MATING SYSTEMS AND SEXUAL SELECTION IN THE SQUID *LOLIGO*: HOW MIGHT COMMERCIAL FISHING ON SPAWNING SQUIDS AFFECT THEM?

ROGER T. HANLON
Marine Biological Laboratory
Woods Hole, Massachusetts 02543
rhanlon@mbl.edu

ABSTRACT

The effect of targeted fishing on spawning grounds is central to the management of commercially valuable squids for at least three reasons: (1) the very short life cycle of about one year; (2) dense spawning aggregations, which are easily targeted by fisheries; and (3) fishing techniques that could remove certain sexes or sizes of squids, thus leading to "unnatural" sexual selection processes that affect recruitment. Recent field and laboratory studies on *Loligo vulgaris reynaudii* in South Africa and *Loligo pealei* off the northeastern United States indicate that the mating systems are complex, that sperm competition is a major feature of the systems, and that alternative reproductive tactics may be flexible enough to withstand targeted fishing pressure, provided that the pressure is not so great that it suppresses reproductive behavior. Behavioral studies combined with DNA fingerprinting to assess paternity of individual egg capsules are helping to resolve some of these questions. In this paper, I outline an approach to studying reproductive behavior in the context of fisheries management, and I speculate on features of the mating system of *Loligo opalescens* that should be understood before high levels of exploitation are permitted.

INTRODUCTION

Evolution has forged ingenious ways for animals to reproduce, and squids are no exception. Like all organisms, squids must survive natural selection, and in the process they must succeed in sexual selection to ensure that their individual genes are passed to the next generation. Squids of the genus *Loligo* school for most of their very short life cycle, and during a large portion of this yearly cycle they are engaged in reproductive behavior. Sexual competition, fecundity, and reproductive success of squids of the genus *Loligo* have only recently been studied in any detail by cephalopod biologists (summarized in chapter 6 of Hanlon and Messenger 1996).

Dense aggregations of sexually active squids are common, and they seem particularly vulnerable to harvesting by commercial fishing methods. For example, *L. vulgaris reynaudii* (South Africa), *L. pealei* (NE U.S.), and *L. opalescens* (U.S. west coast) are fished partly, if not mainly, on spawning aggregations, and they are the basis of large and growing fisheries that are being exploited heavily (e.g., Fields 1965; Dewees and Price 1982; Hixon 1983; Sissenwine and Rosenberg 1993; NFSC 1995; Augustyn 1998). Nevertheless, it is possible that the squids' mating systems are flexible enough to withstand such commercial fishing pressure, although this remains to be demonstrated.

In this paper, I explore the possible ramifications of targeted fishing on spawning aggregations in the context of what we have learned recently about sexual selection processes and mating systems in *Loligo*.

METHODS AND APPROACH

It has been productive to combine field and laboratory studies of *Loligo* spp. Fortunately, spawning loliginid squids do not react to divers or machines, so it is easy to approach and film them with little or no period of habituation (e.g., Hanlon et al. 1994, 1997; Hanlon 1996; Sauer et al. 1997). Technological advances have refined the processes for gathering behavioral data. Scuba diving allows underwater observations under natural conditions, and diver-held video allows careful analysis back in the laboratory or aboard ship. Hi-band 8 mm video, super VHS video, and most recently digital video provide increasingly high-resolution images that allow behavioral details to be recorded and analyzed. Remotely operated vehicles (ROVs) with video cameras allow behavioral sampling as well; when sampling routines for divers and ROVs are coordinated, it is possible to obtain a wide range of behavioral data in a relatively short time, especially with refined behavioral sampling rules and methods (Martin and Bateson 1993). Telemetry devices implanted in squids have allowed longer-term movements to be recorded (Sauer et al. 1997). Field studies under natural conditions make it possible to use noninvasive methods to describe generalities of the mating system, and set the stage and the questions for laboratory experiments.

Significant improvements in methods for keeping squids alive in captivity have enabled researchers to study various aspects of reproductive behavior (e.g., Hurley 1978; Hanlon et al. 1983). Perhaps more important, the advent of DNA fingerprinting methods has allowed verification of paternity in sexual selection studies of numerous taxa (e.g., Queller et al. 1993), both in the field and in the laboratory. With *Loligo*, it is now possible to

determine multiple paternity of field-collected egg capsules (Shaw and Boyle 1997) and to assign paternity after highly controlled mating trials in which the recent mating history of individual females is known with precision (e.g., Hanlon et al. 1997). These powerful molecular and behavioral techniques will permit rigorous studies of reproductive success in cephalopods for the first time.

MATING SYSTEMS, SEXUAL SELECTION, AND FISHERIES

Within a population, the *mating system* refers to the general behavioral strategy used in obtaining mates. It includes such features as (1) the number of mates acquired, (2) the manner of mate acquisition, (3) the presence and characteristics of any pair bonds, and (4) the patterns of parental care provided by each sex (Emlen and Oring 1977). Mating systems can be viewed as outcomes of the behavior of individuals competing to maximize their reproductive success (Davies 1991). The conceptual beginning point of mating systems is promiscuity (all pairings are random and multiple); monogamy represents the other end of the spectrum (Lott 1991). To our current knowledge, there are no monogamous cephalopods. But we cannot yet predict pairings in squid matings beyond saying that, in most species, both males and females will mate with more than one partner.

Sexual selection is defined as the differences in reproduction that arise from individual variations in traits that affect success in competition over mates and fertilizations (Andersson 1994). Hypotheses about sexual selection were first proposed by Darwin, but hypotheses have been tested and actual mechanisms have been determined mostly in recent decades by behavioral ecologists (cf. Andersson 1994; Eberhard 1996; Krebs and Davies 1997).

Fighting among males is a form of competitive aggression (as distinct from protective or parental aggression) that enables males to gain preferred access to females for mating; this is an example of sexual competition (Archer 1988) and introduces a most important concept. *Sperm competition* was defined originally by Parker (1970) "as the competition within a single female between the sperm from two or more males for the fertilization of the ova," but a current definition in common use was provided by Birkhead and Parker (1997) "...a part of sexual selection ... and includes the adaptations which arise as a result of it; e.g., any behaviour, morphology or physiology associated with multiple mating by females, paternity guards and ejaculate characteristics, all viewed from both a male and female perspective."

Sperm competition can occur whenever a female mates with more than one male in one breeding cycle. Thus there is a strong behavioral component to sperm competition. Specifically, sperm competition involves

(1) competition between males for copulations, (2) sperm precedence mechanisms by males (e.g., sperm plugs, last in first out, sperm dilution), as well as (3) possible manipulation of the sperm by inseminated females (Eberhard 1996). Sperm competition is a major component of mating systems in many phyla and is a vigorous field of inquiry for behavioral ecology (cf. Smith 1984; Birkhead and Moller 1992; Andersson 1994; Birkhead and Parker 1997).

Sperm competition typically includes the following features in many phyla: a large testis that can produce large quantities of sperm; sperm packaged in spermatophores; sperm stored by females; appropriate morphologies of the oviduct and spermatheca; polygamous mating systems; multiple styles of mating; delays between mating and egg laying; and intense mate guarding. In squids, many matings can occur over many months, and it is possible that sperm from the most recent matings might displace that from earlier matings. After all, the seminal receptacle of *Loligo* appears to be little more than a series of invaginations and associated glands (Lum Kong 1992), but no one has yet considered the functional anatomy of the seminal receptacle in relation to the hypothesis of sperm competition.

Sexual selection is a vital complement to natural selection (Darwin 1871) and can be a large determinant of the population structure over time. Population structure (i.e., the spatial variation in density and genetic composition of individuals in a species) is affected by fishing techniques and fishing pressure. Because there is a close relation between the population genetic structure and the behavior of individuals in a population (Hewitt and Butlin 1997), the mating system can be altered as population structure is altered, possibly affecting recruitment into the next generation and, ultimately, the fishery.

BEHAVIORAL DYNAMICS OF SPAWNING AGGREGATIONS

Squids of the genus *Loligo* are demersal spawners that usually lay eggs in large communal masses. Spawning aggregations are common for *Loligo vulgaris reynaudii* (e.g., Sauer et al. 1992), *L. pealei* (Arnold 1962; Summers 1983), and *L. opalescens* (McGowan 1954; Fields 1965). Although spawning aggregations are the principal means of reproduction, very small groups or individual pairs of squids also lay eggs in isolation in all three species. Commonly the spawning aggregations comprise hundreds, thousands, or even hundreds of thousands of squids. The behavioral dynamics are at first bewildering, but for *L. vulgaris reynaudii* and *L. pealei* progress has been made in sorting out the general scope of activities (e.g., Hanlon et al. 1997; Sauer et al. 1997).

Figure 1 is a generalized schema of a spawning aggregation of *L. vulgaris reynaudii* in South Africa. The
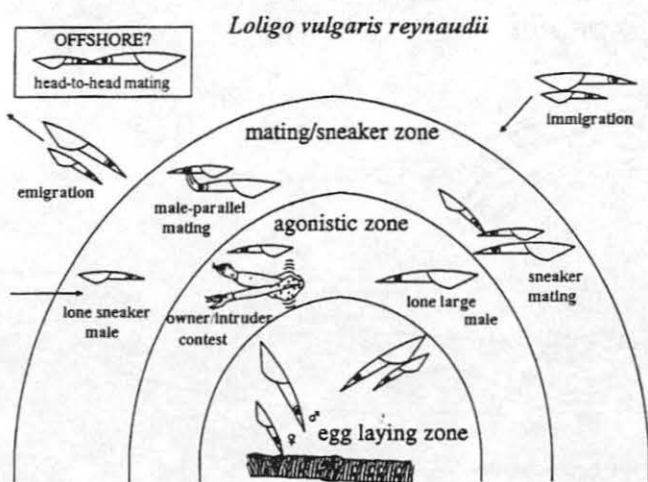
Figure 1. General schema of a spawning aggregation for *Loligo vulgaris reynaudii* off South Africa (modified from Hanlon and Messenger 1996). The "zones" are somewhat arbitrary in their dimensions. "Owners" are large paired consort males, and "intruders" are unpaired large males attempting to become consorts. Offshore head-to-head mating is speculative, but females often have sperm in the seminal receptacle.

main components of the scheme apply generally to the other species as well: (1) an egg-laying "zone" with pairs descending to the substrate and the females inserting individual egg capsules into the communal egg mass; (2) an area with considerable agonistic (fighting) behavior, and (3) an area with mating (several types). In some respects, these aggregations resemble a busy airport in which pairs of squids are circling above and then descending to lay eggs before repeating the cycle. Meanwhile, lone males continually use multiple tactics to obtain mates, both by fighting paired males to replace them as consorts, or by obtaining extra-pair copulations (EPCs); small males are also attempting to gain EPCs. Head-to-head mating has not yet been observed in this species, but it certainly occurs, because females usually have stored sperm in the seminal receptacle; it is possible that this type of mating occurs while the populations are offshore.

Operational Sex Ratios

Although the ratio of males to females is generally 1:1 for *Loligo* populations, in spawning aggregations there appears to be a skew toward slightly more males, which establishes a selection gradient of males competing for females. This aspect of squid biology is poorly known, however, and extensive behavioral observations and quantification are needed to determine the operational ratio of males to females because this is an essential feature of sexual selection processes. Determining how many individuals are actively participating in sexual behavior on any given day or week within a population or restricted geographic area is a challenging task, yet ROVs, telemetry, and divers offer methods to accomplish this.

Multiple Mating Positions and Multiple Mates

Two or three methods of copulation for each individual are known in many loliginid squid and octopus species, and these provide a critical source of variation in cephalopod mating systems. What determines the method to be used by a particular pair of squids at any given mating encounter is unknown. In *Loligo*, it is worth pointing out that in the "head-to-head" position the spermatophores appear to be passed only to the seminal receptacle below the mouth for sperm storage and eventual use by the female (e.g., Drew 1911). By contrast, in the "male-parallel" position the spermatophores are placed inside the female's mantle cavity near the opening of the oviduct (fig. 2). The head-to-head position has been correlated with extra-pair copulations in *L. vulgaris reynaudii* (Hanlon et al. 1994; Sauer et al. 1997) and in *L. pealei* (Hanlon 1996; fig. 3), but no such position has been observed in *L. opalescens*, although there is a seminal receptacle below the mouth as in the other species (see comment in Concluding Thoughts). In the male-parallel position, eggs would have to be extruded and fertilized within minutes or hours to take advantage of those spermatophores, many of which seem to be partially or wholly broken as they are deposited (Drew 1911).

Both sexes have multiple mates, although the absolute number of mates is unknown on natural spawning grounds. In laboratory trials, females of *L. pealei* are known to have up to four mates within several hours, and to lay eggs after mating with several males in succession (Hanlon et al. 1997). These same females lay eggs in bouts that are several days or weeks apart, and in each bout they typically deposit 20–50 egg capsules.

The complexity of sexual behavior in *Loligo* becomes more obvious when the multiple mating positions and mates are analyzed by the different behaviors of each sex. Possibly the most fascinating aspect of this is that female *L. pealei* (U.S. East Coast; Hanlon 1996) and *L. vulgaris reynaudii* (South Africa; Hanlon et al. 1994) perform EPCs with small sneaker males, so that each female may have three or more sources of sperm to fertilize eggs in each egg capsule she deposits (ca. 200 eggs per capsule). These three sources would be from the large paired male, the stored sperm in the seminal receptacle, and the sneaker male, who in *L. vulgaris reynaudii* appears to mate the female when she is holding an egg capsule in her arms. Furthermore, there may be more than one male's sperm stored in the seminal receptacle.

Male Behaviors: Fighting, Courting, Copulating, Sneaking, and Guarding

On spawning grounds, large male *Loligo* strive to form temporary pairs with females, with the goal of having preferred access to copulations. The operational sex ratio
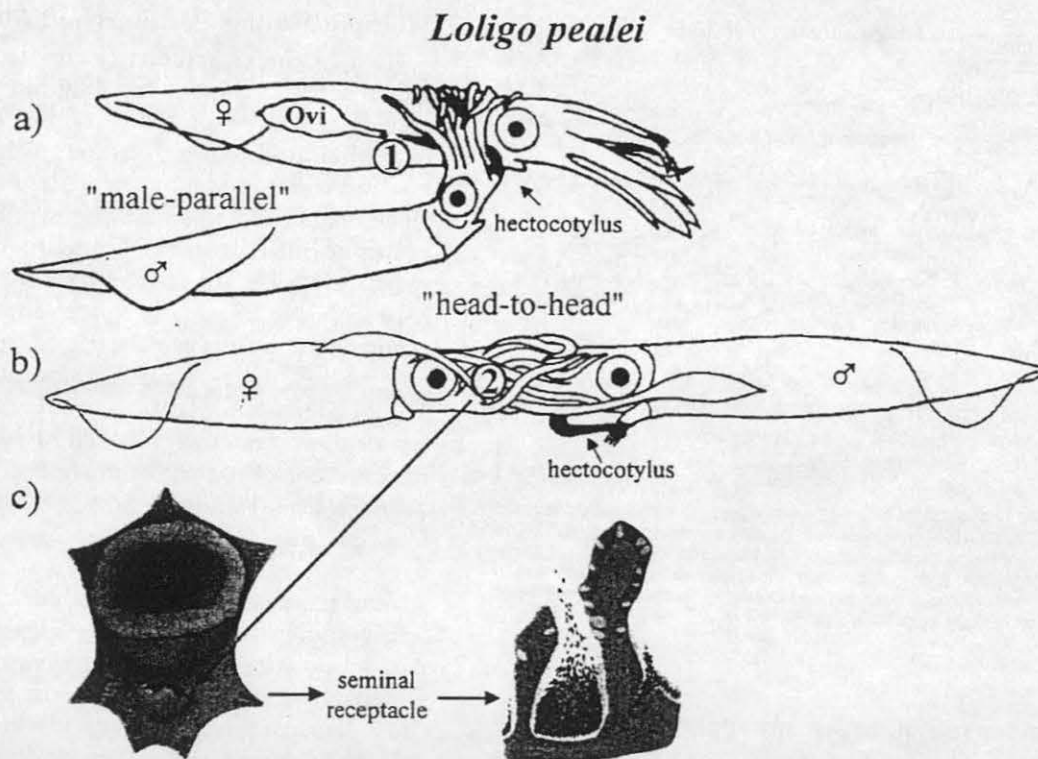
Loligo pealei

Figure 2. Two sperm sources and their placement during different methods of copulation in *Loligo* spp. Drawing is based upon *L. pealei* (modified from Drew 1911 and Hanlon and Messenger 1996). 1. Spermatophores are transferred by the hectocotylus (darkened) and placed near the external oviduct (Ovi) in the mantle cavity of the female during male-parallel mating (*a*). Eggs are usually laid shortly after this type of mating. 2. During head-to-head mating (*b*), males place sperm directly into a seminal receptacle located just below the mouth of the female (*c*). Note stored sperm in the cross-section of the seminal receptacle. Egg laying does not usually take place soon after head-to-head mating.

is skewed toward males, thus males must fight to obtain a mate and then be able to repel the lone rival males. Thus these "consort males" spend considerable energy and time courting and defending individual females, and they have high mating success (Hanlon et al. 1997). By contrast, lone large males spend time trying to become consort males, and focal behavioral sampling of these males has shown them moving from one pair to another, challenging consort males in agonistic bouts that use multiple visual signals and sometimes escalate to fin beating, which is a physical test of strength (Hanlon et al. 1994; Hanlon and Messenger 1996; DiMarco and Hanlon 1997; Sauer et al. 1997).

Yet on all spawning grounds there are smaller males too, and their tactics are very different. They do not engage in agonistic bouts with larger males, but opt to stay distant from pairs and observe them vigilantly. It is worth emphasizing that some small males are sexually mature and active, so that mating is not reserved for large males. The small "sneaker males" rush in and copulate with paired females in the head-to-head position, often with no resistance from the consort male (fig. 3). In 1997, two additional sneaking tactics were observed for *L. pealei*

off Cape Cod (Hanlon et al. 1997). First, small males sometimes became "bold" and moved around the egg mass in groups of 2–4, occasionally darting in for an EPC; thus we have observed both surreptitious and bold sneakers among small males of *L. pealei*. Second, lone large males became "sneakers" on occasion by dashing in and copulating with paired females in the male-parallel position (opposite to that of the small sneakers that mated head-to-head). Overall, five male behaviors have been documented as tactics to obtain copulations (Hanlon et al. 1997).

Finally, the large consort males guard their paired female mates as they descend toward the egg mass to deposit an egg capsule. Such guarding is a common feature of mating systems characterized by sperm competition. However, the degree of vigilance and guarding by consort males varies a great deal, and its meaning remains to be discovered.

Female Behaviors: Choosing Mates and Choosing Sperm

Generally the most obvious behaviors seen in animal mating systems are those of the males, but it is becoming
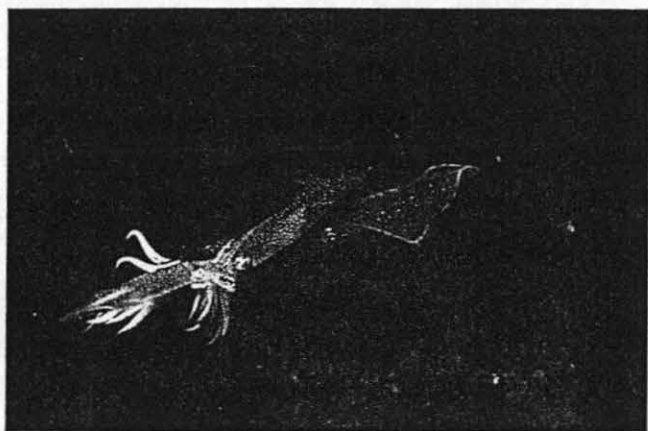
Figure 3. Sneaker male (left foreground) of *Loligo pealei* mating a paired female as the large consort male does not interfere (photo by William K. Macy).

increasingly apparent that females exert several levels of mate choice (Andersson 1994), including methods of sperm manipulation and allotment—a phenomenon known as "cryptic female choice" and elucidated in a provocative book by William Eberhard (1996). Recent studies of sexual selection point out a fundamental discovery: the mechanisms of female choice and their influence on relative paternity by multiple mates are considerable, and may be powerful forces in the ultimate outcome of fertilizations.

Female *L. pealei* (and perhaps the other two species) arrive on nearshore spawning grounds in spring with stored sperm in the seminal receptacle. Thus it is evident that they mate early in their life cycle, and they clearly have at least one source of sperm (a "backup" perhaps). Theoretically they may not need to mate again on the spawning grounds, but squids near shore on Cape Cod engage in high levels of sexual activity.

The curious feature of female *Loligo* behavior is that they appear to be generally receptive to all male mates, and they are relatively passive; i.e., they do not typically show conspicuous behaviors or other obvious signs of rejection of male suitors. Females tend to accept multiple mates even in succession on a single day. But analyses of video tapes of *L. pealei* females on spawning grounds show cases in which females actively jet backwards when males attempt to mate them (Hanlon, Maxwell, and Shashar, unpubl. data). This has happened mostly when sneaker males approach for a head-to-head mating, but has also been seen for male-parallel mating. Such rejections would be cases of "direct" female choice of mate. Most interesting, a recent paper by Wiley and Poston (1996) introduced the concept of "indirect female choice," in which females may set the stage for competition for males before arriving at the spawning grounds, so that any male fit enough to be present and sexually active on the spawning ground has already proved his fitness. In such a system, it might pay females to mate with any male present.

A female *Loligo* may exert choice in the decision of which mating position is used, or whether stored sperm are used when she extrudes each egg capsule, but experimental evidence is lacking for either of these possibilities.

Female fecundity and reproductive output are not well understood in *Loligo* spp., although the information is essential for fishery managers. There is considerable controversy over whether females are terminal "big bang" spawners or "intermittent" spawners over several months (Hanlon and Messenger 1996). Only in *L. opalescens* have dying squids been seen on the mating grounds, which is anecdotal evidence for terminal spawning. There are documented cases in which individual females of *L. pealei* lay eggs over weeks and months in the laboratory. Hixon (1980) documented a case in which a single female deposited 222 egg capsules over 72 days during several bouts of egg laying. Recent trials in our laboratory demonstrate high variability in reproductive output: some small females are as fecund as large females, as determined by measuring the number of mates and egg capsules that are laid over several weeks in captivity (M. Maxwell and R. Hanlon, unpubl. data, 1997). In a single day, one female laid 70 egg capsules; another had at least 6 mating partners over 33 days in the laboratory, so the hypothesis that females commonly have many mates may prove to be true. Clearly more data are required on this subject.

PROBABILITY OF MULTIPLE PATERNITY IN EGG CAPSULES

There is likely to be a rather high degree of multiple paternity in egg capsules of all three of the loliginids considered in this paper, for the following reasons. Pairings of consort males with females are temporary, leading to a high turnover of mates for both males and females. Individuals mate multiple times, often with different mates, even during the same day, and eggs are not always laid after each mating, so that sperm from several males mating in succession could be competing for fertilizations within the egg capsules that are laid that day. There are multiple positions of mating, each with different sperm placement (fig. 2). Females can store sperm for long periods, probably from different males, in the seminal receptacle below the mouth. Females also exercise the option of releasing their stored sperm—or not releasing it—onto egg capsules. When they do release it, however, there is almost certainly going to be multiple paternity.

Sperm competition can take place at multiple levels in such a mating system. First, of course, is the level of whole-animal behavior of males and females that has

been outlined above. To demonstrate this, let us follow the probable course of an egg capsule from its extrusion from the oviduct to the time it is laid in the substrate:

- Egg capsule is extruded from the oviduct into the mantle cavity.
- Free-swimming sperm may be present in mantle cavity from male-parallel mating.
- Sperm enter jelly matrix of egg capsule and swim toward ova.
- Sperm swarm at micropyle of ova[1].
- Egg capsule is drawn by the female into her arms.
- Stored sperm from seminal receptacle may be released and enter jelly matrix and swim toward ova.
- Sperm competition at the micropyle of each ovum may be occurring among sperm from the mantle cavity (male-parallel mating) and from the seminal receptacle (from head-to-head mating).
- In some species, a head-to-head mating can occur just as the egg capsule is held in the arms, so direct deposition of spermatophores on the egg capsule would provide another source of sperm.
- The egg capsule is deposited into the substrate.

Collectively then, multiple paternity must be expected in some percentage of the egg capsules. It is important to know paternity between egg capsules as well as within egg capsules. In both cases the question of "how many" is important, both in evolutionary terms to the individual squids as well as to fishery managers who must be concerned about gene mixing within the population.

How is multiple paternity measured? Field samples of eggs can be analyzed by DNA fingerprinting, which can tell us only that multiple paternity has occurred. Complementary laboratory studies of selective mating combined with DNA fingerprinting of all participants provide detailed information that can elucidate mechanisms of sperm competition. In laboratory experiments, my colleagues and I control the mating sequences; we know the recent mating history of each female in captivity; and we have tissue samples of each potential father to measure paternity with accuracy (Hanlon et al. 1997). The practical difficulty is that many DNA samples must be run for each egg capsule (which contains 100–200 ova), and this is both time-consuming and expensive.

DO COMMERCIAL CAPTURE TECHNIQUES SELECTIVELY REMOVE CERTAIN SQUIDS?

If commercial capture techniques selectively remove certain sizes or sexes of squids, they could create an artificial sexual selection gradient. The consequences of

this artificial gradient would be manifest as differential gene mixing in the next generation.

In South Africa, jigging is the primary capture method for *L. vulgaris reynaudii*. Lipinski (1994) found that jigs undersampled both the largest and smallest squids compared to purse seines (which were presumed to be sampling all sizes equally); this could be extrapolated to mean that the large consort males and the smallest sneaker males, or possibly the smallest females, were undersampled by jigging. Sauer (pers. comm., 1998) found evidence that large paired consort males are less interested in jigs than are lone large males; furthermore, he noticed that females not actively laying eggs were more interested in jigs. These types of observations need to be quantified because they are important to management decisions.

Loligo pealei off the northeastern United States are captured commercially mostly with trawl nets, but also near shore with weir traps. Weirs (which are passive devices) probably capture entire schools, and it would be expected that they reliably sample the adult population. The largest and fastest squids (males in this species) may avoid trawls, and video cameras affixed to trawl nets are now being used in New England to assess such avoidance behavior (Glass and Wardle 1989).

Loligo opalescens off California are attracted with lights, then captured by various types of surrounding nets (purse seines, lampara nets, etc.). If squids naturally spawn at night, it is possible that only some participants on active spawning grounds might be attracted to the lights and captured, while others remain near the demersal eggs and avoid capture. To my knowledge, such information is not available.

A main point here is that practically no information has been gathered to compare the composition of captured squids with the "normal" distribution of squids in an effort to assess the possible deleterious effects of fishing on their reproductive behavior.

For the same reasons, it would be beneficial to study the behavior of squids in relation to jigs, lights, and nets (both passive and actively fished). In addition, the effects of trawls or lampara nets on demersal eggs should be considered. Finally, it is possible that female fecundity is affected by these methods, especially if fecundity partially depends upon the social interactions of schools of squids engaged in intensive sexual competition.

REPRODUCTION, RECRUITMENT, AND FISHERY MANAGEMENT

Reproduction in loliginid squids is a complex system that encompasses a wide spectrum of behavior, a large anatomical investment, and a long period during the short life cycle. This complexity is one measure of the alternative—and flexible—reproductive tactics that should be expected in a short-lived species that migrates to and

---

[1]This process of swarming before fertilization takes up to 10 minutes in laboratory observations (Arnold 1984), which would allow ample time for all the behavioral events of sperm competition to be completed.

from different habitats. What does this mean with respect to managing the fishery?

The underlying notion emerging from this recent work is that the mating systems of squids like *L. pealei* and *L. vulgaris reynaudii* seem to result in genetic diversity in the next generation. This is likely to aid recruitment processes for the next generation, although the dynamics of squid recruitment are not well studied (Rodhouse et al., in press). Much of this diversity appears to result from the multiple paternity that we expect to find not only *among* the many egg capsules (each with 100–200 ova) laid by each individual female, but *within* each egg capsule as well. Ultimately this diversity results from the reproductive behavior of males and females before and during their time on the spawning grounds.

The difficulty of making such assessments should not be diminished. Several other mechanisms might influence paternity, gene mixing, and recruitment. For example, I have been assuming that if a fishing technique selectively removes the large consort males, then gene mixing and subsequent recruitment will be affected insofar as the largest fit males will not be well represented in subsequent populations. But perhaps those same consort males acted as sneaker males months before arriving on the spawning grounds, and their stored sperm were used by some females, perhaps even in precedence over males that the females encountered on the spawning grounds. Although this seems unlikely, it is possible, and DNA studies may turn up cases such as this in laboratory trials. As another example, it is possible that sneaker males are more fit than large consort males, and that recruitment might be strengthened by having more of their genes in the population if large consorts are removed.

As a simple generalization, limited impact on spawning aggregations by targeted fishing will probably not interfere drastically with gene mixing and egg laying, and thus will not have a strongly adverse effect on recruitment. What I mean by "limited impact" is moderate fishing pressure on spawning grounds, and verification that the fishing techniques do not selectively take one segment of the breeding population (e.g., largest consort males, or females, or sneaker males). Unfortunately, such verification is not yet available for any of the three fisheries I have referred to in this paper. This should be a rather high priority for research so that fishery managers will have some biological data upon which to base decisions.

Another practical fisheries consideration is whether commercial fishing takes place during the peak reproductive activity of a species. What sort of disruption would occur if it did? To determine the peak daily time of reproductive behavior, ROVs stationed near communal egg beds could sample around the clock for several days. If, for example, *L. opalescens* spawns predominantly during the day, then commercial fishing at night is likely to disturb mating and egg laying less than daytime fishing directly on spawning squids.

Some of the generalities presented in this paper are likely to apply to *L. opalescens*, but I hasten to add that *L. opalescens* appears to have some differences (Hurley 1978) from the mating systems of *L. pealei* and *L. vulgaris reynaudii*, which have now been studied in some detail (e.g., Hanlon 1996; Hanlon et al. 1997; Sauer et al. 1997). Only one mating position (male-parallel) has been verified in *L. opalescens* (McGowan 1954; Fields 1965). Fields reported that he "might" have observed head-to-head mating once among "scores of encounters," and he noted that it happened to occur "between a small male and a large female." From our knowledge of other *Loligo*, it is likely that Fields observed a sneaker male, but such a concept was unknown at that time.

There is keen competition for mates on the spawning grounds, as highlighted by Hurley's (1978) field observation of five males simultaneously attempting to mate a single female. Furthermore, Fields (1965) noted that "several males may single out one or two females from a group and mate several times with them, ignoring the other females present." Such behavior has not been noted in the extensive observations on the other two *Loligo*.

It is not clear from anatomical studies that female *L. opalescens* can spawn intermittently (Reckseik and Frey 1978), but this requires future behavioral study. Finally, female *L. opalescens* often hold the egg capsule in a horizontal position for long periods of time, even moving it up and down, which would be a plausible way to release stored sperm along the length of the egg capsule, which Fields (1965) suggested. Neither *L. vulgaris reynaudii* nor *L. pealei* have been reported doing this. My colleagues and I have looked for this behavior at communal egg masses of *L. pealei* and have not seen it after dozens of observations.

CONCLUDING THOUGHTS

It is impossible in a short treatise to consider all the features of reproduction that may be affected by, or may themselves affect, a commercial fishery. My point is to highlight the nature of the mating system—particularly its flexibility and multiple tactics—so that fishery managers and teuthologists can consider the possible effects on recruitment if fishing techniques alter the system.

The California fishery for *L. opalescens* is under pressure, not only from commercial fishing but from the influence of El Niño, which has displaced squid populations greatly during 1997 and 1998. It would be prudent to err on the conservative side and protect some known

traditional spawning grounds of *L. opalescens* until some features of the mating system are studied, particularly since this species is so short-lived and recruitment could be affected so directly. Recall, for example, that some of the mechanisms that seem to promote genetic mixing (alternative mating positions, intermittent spawning, multiple paternity within egg capsules) have been shown only in other species, not *L. opalescens*. There is substantial recent literature on the precautionary approach to fishery management, which argues for more restrictive management in the face of uncertainty (e.g., FAO 1997; Serchuk et al. 1997).

Nevertheless, fishermen and managers alike should be encouraged that our current knowledge indicates that the mating systems of *Loligo* spp. can probably withstand a moderate amount of targeted fishing on spawning squids, even though solid scientific evidence is needed to verify this. The problems are known, the techniques are available, and hopefully the opportunity to study these issues will be realized as well.

ACKNOWLEDGMENTS

LITERATURE CITED

Andersson, M. 1994. Sexual selection. Princeton, N.J.: Princeton Univ. Press.

Archer, J. 1988. The behavioural biology of aggression. United Kingdom: Cambridge Univ. Press.

Arnold, J. M. 1962. Mating behavior and social structure in *Loligo pealei*. Biol. Bull. 123:53–57.

——. 1984. Cephalopods. *In* Reproduction. Vol. 7, The mollusca. A. S. Tompa, N. H. Verdonk, and van den Biggelaar, eds. Pp. 419–454.

Augustyn, C. J., and B. A. Roel. 1998. Fisheries biology, stock assessment, and management of the chokka squid (*Loligo vulgaris reynaudii*) in South African waters: an overview. Calif. Coop. Oceanic Fish. Invest. Rep. 39 (this volume).

Birkhead, T. R., and A. P. Moller. 1992. Sperm competition in birds: evolutionary causes and consequences. United Kingdom: Academic Press.

Birkhead, T. R., and G. A. Parker. 1997. Sperm competition and mating systems. *In* Behavioural ecology: an evolutionary approach, J. R. Krebs and N. B. Davies, eds. Oxford, U.K.: Blackwell Science, Ltd., pp. 121–145.

Darwin, C. 1871. The descent of man and selection in relation to sex (ed.1). London: Murray.

Davies, N. B. 1991. Mating systems. *In* Behavioural ecology: an evolutionary approach, J. R. Krebs and N. B. Davies, eds. Oxford, U.K.: Blackwell Science, Ltd., pp. 263–294.

Dewees, C. M., and R. J. Price. 1982. Overview of the squid fishery on the Pacific coast of the United States. New England Fisheries Development Foundation, Inc. Proceedings of the International Squid Symposium, August 9–12, 1981, Boston, Mass. Pp. 197–212.

DiMarco, F. P., and R. T. Hanlon. 1997. Agonistic behavior in the squid *Loligo pealei*: fighting tactics and the effects of size and resource value. Ethology 102:89–108.

Drew, G. A. 1911. Sexual activities of the squid, *Loligo pealii* (Les.). J. Morphol. 22:327–359.

Eberhard, W. G. 1996. Female control: sexual selection by cryptic female choice. Princeton, N.J.: Princeton Univ. Press.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

FAO. 1997. Precautionary approach to fisheries. FAO Tech. Pap. no. 350 (1).

Fields, W. G. 1965. The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. Calif. Dep. Fish Game, Fish Bull. 131, 108 pp.

Glass, C. W, and C. S. Wardle. 1989. Comparison of the reactions of fish to a trawl gear, at high and low light intensities. Fish. Res. 7:249–266.

Hanlon, R. T. 1996. Evolutionary games that squids play: fighting, courting, sneaking and mating behaviors used for sexual selection in *Loligo pealei*. Biol. Bull. 191:309–310.

Hanlon, R. T., and J. B. Messenger. 1996. Cephalopod behaviour. Cambridge, U.K.: Cambridge Univ. Press, 219 pp.

Hanlon, R. T., R. F. Hixon, and W. H. Hulet. 1983. Survival, growth, and behavior of the loliginid squids *Loligo plei*, *Loligo pealei*, and *Lolliguncula brevis* (Mollusca: Cephalopoda) in closed sea water systems. Biol. Bull. 165:637–685.

Hanlon, R. T., M. J. Smale, and W. H. H. Sauer. 1994. An ethogram of body patterning behavior in the squid *Loligo vulgaris reynaudii* on spawning grounds in South Africa. Biol. Bull. 187:363–372.

Hanlon, R. T., M. R. Maxwell, and N. Shashar. 1997. Behavioral dynamics that would lead to multiple paternity within egg capsules of the squid *Loligo pealei*. Biol. Bull. 193(2):214–215.

Hewitt, G. M., and R. K. Butlin. 1997. Causes and consequences of population structure. *In* Behavioural ecology: an evolutionary approach, J. R. Krebs and N. B. Davies, eds. Oxford, U.K.: Blackwell Science, Ltd., pp. 350–372.

Hixon, R. F. 1980. Growth, reproductive biology, distribution and abundance of three species of loliginid squid (Myopsida, Cephalopoda) in the northwest Gulf of Mexico. Ph.D. diss., Univ. Miami, Miami, Fla.

——. 1983. *Loligo opalescens*. *In* Cephalopod life cycles, vol. 1, species accounts, P. Boyle, ed. New York: Academic Press, pp. 95–114.

Hobson, E. S. 1965. Spawning in the Pacific coast squid *Loligo opalescens*. Underwater Nat. 3(3):20–21.

Hurley, A. C. 1978. Mating behavior of the squid *Loligo opalescens*. Mar. Behav. Physiol. 4:195–203.

Krebs, J. R., and N. B. Davies, eds. 1997. Behavioural ecology: an evolutionary approach. Oxford, U.K.: Blackwell Sci., Ltd.

Lipinski, M. R. 1994. Differences among basic biological parameters in a population of chokka squid, *Loligo vulgaris reynaudii*, sampled by three methods. S. Afr. J. Mar. Sci. 14:281–286.

Lott, D. F. 1991. Intraspecific variation in the social systems of wild vertebrates. U.K.: Cambridge Univ. Press.

Lum-Kong, A. 1992. A histological study of the accessory reproductive organs of female *Loligo forbesi* (Cephalopoda: Loliginidae). J. Zool. Lond. 226:469–490.

Martin, P., and P. Bateson. 1993. Measuring behaviour. an introductory guide, 2nd ed. U.K.: Cambridge Univ. Press.

McGowan, J. A. 1954. Observations on the sexual behavior and spawning of the squid, *Loligo opalescens*, at La Jolla, California. Calif. Fish Game 40:47–54.

NFSC. Northeast Fisheries Science Center. 1995. Status of fishery resources off the northeastern United States for 1993. NOAA Tech. Mem. NMFS-F/NEC. Woods Hole, Mass. 138 pp.

Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 45:525–567.

Queller, D. C., J. E. Strassmann, and C. R. Hughes. 1993. Microsatellites and kinship. Trends Ecol. Evol. 8:285–288.

Recksiek, C. W., and H. W. Frey, eds. 1978. Biological, oceanographic and acoustic aspects of the market squid, *Loligo opalescens* Berry. Calif. Dep. Fish Game, Fish. Bull. 169, 185 pp.

Rodhouse, P., E. G. Dawe, and R. K. O'Dor, eds. In press. Squid recruitment dynamics. Rome: FAO Fish. Tech. Pap.

Sauer, W. H. H., M. J. Smale, and M. R. Lipinski. 1992. The location of spawning grounds, spawning and schooling behaviour of the squid *Loligo vulgaris reynaudii* (Cephalopoda: Myopsida) off the Eastern Cape coast, South Africa. Mar. Biol. 114:97–107.

Sauer, W. H. H., M. J. Roberts, M. R. Lipinski, M. J. Smale, R. T. Hanlon, D. M. Webber, and R. K. O'Dor. 1997. Choreography of the squid's "nuptial dance." Biol. Bull. 192:203–207.

Serchuk, F., D. Rivard, J. Casey, and R. Mayo. 1997. Report of the ad hoc working group on the NAFO Scientific Council on the precautionary approach. NAFO SCS Doc. 97/12.

Shaw, P., and P. Boyle. 1997. Multiple paternity within the brood of single females of *Loligo forbesi* (Cephalopoda: Loliginidae), demonstrated with microsatellite DNA markers. Mar. Ecol. Prog. Ser. 160:279–282.

Sissenwine, M. P., and A. A. Rosenberg. 1993. Marine fisheries at a critical juncture. Fisheries 18(10):6–14.

Smith, R. L. 1984. Sperm competition and the evolution of animal mating systems. Orlando, Fla.: Academic Press.

Summers, W. C. 1983. *Loligo pealei. In* Cephalopod life cycles, vol. 1: species accounts. Academic Press, pp. 115–142.

Wiley, R. H., and J. Poston. 1996. Indirect mate choice, competition for mates, and coevolution of the sexes. Evolution 50(4):1371–1381.