survivors, and most of the nitrogen benefits their predators, perhaps increasing the predator's ability to eat fish larvae. It should be better to benefit a competitor 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?

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 (Forsythe 1993, 1997) 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 of the nitrogen collectively assimilated to consume fixed carbon. The squid will compete with fish from various year-classes with varying degrees of effectiveness as they grow. Slower-growing 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 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 squid 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 sufficient numbers to saturate the environment with spawn after a widespread failure or widespread overfishing. Nonetheless, populations that range over a diversity of habitats while maintaining some gene flow are both less likely to collapse and have a greater ability to show recruitment fluctuations.

SQUID v. 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. Table I compares *I. illecebrosus*, which is close to the extreme left, to *Loligo*, which is, in general, more conservative and closer to the fish end of the spectrum. Recent studies resulting from increased commercial interest in the

Table I: Possible life cycle and genetic strategy differences between loliginid and ommastrephid squid

Parameter	*Loligo**	*Illex*†
Sexual dimorphism	Male > female	Female > male
Gene pool	Panmixia	Microdifferentation
Maximum age (months)	12–18?	12
Cannibalism	Male on male	Female on male
Male/female ratio at spawning	>0.6	<0.4?
Spermatheca	Yes	No
Matings	Multiple	2? (Rt. & lt.)‡
Mating time	Minutes to hours	Seconds
Egg cases	c. 10^3	c. 10^1
Fecundity	c. 10^4	10^5–10^6
Egg mass (µg)	200	3 000
Paralarvae	Normal	Rhynchoteuthion
Spawning	Benthic grounds	Midwater drifting
Time/egg case	Minutes	15 seconds
Spawning range	100 km	?
Schooling starts	15 mm *ML*	?
Migrations	Hundreds of km	Thousands of km

* After Hixon (1983) or Summers (1983)
† After O'Dor (1983), Haimovici *et al*. (1998), O'Dor and Dawe (1998) or Sánchez *et al*. (1998)
‡ Sánchez *et al*. (1998) suggest that a single mating leaves spermatophores attached to only one oviduct, but the presence of spermatophores bilaterally implies multiple matings (and handedness in sex?)

Loligo vulgaris reynaudii 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 Agulhas Current and the Gulf Stream are convenient. In fact, this loliginid may be less conservative than most, occupying a niche more similar to those of ommastrephids (Augustyn *et al.* 1992). However, the smaller scale of this pseudo-western boundary current and its less variable traits appear to 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 in returning to the spawning grounds never drops below 14°C, so that there appear to be no thermal limitations on spawning area. The key differences between loliginids and ommastrephids which 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 for *Loligo* to locate in a migration of hundreds of kilometres than ever-moving frontal zones in a migration of *Illex* of thousands of kilometres. The better chance of finding a good site and the poorer chance of being exposed to inclement conditions at that site must increase survival probability such that fewer, larger eggs yield adequate survival. Waves of thousands of *Loligo* 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 mating competition (O'Dor *et al.* 1995, Sauer *et al.* 1997). Recent tagging studies (Sauer 1995) show that squid (particularly males) that spawn in one bay show up at other spawning grounds up to 100 km away. If the smaller females make smaller migratory loops and males survive longer while continuing to move, it would contribute 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, until they intersect with the Agulhas Current which carries them to feeding grounds. Laboratory evidence (Hurley 1976, 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 genetic studies to date; there is little temporal or spatial isolation possible.

Contrast this with the emerging picture of population dynamics of *Illex*. 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 in the laboratory certainly mate more than once (O'Dor *et al.* 1980), and females probably do so as well, although males sometimes represent as few 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 (Carvalho *et al.* 1992) suggest 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 encounter Slope Water sooner, if they are farther out near the continental slope. Egg balloons released in the Gulf Stream will sink to an isopycnic point in the 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 more than 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 homogeneous 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. It is known that some *Loligo* do not begin to school until they reach 15 mm *ML*, but circumstances may allow *Illex* to start much earlier. It has been suggested that the balloon itself, which becomes inhabited by plankton, may provide both food and a stable habitat for hatchlings (O'Dor 1983) which could hold *Illex* hatchlings together until they become compulsory schoolers (Mather and O'Dor 1984). Therefore, the schools travelling the circuit might also be families. Even if the hatchlings disperse from the balloon, as has been recently suggested for *Todarodes 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 upwards against a downwelling current (O'Dor *et al.* 1986), so that the frontal zone could provide a perfect concentrator for squid 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, these are contrasting 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 could produce an enormous population creating the type of genetic bottleneck that might yield the "races" seen in *Illex argentinus* (Carvalho *et al.* 1992). 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 that potentially carry everything in them 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.* 1986) make it clear that *Illex* is a subtropical species that exploits, but cannot really survive, as a species, in temperate waters. *Illex coindetii* is moderately successful in tropical waters, but rarely so successful as to form a major fishery. The big ommastrephid populations are mobile and move through areas of high productivity at times of maximum production. Therefore, their 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, 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, finally, arriving back at the same spot to start the next life-cycle 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 each successful genotype.

Wynne-Edwards (1993) discussed a number of examples of similar situations in marine as well as terrestrial ecosystems and argued that they met Wright's (1931) criteria for unit gene-pools. He held 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 and not widely accepted, this view does seem consistent with the patterns seen among ommastrephids to date. Clearly the term "local units", originally used for territorial species, is wrong 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 collapse. For migratory *uchi*, the risk is high for a highly tuned population to be wiped out by any one of many critical environmental changes at points on the loop. 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 the unusual situation in squid of marked population differentiation with low overall levels of genetic variability at the species and genus level can arise.

Some of these differences may simply reflect how a species is defined; 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 Agulhas Bank region, spawning appears to occur all year round on the inshore sites (Augustyn *et al.* 1992), although hatching shows seasonal peaks, which reflect both variable spawning intensity and 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 much of the recruitment. Therefore, 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 apparent lack of permanent populations in the Benguela upwelling area despite continuous low-level introductions by water movements (*L. vulgaris reynaudii*, Roberts and Sauer 1994) and in Newfoundland waters where occasional vagrants show up (*L. pealei*, Dawe *et al.* 1990).

Despite a high degree of homogeneity within populations, there is also accumulating evidence that loliginids show cryptic speciation with relatively limited geographical isolation (Yeatman and Benzie 1993). Small populations with limited gene-flow have the potential for rapid speciation and adaptation to particular local conditions. This pattern seems inconsistent with the panmixia suggested above, but with complex loliginid mating behaviours either situation could arise.

CONCLUSIONS

This broad overview attempts to shed some light on recruitment patterns by relating the differences between the life-history strategies of squid and fish to differences in their reproductive strategies, ecological roles, behaviour, physiology and, finally, their genetics. Although the information available for comparison is still scant, "the effect of genetic differences among individuals and the linkage between selection pressure under different environmental regimes is critical" (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 physiology within narrow limits and then stabilize their environment through homeothermy and behaviour such as making dens. Many poikilotherms maintain alternative 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, including 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. There are only hundreds of species of cephalopods, compared to thousands of species of fish. In general, cephalopod species are widely dispersed and opportunities for gene-flow between populations seem particularly large among oceanic squid. Fish have high standing biomass made up largely of old animals, whereas cephalopods have high production focused on the young of the year. These cephalopod trends are all consistent with life-history strategies of genetic adaptation, more like the bacterial model than the vertebrate one.

Summarizing, the selection of the fastest growing juveniles in a particular environmental regime through cannibalism 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 environmental changes took place over the entire range. Therefore, organismal change could keep pace with rapid environmental change or with opportunities for colonization. Trends toward interbreeding between annual cohorts would stabilize the population, but reduce the flexibility of the population. If squid were iteroparous it would restrict the rapid responses to changes in environmental production or competition that characterize this life-history strategy. The hustler might say, "Gene-pool is like nine-ball, what you leave behind is more important than how often you score."

MANAGEMENT CONSEQUENCES

From a management perspective there are several practical consequences of this squid or "gonzo" pattern of population dynamics and life-history strategy which constrain dynamic management.

(i) The most critical is that management of squid stocks according to the "precautionary principle" requires defining individual microcohorts genetically, temporally and spatially.

(ii) Virtual Population Analysis models must be adjusted to work on a monthly or weekly basis, and much better information on early life-history mortality rates is required.

(iii) Migrations must be documented and models which assume no immigration or emigration cannot be used.

(iv) Information must be supplied with as much lead time as possible, so continuous monitoring for gladius growth history reconstructions of waves of juveniles may provide an index of the state of various microcohorts.

Simple tests of pre-season abundance (Kawahara *et al.* 1993) are not adequate unless the fishery remains focused on the early microcohort and moves with it, rather than continuing to fish the succession of microcohorts passing a point. Stationary fisheries must, at minimum, monitor catch per unit effort continuously to avoid destroying individual stock units as they pass by. Aggressive dynamic management to maximize yields will only be possible with sensitive indices, rapid changes in exploitation rate and a flexible and responsive fleet.

The cost of such dynamic management will be high and must be weighed against the difference in value between the sustainable catches under dynamic management and sustainable catches under passive management. Given the recognition that squid are migrating continuously, passive management approaches can be quite effective if the fisheries are not allowed to pursue squid relentlessly. Protection measures must include both closed seasons and closed areas, because a closed season primarily protects a major microcohort during a spawning season, whereas closed areas provide some measure of protection to all microcohorts in the region. Given their distribution in time and space, the best protection for squid may result from several short closed seasons and several closed spawning reserves distributed throughout the range.

The precautionary principle clearly requires that situations that put stocks at risk be avoided. For annuals such as squid, this is a major problem because of the likelihood of rapid oscillations in abundance. O'Dor and Coelho (1993) point out that collapses of squid fisheries are often associated with the build-up of local fleets during periods of high squid abundance, followed by relentless fishing in a year of low abundance, driven by powerful local financial and political interests. Although particularly common for squid, the pattern is seen in all fisheries (Mace 1997). Given the global excess fishing capacity and the evidence of the relatively stable Falkland Islands squid fisheries, the earlier recommendation to stabilize local squid fleets at sizes capable of catching and surviving financially on average or below yields still seems sound (O'Dor and Coelho 1993). Highly mobile, global fleets will contribute to local economies with license fees when squid are abundant, but can move to other areas when abundance is low locally, without causing financial ruin.

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