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A REVIEW OF CEPHALOPOD FISHERIES BIOLOGY

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Abstract

The status of knowledge of the biology of cephalopods applicable to fisheries management is reviewed, especialy relating to life span, age at maturity, fecundity, spawning, recruitment, migration, populations and prey/predator relationships. Data are summarized and major areas of lack of information are indicated. It is concluded that probably no species of squid or octopus has been sufficiently studied to afford proper data for management. Of approximately 650 species of cephalopods some data are available for only 23 species or about four per cent, some of which have no commercial value. The need for support of biological studies relating to the fisheries is stressed.

Introduction

A basic tenet of fisheries science is that stocks cannot be meaningfully managed without a solid basis of biological information on such factors as (1) life span, (2) age at maturity, (3) fecundity, (4) spawning, (5) recruitment, (6) migrations, (7) populations, and (8) prey/predator relationships.

If information on all or most of these subjects is necessary, then very few of the actual or potential commercial species of cephalopods have been sufficiently studied, as such data are unavailable. Fisheries officers may well question why data necessary for stock management are not available but the answer is simple; most cephalopod fisheries are relatively new and governments have allocated few funds for studies of a fishery that, except in one or two countries, is still not considered to be of major economic value. This view is now changing because of the increasing value of the fisheries. The following account is an attempt to review briefly the present status of the fisheries biology of cephalopods so that we may identify the gaps in our knowledge and make plans for future research.

Fisheries Biology

Japan, almost alone of the fisheries nations, has conducted biological studies of commercial species of cephalopods. This is understandable when one considers that for years Japan has been the major world consumer of both squid and octopus. Indeed, the world squid fisheries are primarily dependant upon the Japanese market and only secondarily upon the demands of Spain, Portugal, Italy, Greece, and recently the Soviet Union. Only in the last ten to fifteen years have other western nations, France, England, Germany, Poland, certain South American nations, Mexico, and the United States begun to realize the importance of cephalopods, either for their own consumption or because of interest in the Japanese market. But all of these nations are consumers and have little regard for management or resource conservation. This attitude is a result of several widely held premises among which the most common are beliefs that cephalopods represent a one year crop which will be wasted if it is not harvested, and that the supply is nearly inexhaustible. Thus there has been little incentive for the kinds of fisheries studies long undertaken on fin fish. Only when wide fluctuations in stocks appeared and fishing vessels were forced to go further and further afield did even the Japanese begin to undertake squid studies.

In the United States and Canada squid have been harvested for many years either for bait or for fish meal. As a result the price to the fisherman was low and agencies were uninterested in supporting fisheries investigations. In the last five years or so the picture has changed and much interest is being shown in the squid fisheries. Squid biology related to the fisheries, however, is still fragmentary and in its infancy.

On the other hand, scientists in France, England and the United States have long been interested in cephalopods for different reasons. Their interests have been based upon elucidating basic biological information: physiology, biochemistry, neuro-physiology, behaviour, genetics, phylogeny, systematics, zoogeography and others. This interest has been generated by medical importance, the search for basic scientific knowledge, and heuristic approaches. The great advances in the last decade in rearing and maintaining squid and octopus have not been primarily from attempts to aid mariculture but to provide animals for research.

Thus we see that there has been a polarization of research efforts, one based upon applied fisheries needs and the other on basic research and medical requirements. It is time that these two reservoirs of biological data are brought together and integrated for the mutual benefit of both interests.

This review draws heavily upon information from studies conducted at three widely separate areas: Newfoundland on *Illex illecebrosus*, California on *Loligo opalescens*, and Japan on *Todarodes pacificus*. The California study was the only planned, broad, biological program done purely for fisheries management in the United States. From lack of funds it was terminated after three years just as the program was beginning to yield useful results (Recksiek & Frey, 1978). The Japanese have led the field in squid studies and numerous papers have appeared in Japanese journals on practically all phases of squid biology related to the fisheries. Many of these are mentioned in FAO Fisheries Technical Paper 173 (Okutani, 1977). Most, however, are in Japanese with only brief English abstracts and are of limited value for western workers.

An indication of the growing interest in the cephalopod fisheries is the appearance in the last ten years of four major reviews of the fisheries on a world wide basis (Arnold, 1979; Okutani, 1980; Voss, 1973, and Zuev & Nesis, 1971). Another valuable aid for fisheries biologists has been the publication of the FAO Identification Sheets for the various fishing fishing areas of the world (Roper, 1977; Roper & Sweeney, 1982).

The following pages review the problem areas in our knowledge as given in the Introduction.

Life Span. There is little solid information on the age and life span of cephalopods. No reliable method has so far been developed for aging either squid or octopus. Most data on age have been derived either from rearing studies or from length/weight frequencies and size at maturity. Aquarium studies, until recently, have been conducted mainly on octopods. *Octopus vulgaris*, as well as other species, can be easily maintained and will spawn and brood their eggs in aquaria. Usually the female dies after her eggs have hatched. Because the females attain sexual maturity in one year or less, mate, brood their eggs, and die, it has been assumed that the females live for only one year. It has been axiomatic that female octopus do not feed during egg brooding, waste away and die, despite occasions on which the females fed and continued to live. So general has the belief become that some females die after their brooding in aquaria is finished because they have been starved to death.

Probably in nature some octopus live to brood several times and to attain a much larger than average size. Operations on the optic gland (Wodinsky, 1977 and pers. comm.) may prevent sexual maturity and the animals may live to considerable age and attain great size. Possibly the very large animals occasionally reported may represent those in which sexual maturity has been repressed. It may also be that they are animals that have survived several spawnings. Small octopus such as *O. hummelincki*, a tropical western Atlantic species, frequently live after brooding (Reisinger, unpubl. data).

The other method of aging is by sampling populations to obtain either length frequencies or weights or both over considerable time periods, mostly from the commercial fisheries. It is thus possible to follow the young squid through the year, assess their monthly growth and determine when they have reached maturity. This method is standard practice in squid studies but also has its drawbacks. Size at maturity is not necessarily representative of life span unless one assumes that squid die after mating and spawning and that they spawn only once. This assumption is based primarily upon the many records of mating/spawning frenzies in *Loligo opalescens* in California as reported by Fields (1950), McGowan (1954) and others.

This kind of aggregation and frenzy has not been reported for other species and may be atypical. Length and weight frequencies may also become less reliable and fail completely as far as age is concerned as immature animals enter the mature population and size groups are lost in the adult weight and length ranges.

The importance of an accurate aging method has long been recognized and attempts have been made to use the few hard structures of teuthoids, their beaks, gladius, sucker rings, and statoliths, by searching for growth rings comparable to those found on fish scales and otoliths. Statoliths are the only structures so far that have shown possibilities but considerable difficulties are encountered in interpretation of rings in certain areas of the statoliths (Spratt, 1978; Kristensen, 1980). Nonetheless, this structure is promising and may soon prove useful.

The cuttlebone of *Sepia* was first shown to be of value in aging by Choe (1963) who found that in aquaria and large cisterns a chamber or striation was laid down every one to three days and could thus yield a fairly reliable age determination. Boletzky (pers. comm.) is now working on this and the effects of various factors on the deposition of chambers using European cuttlefish.

Realizing that no definitive method has been developed, Table 1 has been derived from references in the literature. Examination of these data shows that cephalopods in general appear to have an average life span of one to two years but that, depending upon the species, it may range from about four months or less to five years or longer. Small species such as *Octopus joubini*, and probably the pygmy cuttlefish *Idiosepius*, and other small forms are very short lived and may produce one to two or even three generations a year. The estimated ages of *Octopus vulgaris* based on size may be due to abundant food and fast growth as appears to be the case with the giant *Octopus dofleini* of the North Pacific.

Even though *Loligo opalescens* dies shortly after mating and spawning, age estimates both by length frequencies and statolith examination indicate that they live for one to about three years. Studies on *Loligo pealei* and *Illex illecebrosus* also indicate this age range. This has been explained by Summers (1971) and Mesnil (1977) as a result of winter/spring or summer/fall spawning. In the first case the females would spawn at one year of age or thereabouts while in the second case conditions would delay or inhibit growth in the late hatchlings so that they would not mature until the following summer and would spawn at an age of one and half to two years of age or even later.

The age of oceanic squid has not been determined using statoliths and has depended upon estimates resulting from frequency curves. No one has attempted to estimate the ages of the giant squid *Moroteuthis* or *Architeuthis*. Although nothing is known of age at spawning, females of midwater squid such as *Chaunoteuthis* and some of the cranchiids show strong mantle deterioration; the wall becomes soft and flabby, and it appears that these females do not recover and also die shortly after spawning.

The ages of deep-sea squid and octopods are unknown. Possibly reduced metabolism in cold waters and low food availability may contribute to longer life spans. The question cannot be resolved at this stage of our knowledge.

It is obvious that special effort is required to attempt to resolve the age question before satisfactory fisheries models can be constructed.

Age at Maturity. This has two built-in difficulties: determining age as discussed above, and recognizing sexual maturity or stages thereof.

Sexual maturity in males is usually considered to occur when spermatophores are found in Needham's sac. Studies now being conducted at Miami by Hess indicate that the first spermatophores manufactured may be incomplete and that the male makes spermatophores over a considerable period of time (Hess, pers. comm.). It is obvious that the sperm in the earliest spermatophores must either have an inhibitor or a long viability in order for them to remain active until spermatophore manufacture is completed and the male is functionally "mature". Body growth continues throughout the time of spermatophore construction so that from initiation

TABLE 1

Estimated life span of selected species of cephalopods based upon various methods of analysis found in the literature.

Species	Estimated span	Method	Authority
SEPIOIDEA			
Sepia officinalis	2-3 years	?	Mangold, 1963
S. orbignyana	1-1½ years	length frequencies	Mangold, 1963
S. elegans	1 year	length frequencies	Mangold, 1963
Rossia macrosoma	1 year plus	length frequencies	Mangold, 1963
Sepiola rondeleti	1 year ?	?	Mangold, 1963
Sepietta oweniana	less than 1 year ?	length frequency	Mangold, 1963
TEUTHOIDEA			
Loliginidae			
Loligo vulgaris	males 3-4 yrs., females 2-3 years	?	Mangold, 1963
L. forbesi	1 year	length frequency	Holme, 1974
L. pealei	1-1½ years	length frequency	Hixon, 1980
	14-24 months, Max. 36	length frequency	Summers, 1971
L. opalescens	1-1½-3 years	length frequency	Authors
	1-1½-3 years	statoliths	Spratt, 1978
Doryteuthis plei	1-1½ years	length frequency	Hixon, 1980
Sepioteuthis sepioidea	less than 1 year	rearing	LaRoe, 1971
Lolliguncula brevis	1-1½ years	length frequency	Hixon, 1980
Alloteuthis media	M, 1 year, F, 1-1½ years	?	Mangold, 1963
Ommastrephidae			
Illex illecebrosus coindeti	M, 12-20 months, F, 24 months	?	Mangold, 1963
Illex i. illecebrosus	1-2½ years	length frequency	Mesnil, 1977
Todaropsis eblanae	M, 24 months; F, 2-3 years	?	Mangold, 1963
Todarodes pacificus	1 year	length frequency	Hamabe & Shimizu, 1966
Ommastrephes bartrami	1 year	length frequency	Araya, this volume
O. pteropus	1 year	length frequency	Hixon *et al.*, 1981
Dosidicus gigas	16-20 months	length frequency	Ehrhardt *et al.*, this volume
OCTOPODA			
Octopus vulgaris	1-5 years, av. 2 years	length frequency	Mangold, 1963
O. salutii	2 years to maturity	length frequency	Mangold, 1963
O. briareus	12-15 months	rearing	Wolterding, 1971
O. joubini	4-12 months plus	rearing	Thomas & Opresko, 1973
Eledone cirrhosa	M, 14-15 months, F, 16-18 months	length frequency	Mangold, 1963
Bathypolypus sponsalis	2 years	length frequency	Mangold, 1963

of spermatophore production to completion, size increases steadily.

Whether, for fisheries purposes, maturity should be considered to be whenever one or any spermatophores are present or only when the sac is full is open to discussion. The average number of spermatophores in adult males ready to mate has been determined for very few species of squid. Also the number varies greatly from group to group. In octopods the number of spermatophores may be very high in some species (more than 100) while in others only one or two may be produced. The process of spermatogenesis in *Loligo opalescens* has been described by Grieb and Beeman (1978).

Maturity in females is also difficult to determine. Females of some species produce thousands of eggs while others may produce only a dozen or so. The degree of maturity is difficult to determine and each species requires careful study. Size of the eggs, size of the ovary, size and condition of the nidamental glands and accompanying colour changes are all possible indicators.

In view of the difficulties described above as to when males and females are actually sexually mature, the assessment of age at this stage is more difficult. In examining Table 1, it can be seen that in general males may have a shorter estimated life span than females. This is based on the postulation that males die shortly after mating, which happens in *Loligo opalescens* (McGowan, 1954), but not necessarily so in others, and that the females have a delay between mating and spawning and may spawn over a number of days or weeks. In octopods the life span may be longer because the females brood their eggs for up to two months or more after spawning and may live for weeks to months thereafter. Thus for the females, age at sexual maturity may be considered about equal to the age of males at death in those species in which the males die after mating.

Correlation of sexual maturity with mantle length may afford a means of aging species when aquarium rearing studies have provided growth data, although all aquaria studies must be viewed with caution.

Fecundity. Fecundity is usually determined by counting the number of eggs contained in the ovary of mature females. If the species is one that spawns completely in either one spawning or in several spawnings over a short period, this method of establishing fecundity may be reliable. This condition may possibly be determined if all of the eggs in the ovary are at the same or nearly the same stage of development. The presence of eggs of various sizes and stages usually indicates a prolonged spawning period during which new eggs may be produced and others have the time to develop. In this latter case egg counts at any one time may be very misleading.

Hixon (1980) reported that *Lolliguncula brevis*, a one time spawner, laid 2 024 eggs in the laboratory (previous estimates 1 400-6 350). Three female *Loligo pealei*, also in the laboratory, laid 21 315-53 072 and 55 308 eggs respectively over periods of from 5 days to one month. Previous estimates of from 980-15 000 were made from egg counts (Haefner, 1959; Summers, 1971) or by gravimetric extrapolation (Vovk, 1972). Another loliginid, *Doryteuthis plei*, was determined to spawn 14 310 eggs by spawned egg count (Roper, 1965) and 218-2 500 by ripe egg count (LaRoe, 1967). It can be seen from these figures that fecundity based upon egg count can be off by several orders of magnitude unless it is known whether it is a one time (several days) spawner or whether it spawns over one or more months.

Examination of Table 2 shows that cephalopods may spawn as few as 25 eggs or as many as 6 000 000 eggs. These numbers depend primarily upon either the absolute size of the eggs as in *Octopus maya* which is a large octopus that produces large eggs (17 mm long), or the relative size as in *Idiosepius pygmaeus* that is the smallest cephalopod known (mantle length 8 mm) and produces eggs less than 1 mm long. All of the species producing large numbers of eggs (greater than 5 000) have small eggs (less than 3 mm), but within this group the size of the eggs may vary. As a general rule, the greater the number of eggs, the smaller they are. Unfortunately, as can be seen from the table, little information is available on fecundity and much that is given here is subject to reservation.

Spawning. Spawning time, place, and mature eggs are known for very few species of squid. Information in nearly all species is fragmentary and much of the available information is derived from catch statistics from which deductions have been made.

The spawning of cuttlefish has been recorded from classical times. *Sepia officinalis* spawns nearly or entirely around the year, coming into shallow water and attaching the eggs one at a time to hard objects on the bottom. Many other cuttlefish follow the same pattern. Grimpe (1928) wrote that *Rossia macrosoma* spawned around the year on the northern European coast and the North Sea, fixing its eggs to hard objects on the bottom. *Idiosepius*, according to Natsukari (1970) is a summer spawner but it is possible that it has several generations a year.

Despite the long interest in *Loligo*, its biology has been little studied. According to Tinbergen and Verwey (1945) *Loligo vulgaris* spawns in the summer in Dutch waters but Holme (1974) could not verify that it spawned in the English Channel. *Loligo forbesi* has its major spawning in Great Britain in December and January (Holme, 1974), coming into shallow water and attaching the eggs to objects that keep them off

TABLE 2

Fecundity of various species of cephalopods, derived from the literature.

Species	Number of Eggs	How Determined	Source
SEPIOIDEA			
Sepia officinalis	about 1000	egg count	Mangold, 1963
Rossia macrosoma	about 40	egg count	Mangold, 1963
Idiosepius pygmaeus	25-64	eggs spawned	Natsukari, 1970
TEUTHOIDEA			
Loliginidae			
Loligo vulgaris	about 6000	egg mops	Mangold, 1963
L. pealei	21 315-55 308	egg mops	Hixon, 1980
L. Opalescens	14 000	egg mops	Fields, 1965
Doryteuthis plei	14 310	egg mops	Roper, 1965
Lolliguncula brevis	1400-6360	egg count	Hixon, 1980
Sepioteuthis sepioidea	260	egg count	Voss, unpubl.
Alloteuthis media	1000-1400	egg count	Mangold, 1963
Ommastrephidea			
Illex illecebrosus coindeti	5000-12 000	egg count	Mangold, 1963
	50 000-100 000	egg count	Boletzky *et al.*, 1973
Illex i. illecebrosus	440 000 plus	?	Durward *et al.*, 1979
Todaropsis eblanae	5000-10 000	egg count	Mangold, 1963
Todarodes sagittatus	12 000-15 000	egg count	Mangold, 1963
T. pacificus	70 000 mature eggs	egg count	Joo Youl Lim, 1967
T. filippovae	about 500 000	estimated	Dunning, 1981
Ommastrephes pteropus	52 618-186 461	egg count	Hixon *et al.*, 1980
O. caroli	360 000	?	Clarke, 1966
Dosidicus gigas	1-6 million	?	Ehrhardt *et al.*, this volume
OCTOPODA			
Octopus vulgaris	127 000-402 000	egg strings	Mangold, 1963
O. briareus	100-500	egg strings	Wolterding, 1971
O. joubini	40-95	egg strings	Thomas & Opresko, 1973
O. maya	1500-2000	egg strings	Solís, 1967
Eledone cirrhosa	1010-3800	egg count	Mangold, 1963
E. moschata	280-370	egg count	Mangold, 1963
Bathypolypus sponsalis	70-120	egg count	Mangold, 1963

the bottom. Aggregations have not been seen. *Loligo pealei* spawns in New England waters around May (Summers, 1971) but it may spawn later further south. In Texas it spawns in summer and fall (Hixon, 1980). Spawning is usually communal but not in major aggregations. The eggs are attached to the bottom in mops in shallow water. *Loligo opalescens* spawns in the winter in southern California but progressively later in the northern regions. It forms large spawning aggregations in shallow water and attaches its mops to hard objects on the bottom (Fields, 1965). *Loligo edulis budo* in Japan spawns late fall apparently offshore (Ikehara *et al.*, 1977). The tropical *Doryteuthis plei* spawns year round in Texas according to Hixon (1980). The Japanese *Doryteuthis kensaki* spawns in August attaching its egg mops to sandy bottom (Natsukari, 1976). *Doryteuthis bleekeri* (Matsui, 1974) spawns in inshore Japanese waters in December through May.

The east American *Lolliguncula brevis* spawns all year, attaching its eggs in mops in shallow estuarine areas (Hixon, 1980). The Caribbean Reef Squid, *Sepioteuthis sepioidea*, spawns all year round throughout its range (LaRoe, 1967), while the Australian calamary, *S. australis*, spawns from July through November (Potter, Winstanley & Caton, this volume); both attach their eggs to algae and rocks.

The time and place of spawning of the ommastrephids are practically unknown for any species. Almost all published information on spawning time is based upon capture of mature females in the fisheries but almost no records contain any information on whether the eggs were found in the oviduct, the only sure indication of mature, ready to spawn, females.

According to Squires (1957) *Illex illecebrosus* spawns in December through March but no spawning sites of *Illex* have ever been reported unless an aggregation off the Florida coast in about 1 000 metres was a spawning event. An egg mass was spawned in an aquarium (O'Dor and Durward, 1978) but the major spawning areas are unknown. *Todaropsis eblanae* and *Todarodes sagittatus* in the Mediterranean spawn in December to March and September to November respectively, based upon supposed mature females (Mangold, 1963).

Todarodes pacificus apparently has at least two and possibly three spawning periods. Joo Youl Lim (1967) stated that *T. pacificus* spawns from July to November in Korean waters while Kasahara *et al.* (1969) stated that there are two spawning periods in Japan, winter and summer; these yield three populations. While the spawning times are well known, the actual spawning areas and distribution of eggs have yet to be delimited. *T. pacificus* has been studied biologically from the fisheries standpoint more than any other oceanic squid (Okutani, 1977) but many questions remain to be answered.

Of the three species of *Ommastrephes*, only *O. bartrami* has been studied biologically. Araya (this volume) believes, based upon mature females in the catch, that it spawns in January through May in the warm Pacific waters. They are thought to breed and spawn in deep water. Little is known of their biology in the Atlantic. Hixon *et al.* (1981) have provided some information on *O. pteropus* in the Gulf of Mexico, especially related to fecundity. Ehrhardt *et al.* (this volume) reported upon the biology of *Dosidicus gigas*. According to them it spawns during early winter both in the Gulf of California and along the slope on the western edge of Baja California but data are lacking on spawning grounds, egg clusters and eggs. According to Potter, Winstanley & Caton (this volume) *Nototodarus sloani gouldi* in the Bass Strait area appears to spawn in winter, summer and fall but spawning areas, eggs and larvae are unknown. It appears from this review that there is little reliable data on any aspect of spawning as far as ommastrephids are concerned.

Our knowledge of these events in octopods is much more reliable. Many species of octopus lay eggs and brood in shallow water where they are available for observation and they are amenable to rearing in aquaria. *Octopus vulgaris* in Europe and in many other areas of the world spawns in summer. The eggs are attached in festoons on the underside of rocks, in caves, large shells and other objects. *Octopus briareus* has its peak spawning during January through March. The eggs are laid in short festoons or rarely in a single layer on the underside of coral slabs, in caves, or empty conch shells, all in shallow water. *Octopus joubini* is a small species and lays few eggs usually in old gastropod or bivalve mollusc shells. Two broods probably occur in South Florida, one in the winter and the other in the summer, but only one brood per year occurs in North Florida (Thomas & Opresko, 1973). *Octopus maya* of the Gulf of Mexico and Campeche spawns during the winter in waters less than twelve feet deep, the eggs attached in festoons on rocks, in dead shells and other hard objects (Solís, 1967).

Recruitment. Recruitment refers to the number of young cephalopods entering the fisheries each year as a result of the last spawning season. In a species with a life span of one year, a constant and rather high recruitment is necessary to maintain the stocks against fishing and predation mortality.

Recruitment in the squid fishery is determined by analyzing the length frequency modes in the catch and noting the numbers and times of young squid entering the fishery. In a fishery conducted by jigging, the size of the recruits caught is determined by the catch characteristics of the commercial jigs; small animals are unable to take the jig. Similarly in the trawl fishery the size of the animals caught is determined by the mesh size. Thus the size available for recruitment determination is limited.

In finfish fisheries, the recruitment is determined, in many cases, long before the young show up in the catch and thus there is a predictive capability. Squid eggs, larvae, and early juveniles are seldom taken by any means and apparently never in sufficient quantities to have a predictive value. As the life span is so short in many species, this lack may not affect fisheries management to any great degree. Most of the commercial species of squid have a high fecundity and, unless there is heavy overfishing or a strong ecological perturbation, they should maintain themselves.

It is probable that little progress can be made in stock predictions and early recruitment figures until more is learned about the areas and times of spawning and the depth levels sought by the hatchlings and early juveniles. Obviously nets are available to catch them if their whereabouts were known. Much more exploratory work is needed in this area of squid research.

Migrations. It is well known that some squid migrate but it is less known that octopods do also. Rees (1952) and Rees and Lumby (1954) have reported upon *Eledone cirrhosa* 'invasions' of the English coast and the sighting of octopus swimming in assumed migrations. Octopus also have a winter/summer movement inshore and offshore in relation to changing water temperatures.

The situation with regard to squid is of a more classical nature. It has long been known that *Todarodes pacificus* migrates in Japanese waters (Okutani, 1977). Squires (1957) described the inshore feeding migrations of *Illex illecebrosus* in Newfoundland waters in summer and fall but the other end of the migration is not known although it may be a southward movement as far as Florida. In the loliginids Tinbergen & Verwey (1945) described a seasonal migration of *Loligo vulgaris* on the Dutch coast while Holme (1974) demonstrated a migration along the British Isles for *L. forbesi*. *Loligo opalescens* has inshore spawning migrations and aggregations along the California coast but offshore and longitudinal movements have not been noted (Fields, 1965).

There is little information on the movements of most squid and in some cases disappearance in one area and abundance in another may be due to migrations or to long term ecological changes or they may reflect local population fluctuations. *Dosidicus gigas*, long abundant on the Chilean coast as far south as Concepción, practically disappeared from Chile for the last 15 years (Gallardo, pers. comm.) only to become abundant off northern Mexico and in the Gulf of California. In 1982 the species appears to have moved southward and has practically disappeared from the Gulf of California (Ehrhardt, pers. comm.).

The causes of migrations are multiple, including mating and spawning, feeding, seasonal temperature changes, and others. Unfortunately in most species the fisheries are not carried out year round with the vessels following the squid movements. Thus knowledge of the total migratory patterns for most species is fragmentary both in space and time.

Populations. Little is known concerning populations except for a few species and most of the information deals with seasonal populations rather than geographical ones. Verrill (1882) apparently noted population differences when he described several varieties of *Loligo pealei*. Mullin (pers. comm.) noted that the populations of *L. pealei* seemed to change seasonally off the Maryland coast and investigations indicated differences in sucker dentition on the tentacular clubs. Studies of *Lolliguncula brevis* (Voss, unpubl.) showed that stocks could be distinguished on the Georgia/Florida shelf, South Florida, and the Gulf of Mexico by multiple character indices, especially fin size.

Most population distinctions are based upon the times of spawning and appearance of the recruits in the stocks. Holme (1974) thought there were winter and summer spawning populations for *Loligo forbesi* in British waters. Okutani (1977) has reviewed the summer and winter populations of *Todarodes pacificus* in Japanese waters. Seasonal populations are less well documented for other species but data are accumulating that shortly may be useful in distinguishing populations in other species.

Seasonal populations may not be as important from a fishery management viewpoint as are geographical ones but the latter are much more difficult to recognize. It seems unlikely from a longitudinal distribution viewpoint that *Loligo pealei* on the American Atlantic coast and *L.*

opalescens on the Pacific coast should each belong to a single population. This is especially true for *L. pealei* where semibarriers occur at such points as Cape Hatteras and south Florida; nonetheless separate populations have not been discriminated. Along the west coast of North America no apparent barriers exist and *L. opalescens* is found from western Canada to Baja California, a range of approximately 1 500 miles. Various techniques have been used in an attempt to identify populations of this species: morphological characters (Kashiwada and Recksiek, 1978), biochemical-genetic studies (Ally and Keck, 1978), and protein electrophoresis (Christoffersen *et al.*, 1978) but no definite conclusions on the recognition of populations could be reached by any of these methods. Existence of populations, however, seems possible and more extensive studies may well provide answers to these perplexing questions. For the time being the greatest possibility of success seems to lie in detailed morphological studies of characters and combinations of characters showing geographical variation.

The same problems apply to the octopods. Thomas & Opresko (1973) believed that there were summer and winter populations of *Octopus joubini*, which has a short life span. Seasonal populations may be a widespread phenomenon in temperate and cold water species but in strictly tropical waters seasonal populations probably do not occur because of the long duration of spawning or year round spawning.

Population fluctuations of various species of squids and octopuses have been well documented but despite this, normal fluctuations are often misinterpreted as representing changes due to fishing pressure or other factors. The decline of the catch of *Todarodes pacificus* in recent years was considered to be due to overfishing (Okutani, pers. comm.) but in 1980-81 the population rose significantly, leading some biologists to consider that this was a natural population fluctuation or cycle. Fields (1965) showed population fluctuations in *Loligo opalescens* on about a 15 year cycle. Squires (1957) analyzed data on *Illex illecebrosus* in Newfoundland waters and found strong fluctuations in abundance but no definite cyclic pattern.

Prey/Predator Relationships. Cephalopods are active, top level predators. They feed upon numerous invertebrates, especially crustaceans, and many species of fishes, as well as other cephalopods. Cephalopods, in turn, are eaten by large fishes, marine mammals, and many sea birds, forming a large percentage of their diet. Clarke (1962) pioneered the study of mammal predation on cephalopods using the characters of the indigestible chitinous beaks for identification and squid biomass, relating beak size to body size. Much information is now accruing from the identification of cephalopod beaks in whale (Clarke, 1980), fish, and bird stomachs although in many instances identification can be taken only to genus or even family, with a few unknowns even at this level. These hard parts are retained for a sufficient time that a rather accurate estimate may be obtained of the percentage of squids eaten in comparison with other groups of prey animals. Nearly every species of large fish and marine mammal eat squid and the pressure upon the stocks of squid must be formidable (Clarke, this volume).

The major predators upon cephalopods, however, have been greatly reduced as a result of the whale fisheries, depletion of the fur seals, and the heavy inroads upon the large fishes as a result of the high seas longlining and the tuna fisheries. Toll & Hess (1982) have studied the diet of the swordfish in Florida waters where *Illex* spp. constitute over 90 per cent of their diet. Voss (1953) showed that nearly 17% of the diet of sailfish consisted of mixed cephalopods. The result of the depletion of these fishes and others may have resulted in a dramatic increase in available cephalopod stocks. Voss (1973) based part of the estimates of cephalopod resources on data derived from squid consumption by large predators.

Squid predation is much less understood. Cephalopod workers have been remiss in studying stomach contents. The general picture that emerges, however, is that young and small adult squid feed primarily upon small crustaceans: amphipods, copepods, euphausiids, mysids, cumaceans, ostracods, and others, and larval stages of larger crustaceans. As the squid grow there is a move toward larger prey such as other squid and fishes. In large squid the prey may become almost exclusively squid and fishes. The stomach contents of a giant squid *Architeuthis* taken off South Africa contained only remains of large squid (Peréz-Gándaras & Guerra, 1978).

The most detailed study of the position of a species of squid in a food web was carried out at Moss Landing, California, on *Loligo opalescens*. Karpov and Cailliet (1978) studied the stomach contents of *L. opalescens* from various areas and times of day. They found that this rather small squid fed mainly upon crustaceans throughout its life cycle and even as adults, fishes and squid formed a minor part of their diet. Morejohn, Harvey & Krasnow (1978) examined the gastrointestinal and stomach contents of 1 928 fishes of 86 species and 33 families, 513 sea birds of 28 species and eight families, and 143 marine mammals of 15 species and eight families. On the basis of these two studies the latter writers gave several depictions of the complicated food web of this squid. While these studies can be used for management purposes in California, they cannot be used for the oceanic squids that attain much larger sizes and do not compare with our knowledge of the prey/predator relationships of other species of *Loligo*.

Obviously we know very little concerning the position of squid in oceanic food webs and if squid stocks are to be subjected to heavy fishing pressures such data are needed in order to avoid causing major perturbations in stocks of other groups.

Conclusions

With this review of fisheries biology it becomes readily apparent that few, if any, species of cephalopods have been studied sufficiently to yield information needed for proper management. At least some data are available for the following cephalopods. For others, information is either sparse or lacking altogether.

Eastern Atlantic

Illex illecebrosus coindeti, Todarodes sagittatus, Loligo forbesi, L. vulgaris, Sepia officinalis, Octopus vulgaris, Eledone cirrhosa, E. moschata.

Western Atlantic

Loligo pealei, Doryteuthis plei, Illex illecebrosus, Octopus briareus, O. joubini, O. maya.

Eastern Pacific

Loligo opalescens, Dosidicus gigas, Octopus dofleini.

Indo-West Pacific

Loligo edulis, Doryteuthis bleekeri, Todarodes pacificus, Nototodarus sloani, Symplectoteuthis oualaniensis, Ommastrephes bartrami, Onychoteuthis borealijaponicus, Octopus dofleini, O. cyanea.

It is apparent that of approximately 650 species of cephalopods, there are some management data for only 23 species or about four per cent, some of which have no commercial value. This is only a small fraction of the total number of actual or potential economic species of cephalopods attaining a figure of perhaps 150 species. It should be pointed out that this information is only for restricted areas of the species range and in widely distributed species populational data for one region may not be applicable for another. It is certainly true that data obtained for one species of cephalopod may have little or no value when applied to another.

The biology of no species of cephalopod is as well known as that of almost any commercially exploited fin fish. One only has to look at the wealth of knowledge about cod, hake, sole, halibut, herring, mackerel, anchovies and dozens of others to realize the inadequacy of cephalopod data. Our information on the ecological factors controlling squid distribution and abundance is even more inadequate.

Present cephalopod fisheries practices are based upon the concept that squid live for one year only. While this broad generalization does fit some species, examination of the data given above shows that life spans vary in known species from 4 months to 4 years and accurate knowledge of the life span of heavily fished oceanic squid is still lacking. Similarly, fecundity figures are so widely varying in the same species between different authors that present figures are unconvincing.

More ship time and laboratory research has been expended on plankton studies than any other phase of marine biological work. Yet few cephalopod eggs have been obtained and larvae are sparse. For most oceanic species spawned eggs are unknown and larvae undescribed. Surely these fundamental phases of cephalopod life cycles could be uncovered with adequate funding, a fair share of ship time, and properly planned research programs.

At present we are at a complete loss to explain the questions of squid disappearance from an area for years only to reappear in almost original numbers as occurred with *Todarodes pacificus* in Japan with drastic effects upon the world squid market. Similarly *Dosidicus gigas* appeared and disappeared in the Gulf of California. Thus a promising new fishery was developed and left stranded. Even seasonal movements are unknown for most species simply because research ships are not involved except when the fishery is in operation. Millions of dollars have been spent on seeking the pathways and spawning grounds of the European and American eels with little foreseeable impact upon either the eels or their fisheries. How much has been spent to track squid migrations and discover squid spawning grounds other than in Japanese waters?

From a fisheries viewpoint can we afford to gamble on investments in ships, gear and men at a time when foreign vessels are being more and more restricted from national waters? The time seems to be approaching when, if a national fishery fails, ships cannot move to another country to exploit new stocks. This is as much a political problem as it is a biological one.

This review makes it clear that much more attention must be paid to the biological factors. While mathematical models based upon catch figures may suffice for management of a healthy fisheries, they do not show the causes of declines based upon other than overfishing. Real figures are required, derived from knowledge of the biology of the species exploited.

The cephalopod fishery today amounts to about 1.3 million metric tons. Its potential on the continental shelf alone is estimated at between 7-10 million metric tons. It is perhaps the largest source of harvestable but underexploited protein in the oceans. Yet the amount of money expended in biological research on our squid fisheries on a worldwide basis is not as large as that expended on the study of only one family of pelagic fishes alone, the Scombridae. Surely cephalopod fisheries biology deserves better treatment from the hands of the fishery services of the world.

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There is a very large and diverse literature dealing with cephalopod biology. Much of it is in obscure journals, widely ranging fisheries sources, and often in languages difficult for workers of western European origin. Leads to much of this, however, may be obtained through searching the bibliographies in the following sources. A full bibliography of cephalopod fisheries papers is much to be desired.

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