II. Collection, Maintenance and Population

DYNAMICS OF THE SQUID.

Capture

Squid are captured by an amazing variety of devices representing most kinds of fishing gear. This is not surprising because many were originally designed to catch pelagic or demersal fish species. Included are: fixed nets, surround nets, midwater trawls, otter trawls, fish pumps and hook and line fishing (an especially useful reference is von Brandt, 1964). World-wide, commercial quantities of squid are taken most often by surround nets, otter trawls, fish traps and squid jiggers (hook and line fishing with special lures called "jigs"). *L. pealei* was often taken in fish traps when traps were common along the Eastern Seaboard. The recent Japanese fishery for this species and other offshore capture is based on the use of large trawl nets, probably mostly otter trawls. Mechanized squid jigging has been introduced in Newfoundland with considerable success. There, as in Japan where mechanized jiggers were developed, the fishery is centered on non-breeding populations of Oegopsid squid. Jiggers are of little value in capturing *L. pealei* during the inshore season (Summers, unpublished results); perhaps because of life history differences between these squids. Surround nets and fish pumps have been used on other species of *Loligo* and are successful where aggregations are found; these have not been fully tested for consistent use on *L. pealei*.

For several years, the Marine Biological Laboratory at Woods Hole, Massachusetts, has supplied investigators with live squid taken by groundfish otter trawls from a chartered fishing vessel. Some 10,000 to 15,000 live animals are landed this way in a ten week period each summer. Prior to vessel charter, the laboratory obtained squid from various fish traps along the coast.

The principal advantage of an otter trawl in the inshore fishery for *L. pealei*, is its reliability. Set nets and their mobile variant, surround nets, can catch immense quantities of squid when aggregations are encountered. Locating squid aggregations remains an imprecise art at best, relegating set and surround nets to irregular productivity. Trawls, on the other hand, can be deployed over any good bottom with no special problem, are readily moved from place to place to suit the fishing conditions and are towed considerable distances, thus greatly increasing the chances of encountering squid. Furthermore, *L. pealei* is known to be more available to otter trawls in daylight hours when it apparently becomes demersal and may have less tendency to form schools (Summers, 1969).

Several modifications of trawling procedure improve the chances of catching relatively undamaged, live squid. None of these ordinarily yield the quality of squid taken by traps or set nets or, perhaps, by jigging. Considerable damage appears to be rendered to squid by other animals in the trawl. For this reason, we find it advantageous to rig the trawl to fish lightly on the bottom in an attempt to minimize the simultaneous capture of skates and rough invertebrates. A fine-mesh, knotless liner is useful in the cod end of the net, and a hoop between the liner and the cod end prevents the catch from being crushed when the net is drawn on board. A quick release cod end closure is desirable because the catch must be dumped quickly into water if live squid are to be obtained. Short tow durations and smaller sized nets re-
duce the overall catch, but enhance the probable survival of individual squid. In spite of these modifications, it is only through redundancy that sufficient numbers of live squid are taken by the trawl.

**Handling and Maintenance**

Squid are active animals which ordinarily gain safety through flight. As a result, they avoid any form of confinement and become very agitated when trapped, often with the result that they damage themselves in attempts to escape. It is not practical to anesthetize them for ease in handling. The best general rule is to avoid handling as much as possible. We have had some success in moving squid short distances with 40 liter, plastic containers filled to the top and closed with a tight lid. Water circulation, aeration and no more than moderate crowding are required for any tankage used to transport squid. Reduction of the free surface appears to be highly desirable.

Dip nets, when used to transfer squid, should be at least 20 cm in diameter to accept the squid crosswise without distortion. The bag should be made of knotless netting, blunt at the bottom and of a length which will not allow the squid to get caught behind the rim when the net is turned over. Squid are best caught end on with a dip net, and it is often easier to approach them from the tail end because this is their normal avenue to escape when alarmed. On the other hand, they often squirt ink when netted, and their range of targets can be more controlled if they are caught from the head end. The latter approach has the disadvantage that the captured squid is more likely to tangle its arms in the net (or even bite the netting) than with tail-first capture.

Formulas for the maintenance of squid under laboratory conditions have been the subject of many rumors and unscientific practices at the Marine Biological Laboratory and elsewhere. These almost never appear in the literature for what one may suppose are obvious reasons. The simple fact is that squid in general, and representative *L. pealei* in particular, do not survive long in captivity. Summers and McMahon (1970) have reviewed some of the literature on squid maintenance and report a half-life of two days for *L. pealei* under rudimentary conditions. In recent work, the same authors have extended the mean survival of several batches of *L. pealei* to as long as two weeks through the use of more commodious facilities. The record survival of individual animals extends over one month. Mr. Stuart Jacobson of Boston University kept one isolated squid for 36 days in a standard sea table at the Marine Biological Laboratory during the fall of 1970 and Summers (unpublished) kept individuals 47 days and 59 days in recent experiments. Longer records may well exist, but little can be learned from them.

Summers and McMahon (in manuscripts) completed a series of 16 experimental survival runs employing a total of 468 squid during the period of May through November, 1970. Mean survival of squid in these runs was 4 days. The experiments employed a 2^6 factorial design where three imposed factors were studied simultaneously, each at two different levels. Imposed factors were: relative water temperature, crowding, feeding and tank shape. Analysis of variance demonstrated that tank shape was highly significant in squid survival (rectangular tanks superior to square ones); that relative water temperature was occasionally significant, though not consistent in its effect; and that the other factors were not found to be significant.

Water temperatures ranged from 6° to 23° C during the course of the 1970
survival experiments, even though squid were not encountered at ambient temperatures below 8°C. Those held in sea water chilled below 8°C were aberrant in behavior. No single range of water temperatures was demonstrated as beneficial to squid survival through these experiments. Crowding at levels of one to eight individuals per experimental cell (18 square feet by one foot depth) did not produce testable differences in the mean survival; neither did the chance isolation of one sex as contrasted to experimental cells holding mixed sexes. Breeding and egg deposition are thought to bring about mortality in both sexes. These experiments may have failed to demonstrate this factor because sexually mature, virgin individuals are unobtainable. No survival significance could be attributed to the upstream-downstream position of the particular experimental cells or the potential effects of zinc leaching into the chilled sea water tanks from a galvanized heat exchanger.

Age groups were identified among the experimental squid on the basis of a population dynamics study (Summers, 1971). The assemblage of animals used in survival experiments conducted in 1970 were composed of approximately 10%, 58%, and 32% of age groups 0, 1 and 2 years, respectively, and generally favored males among the older groups because of inadvertent selection for larger sized individuals. When mixed, the older (larger) individuals survived better than younger ones. Among actively breeding one year olds, male survivorship was greater on an average than that of females.

Extensions of these studies were carried out in 1971 by these same authors and G. N. P. A. Ruppert employing 246 squid in 8 experimental runs. Preliminary results of this latest work indicate a mean survival time of one week, and demonstrate the survival advantage of shock-absorbing inner tank walls and large tank sizes (2 and 3 times larger than in the previous experiments). Vertical pieces of polyethylene sheeting weighted on the lower edge and held away from the inner tank wall by a line of small diameter floats provided the shock absorbing material. Only clear sheeting has been used, but colored or opaque material could be employed.

Age groups in the 1971 survival experiments were composed of approximately 28%, 62% and 10% of 0, 1 and 2 year olds, respectively, similar to the previous years' breakdown, though more equal in sex ratio. Early in the season, when sexually mature 1-and 2-year-olds were mixed together, males appeared to hold a small survival advantage, but neither age group held a clear advantage. The mean survival of one-year-olds increased through the 1971 experiments and demonstrated a distinct advantage for non-breeding females late in the year. Mixed populations of 0-and 1-year-olds indicated a marked survival advantage for the larger one-year-olds. Mean survival of one-year-olds through the 1971 experiments was over 9 days.

Results of all these experiments suggests the following points of departure for the maintenance of adult *L. pealei*. The holding tanks should be clean (at least initially) and provided with a copious supply of running sea water. Squid are easily "spooked" and opaque tank walls and bottom are an advantage if movement near the tank is necessary. A tank cover can be used to physically contain the squid and may, if properly chosen, serve to provide diffuse and/or colored illumination. Constant illumination reduces the activity of the squid and simulates the conditions under which they are found near the bottom in nature (Summers, 1969). Feeding is not necessary for squid held for short periods of time (a few days); however, *Fundulus* or other live fish are suitable for feeding healthy squid for longer maintenance. The crowding of animals both by number and by biomass is not critical so
long as they have room enough to form schools and move about without contacting the tank walls. Shock absorbing inner tank walls should be employed in large tanks for maximum survival (see above).

**Laboratory Rearing**

It might seem that an alternative to the cost and effort of collecting and maintaining adult *Loligo pealei* would be rearing animals in the laboratory, since the eggs can be obtained in abundance. Thus far, all such attempts with *Loligo* have been futile. Several investigators such as Fields (1965), Boycott (1965), and Summers (personal communication, unpublished data) have tried with various levels of sophistication and been unsuccessful. Recently, LaRoe (1971) has succeeded in rearing another loliginid, *Sepioteuthis sepioidea*, from eggs to adult size in the laboratory. Unfortunately he was unsuccessful in his attempts to rear *Doryteuthis (=Loligo) plei* in the laboratory, and *Sepioteuthis* lacks the large axon size of *Loligo*. The major problem in rearing larval *Loligo* sp. seems to be finding an acceptable and abundant food source. With *Sepioteuthis sepioidea*, LaRoe found that newly hatched larvae would attack small mysids but ignore other food for several hours, feeding on it only if starving. With sepioïds, Choe (1966), Boletzky *et al.* (1971), and Arnold *et al.* (1972) found various species of mysids also to be acceptable food for the newly hatched larvae. All these species are relatively large egged, slowly developing animals with very short or no pelagic larval periods. Although they too lack the large axon so beloved by neurophysiologists, these species do offer large eyes, an easily accessible brain, and many other cephalopod attributes. Recently Boletzky and Boletzky (1969) successfully reared an individual *Octopus joubini* from an egg to sexual maturity. Opresko (personal communication) has also successfully reared *O. joubini* and *O. briareus* through several generations so the techniques for handling these species are well in hand. These large egg species also lack a planktonic larval stage and take up benthic life immediately upon hatching. Richard (1967a, 1968) has considerable data on the sexual cycle of *Sepia officinalis* and has successfully induced gonad maturation in this species by varying light cycles.

It would appear from these few successful rearings of cephalopods in laboratories that because of its planctonic larval life rearing *Loligo pealei* under completely artificial conditions would be quite a feat using our current techniques.

**Age**

There are no natural markers on *L. pealei* which can be used to quickly establish the age of a particular specimen. The beak and pen both bear faint growth “rings”, but the former wears away in life and does not display pattern which shows any direct relationship to age. Statoliths, which occur in this squid, grow at a slower rate than the whole animal. These are difficult to dissect, spongy in texture and, in our hands, devoid of useful markings even after various heat and chemical treatments.

The short survival of captive squid does not allow the determination of growth rates in aquaria. Ideally, one might measure, tag and release squid with the hope of capturing them again at a later time. Some work of this kind has been performed in Japan with the Oegopsid squid, *Todarodes pacificus*, though the emphasis was on migrational studies and not growth. Owing to the low probability of returns, the prospects of tagging *L. pealei* for growth studies are not good except under limited conditions (e.g. where a fishery already exists). Preliminary efforts to tag and re-
cover squid near Woods Hole were begun in the summer of 1970 using fin notches, plastic fish tags and numbered metal tags. Results of this initial work were not conclusive because of limited returns (Summers, unpublished).

One remaining option in determining the age of *L. pealei* is to examine its population dynamics. Various authors have proposed squid growth schemes based on changes in the mean or modal sizes of samples taken at different times of year. Verrill (1882) outlined the growth of *L. pealei* by setting generous size ranges for various, interpreted age groupings during the inshore season. Other authors have tabulated upper size ranges or extreme sizes of certain squids (Summers, 1971). These sources leave some doubt as to the adequacy of the sampling, especially in those cases where the squid represented a portion of a commercial catch. Because squid are good swimmers, the size bias of the collecting gear and any possible effects of migration have to be carefully accounted for in any growth scheme.

The population dynamics reported here are summarized from a recent study (Summers, 1971) representing sampling principally with large otter trawls, both inshore and offshore, through the period 1967 to 1970 inclusive. Some of the collections were reported previously relative to other data (Summers, 1967, 1968, 1969; Summers and McMahon, 1970). Offshore collections resulted from cruises ranging from Georges Bank to Cape Hatteras. Two of these were in the winter and one trip was made during the summer of 1969. Inshore collections were made on approximately 45 dates between early May and late November near Woods Hole. Freshly caught *L. pealei* were measured (dorsal mantle length) to the nearest centimeter and placed in one of three categories: males, females and unsexed young-of-the-year. Each sexed group averaged approximately sixty individuals per collection. Unsexed young-of-the-year squid were considerably more numerous, but in no case were fewer than twenty individuals used in the analysis. A size class separation was performed on each group following the method described by Cassie (1954); normal size distributions were assumed for sexed animals and lognormal models were used for young-of-the-year squid (see Summers, 1968 and 1971). The size class mean values, weighted by the percentage representation of that class, were pooled in units of one month by one centimeter mantle length (Figure 1). Each column (month) was again evaluated by the Cassie method and consistent breaks in size classes were taken as the intersections between year classes. Data for the young-of-the-year animals and for the offshore collections were treated qualitatively because gear selectivity of these samples was different than for the others.

It is of interest to note that these size class breaks were not always apparent by observation. The average squid caught near Woods Hole is 12-14 cm in mantle length, and year classes are not distinctive except for young-of-the-year animals (which increase in sample abundance through the fall) and two year old squid taken early in the season. A proposed age class scheme, the range of size class means and the mean size of sampled squid are shown in Figure 1. As illustrated, samples in the month centering on May first are exclusively two year old squid. During the following five months (1 June - 1 October), one year old animals dominate. By the first of November, young-of-the-year squid are more common in the samples than others, and that situation extends into the next month when the last squid leave the inshore waters near Woods Hole.
FIGURE 1. Proposed age groups and monthly occurrences of sexed squid (those over seven centimeters dorsal mantle length) from inshore samples taken near Woods Hole, Massachusetts from 1967 to 1970. Vertical bars represent the range of size class means resulting from graphical (Cassie method) size class analyses. The range of sizes for the predominant one year olds has been stippled for emphasis and a dashed line is shown at the approximate mid-range.

FIGURE 2. Proposed growth scheme for the squid, *L. pealei*. The mean size is indicated by sex for each of two broods observed annually from sampling conducted along the mid-Atlantic coast in the period 1967 to 1970. Stippled areas are reiterated from Figure 1.
Various aspects of the population are not shown in Figure 1. For instance, *L. pealei* is generally sexually mature when it first comes inshore in the spring and it is almost entirely sexually immature when it migrates offshore in the fall. A dramatic change in the sexual maturity of the population occurs in both sexes about the first of September. Two year old males remain sexually mature throughout the season and two year old females are not found beyond late June. The blending of young-of-the-year and one year old squid is gradual and extends from about the first of October through to the end of the inshore season.

In Figure 1, the one year old size range is arbitrarily divided by a dashed line at the mid-range. Based on the winter collections, it appears that there are two major hatching periods for *L. pealei* each year: one regularly observed near Woods Hole about the first of July and a second as much as four months later which probably is most successful in recruiting to the population in the southern half of the mid-Atlantic Bight (Summers, 1969 and 1971). The dashed line, then, is an attempt to segregate these two hatching periods of year old squid. If correct, the larger year old squid (approximately 1 July hatch) are dominant in the samples in June and July and give way to smaller year old squid (early November hatch) from August through the end of the season. Most of this latter grouping do not mature sexually before the following year and it is likely that they produce most of the two year old squid seen the following spring, as indicated in Figure 1. Abundance of Fall hatched squid is apparent in the reduced sexual maturity of squid after the first of September and the growth of mean mantle length of samples over the month of September.

The growth scheme is summarized in Figure 2. It is founded on an unbiased mathematical technique which aids in the identification of size classes and, therefore, is independent of earlier work. It should be noted that both sexes of the California squid, *Loligo opalescens*, and other more distantly related cephalopods are known to die soon after spawning (McGowan, 1954; Hobson, 1965; Fields, 1965). Complete evidence of a similar breeding-related mortality is lacking for *L. pealei*, but it is consistent with the growth scheme given here and assumed to be a common feature in squid biology. Owing to the persistence of two year old male squid and the occasional report of individual males approximately 45 cm in mantle length (Verrill, 1882; Summers, 1969; Vovk, personal communication), it seems likely that some of the males survive to reach an age of three years.

Nevertheless, the implication intended here is that squid of 19 to 20 months of age breed in waters near Woods Hole between approximately April and early July. Some of these may alternatively breed with year old squid (11-12 months of age) after late May when sexually mature year old animals become common. Some inter-breed between year classes involving the continuing small fraction of two year old males is possible as late as September. Breeding-related mortality would account for the consecutive disappearance of these age groups from the samples during the season. The fall hatched squid, especially males, show the inception of sexual maturity at about 12 months of age, and it is supposed that they would breed farther to the south where temperatures remain warmer later in the year. North of Cape Cod, a single breeding period of the July hatch observed near Woods Hole. This evidence supports the thesis that the northern range limit of *L. pealei* is set by the proximity of suitably warm breeding grounds. Studies comparable to Richard's (1966 to 1971) work on the influence of migration, day length, water temperature, and season of hatching on sexual maturity in *Sepia officinalis* have not been done on *L. pealei* but such data would be extremely useful.
ORGANISMIC LITERATURE CITED


