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A REVIEW OF THE LABORATORY MAINTENANCE, REARING AND CULTURE OF CEPHALOPOD MOLLUSCS

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Abstract

The historical and current developments associated with keeping cephalopods in captivity are reviewed. While cephalopod maintenance is straightforward for many species, rearing and culture are still in the early stages of development and have been accomplished only on a relatively small scale, although recent advances have been substantial. A detailed review of cephalopod diets shows that cephalopods are active carnivores from hatching to adulthood and that they feed primarily on crustaceans, although shelled molluscs, fishes and other cephalopods also are consumed. To be maintained, reared or cultured successfully, they generally need: (1) careful handling to avoid skin damage, (2) tank space appropriate for their benthic or nektonic mode of life, (3) a good supply of high quality water, and (4) a sufficient supply of live food. Diseases in captivity in only a few cases have been a major problem. Culture is a useful means of providing animals as research models and of obtaining life cycle information, particularly that of the critical early developmental periods. A major economic impediment to large-scale culture is the development of a cheap, reliable artificial food.

Introduction

Previous reviews of cephalopod maintenance and culture have been provided by Grimpe (1928), Boletzky (1974a) and Shevtsova (1977). In view of the fact that there has been a resurgence in worldwide interest in cephalopods during the past few years, we present here an updated review that concentrates particularly on the diets of cephalopods as well as current advances in culture methodology and the future potential of culture programs.

What is to be learned from the culture of cephalopods? These dynamic predators occupy a dominant position in the trophic relationships of the marine ecosystem. They are an important food source for human consumption and they are unique and versatile research models. The first International Workshop on the Biology and Resource Potential of Cephalopods has clearly shown how little is known about their early life histories, recruitment into populations, predator-prey relationships and other facets of their life cycles. The scientific community is forced to depend largely upon culture programs to provide such information, especially on early life histories, because it is extremely difficult to make direct and detailed observations of cephalopods in nature due to their mobility, excellent vision and generally nocturnal habits. Culture programs also may become useful in providing selected species as biological models in experimentation, as for example the retina, the giant axon of the squid and the brain of the octopus. Culture therefore can be considered a means by which a number of pertinent problems of basic and applied science can be solved.

We have attempted to provide an overview as informative and detailed as possible, but inevitably there will be gaps and inaccuracies that escaped our attention. Nevertheless we hope that this article may prove useful as a source of information and stimulation to biologists and culturists interested in specific aspects of the 'indoor' biology of cephalopods.

A. TERMINOLOGY

In reviewing the literature we found little uniformity in the use of terms that relate to culture. In an effort to standardize their usage, we follow the definitions introduced by Paffenhöfer and Harris (1979) for plankton culture, but we have modified them slightly so that they apply more specifically to cephalopods.

Maintenance: Holding wild-caught late juvenile or adult stages in the same approximate developmental stage for varying periods, with no direct intention of growing them to a more advanced stage (e.g., maintaining sexually mature adults until they lay eggs for rearing studies, or holding wild-caught animals until needed for experiments).

Rearing: Growing a cephalopod over a certain period of time without achieving a second generation. Specifically it refers to any attempt to grow hatchlings or young juveniles to full size and sexual maturity.

Culture: Growing a cephalopod at least from hatching, through the complete life cycle (juvenile and adult stages, sexual maturity, mating and egg laying), to hatching of viable young of the first filial (F_1) generation. The term culture also may be used in the sense of collectively referring to maintenance, rearing and culture. These definitions do not apply to existing literature because terms often have been used interchangeably, especially the terms rearing and culture.

The standard measure of body size of cephalopods used throughout this paper is dorsal mantle length = ML.

The popular and scientific names of prey animals are given as quoted in the original papers.

B. HISTORICAL PERSPECTIVE

Cephalopods have a somewhat undeserved reputation for being delicate sea creatures that do not survive well in captivity. It is true that, among the approximately 700 species inhabiting all the world's oceans, a great majority would require specialized capture and maintenance techniques that cannot practically be provided. But there are many species living in the continental shelf waters of the world that thus far have proved fit for life in captivity and some of these hold great interest from the scientific perspective.

In a very detailed review with a translated title of 'Maintenance, handling and breeding cephalopods for zoological and physiological purposes', Grimpe (1928) presented the state of the art in cephalopod maintenance. He was particularly acquainted with these problems through years of experimental cephalopod research, mostly in the Zoological Station in Naples, Italy. Unfortunately, Grimpe's review marked the end of a period of very active cephalopod research. By the end of the 1920's only a handful of scientists remained who worked with living cephalopods. If the economic conditions had been more favorable then, cephalopod research and culture attempts quickly might have reached the state that was actually realized a full 30 years later. With the new drive of marine biology in the 1950's and 1960's, with possible applications in 'sea farming' or 'mariculture', it appeared to be a mere matter of time and technical improvement before large-scale cultures of cephalopods for human consumption would begin. Everyone now knows that this was unrealistic. Even now, most natural cephalopod stocks are so far from depletion that there is no sufficient market pressure towards alternative modes of cephalopod production.

Meanwhile, a different market opened and is expanding in the biological sciences. It comprises two sections: one for life cycle analyses, another for the production of cephalopods as experimental animals. The former is important for basic biological and ecological research as well as for fisheries biology dealing with cephalopod stocks, their exploitation and protection. The latter is important for many research projects in cell biology and neuroscience, in particular as a means of providing giant axons of squids all year long. The extent to which this market expands will set the pace of future culture work on cephalopods. The following chapters address technological limitations of culture faced by the culturist as well as biological limitations of culture imposed by the nature of cephalopods.

Collection Methods

The procurement of healthy eggs, juveniles or adults of marine animals for laboratory study often is difficult because collection and transportation procedures must be adapted to: (1) temperature and salinity requirements of each organism, and (2) the degree of stress that each species can tolerate from the trauma of capture, shipboard handling and transport, and transfer procedures into the laboratory tanks. These limitations are particularly strict with cephalopods that move very actively and tend to damage their integument. Recent reports by Leibovitz *et al.* (1977) and Hulet *et al.* (1979)

have described the consequences of skin damage in pelagic squids and they reemphasize the importance of developing atraumatic capture methods for squids and other cephalopods.

It is not within the scope of this review to list all the collection methods for cephalopods, but some techniques will be listed below for the three general stages that interest culturists. Some general reviews on collection techniques are given by Voss (1973), Zuev and Nesis (1971), FAO (1975) and Tomiyama and Hibiya (1978). These methods do not always emphasize the atraumatic capture of animals and therefore their use in obtaining healthy animals for laboratory study and breeding often is limited. Obtaining experimental animals from existing fisheries generally is the easiest and most inexpensive solution to collection, especially when it is not necessary to obtain animals in perfect condition. Slightly damaged animals often are able to spawn in the aquarium, and this allows one to take care of the egg masses from the beginning of embryonic development.

Eggs of species that spawn on open stretches of sandy or muddy bottom can be collected with bottom trawls, but care must be taken to limit the mechanical disturbance of the egg masses, especially when the net is taken onboard for sorting of the material and when temperatures rise during sorting on deck. These problems are more easily dealt with when eggs laid inshore (not deeper than 40-60 m) are collected by SCUBA diving, which in addition allows one to have access to rocky bottoms where trawling is impossible. Indeed, squid eggs often are deposited under rocky overhangs. In addition to this mode, Takeuchi (1969, 1976) has observed that *Doryteuthis bleekeri* spawns on the abdomen of the giant spider crab *Macrocheira kaempferi*. Eggs of some cuttlefishes and squids such as *Sepioteuthis lessoniana* may be collected by placing tree branches on spawning grounds to which females attach their eggs (Mangold-Wirz, 1963; Choe, 1966a; Tomiyama & Hibiya, 1978). For many species, it is easier first to obtain adult animals by trawling, maintain them in aquaria until spawning and then collect the eggs there. In loliginid squids and cuttlefishes, egg-laying can be triggered by certain visual stimuli, especially by natural or artificial egg masses placed in the aquarium (Arnold, 1962).

The collection of young juveniles generally is the most difficult undertaking. Even very small cephalopods are able to avoid most collecting gear, and if caught, they accrue considerable stress and injury to a degree that drastically limits their survival. The young of many species have more rigid feeding requirements than the adults, and the trauma of capture often upsets highly specific feeding responses. Lighted traps set at night probably would be the best collecting device for fragile cephalopod juveniles, but this technique has not been used frequently. Most of the cephalopod juveniles described in the literature have been captured with plankton nets and midwater trawls. Very small benthic sepioids, especially sepiolids, are regularly captured with a small sled-dredge used for various purposes by the Laboratoire Arago in Banyuls.

The collection of adult cephalopods is more straightforward but varies considerably for different ecological situations. Most cuttlefishes and sepiolids are collected by bottom trawl. When the duration of tows is limited (20 min. to 1 hr.) and net retrieval and sorting of catch are carried out carefully, a fair percentage of the captured sepioids survive with minimal skin damage. Many squids (loliginids and oegopsids) are caught routinely with bottom and midwater trawls, but a very small fraction of the catch avoids major skin and fin damage. This is not a very desirable collection method for most squid species if long-term maintenance is required (but see Hulet *et al.*, 1980 for successful trawl capture of *Lolliguncula brevis*). Collections by static pound nets (cf. O'Dor *et al.*, 1977 for *Illex illecebrosus*) or encirclement nets (e.g., purse seines, lampara nets) are good methods because the squids do not incur much net contact. Attraction to night lights and subsequent capture by dipnets or squid jigs is a favorable method of capture because the squids are nearly injury-free and the chances for survival are high. Some species, especially reef-dwelling loliginids, may be hand-collected during diving at night by mesmerizing individuals with bright lights. Octopods are most often caught with bottom trawls, but in many fisheries they are trapped in empty pots in which the animals seek refuge (Lane, 1960; Inoue, 1969). Small benthic octopodids (members of the only benthic family—Octopodidae—within the Incirrata) may be collected by hand while SCUBA diving.

Atraumatic capture methods are of little use if the subsequent acclimation to laboratory conditions fails. This acclimation must be coupled with the transport procedure from the moment of capture. Transfer from water-to-air-to-water should be avoided or kept to a minimum, and particularly temperature, salinity, and pH of the water and lighting in holding tanks should be monitored in order to avoid physiological shock. Cephalopods generally need high quality water and adequate oxygenation. Recent investigations by commercial fish dealers show that many marine organisms transported in small volumes of water for long periods of time produce nitrogenous wastes that reach lethal levels and drop the pH before oxygen is depleted. Recent experiments carried out with squids at the Marine Biomedical Institute at Galveston show the same effect. It is important to provide an adequate volume of clean sea water for each animal *at all times*, beginning immediately after capture and continuing throughout the period the animals are kept in aquaria.

In general the culturist will have to judge the best collection and acclimation methods for a given species. Both availability and habits of cephalopods vary from one species to another, and consultation with local fishermen and scientists familiar with the desired species always is advisable.

General Culture Requirements

A. WATER QUALITY

The quality and quantity of sea water available to each animal represent the most essential aspects of culture. Cephalopods generally require fairly large quantities of clean, oxygenated sea water within a relatively narrow range of salinities. Unlike some of their sedentary molluscan relatives who can tolerate or shut out undesirable water, the cephalopods must rely on locomotion to avoid unsuitable water. In captivity they lose this option and the culturist must insure that water requirements are met at all times.

The most important parameters of water quality (but certainly not all) for consideration in culture are: temperature, salinity, pH, O_2, ammonia (NH_3), nitrite (NO_2) and nitrate (NO_3). In open systems usually only the temperature and salinity are likely to fluctuate, whereas in closed systems the remaining parameters are more likely to fluctuate. Because food items decompose and the cephalopods excrete nitrogenous wastes, especially the levels of toxic ammonia, nitrite and nitrate must be monitored most carefully. No tolerance levels have been clearly established for cephalopods. Temperature tolerances are species-specific and range widely, but salinity tolerances are more restrictive since most cephalopods are stenohaline (except *Lolliguncula* spp., cf. Hendrix *et al.*, 1981). Still, most species lie within the range of 27 to 38 ppt. The range for pH is restricted to that of sea water, usually 7.7 to 8.2. Dissolved oxygen levels always should be near saturation, particularly for the active, pelagic teuthoids, although some benthic octopods are surprisingly tolerant of low oxygen levels. For example, Maginniss and Wells (1969) found that *O. cyanea* did not show signs of distress until oxygen levels fell to 0.6 mg/l, only 11% of saturation levels. The limits for nitrogenous waste levels should follow those proposed by Spotte (1979) for most marine animals: <0.10 mg/l ammonia, <0.10 mg/l nitrite and <20.00 mg/l nitrate. The tolerance limits for some species certainly are above these figures. Vevers (1962) reported that *Octopus vulgaris* lived for nine months, mated and laid viable eggs in a closed system with levels up to 10 mg/l nitrate. Hirayama (1966) found that *Octopus vulgaris* withstood 1400 mg/l nitrate for ten hours before dying. Forsythe and Hanlon (1980) found that *O. joubini* tolerated 150 mg/l nitrate for several days with no adverse effects, and Hanlon and Forsythe (unpublished data) determined the 96 hour medium tolerance limit of *Octopus joubini* hatchlings to be near 15 mg/l nitrite, a level far higher than anticipated. In closed systems it is highly recommended that accurate colorimetric methods be used periodically to monitor levels of ammonia, nitrite and nitrate (see methods in Rand *et al.*, 1976; Spotte, 1979; Strickland & Parsons, 1972).

The exact quantity of sea water needed per individual cephalopod is unknown. In open, or flow-through, systems one need only regulate the flow rate through the rearing chamber to insure that used sea water is constantly replaced. But in closed, recirculating systems both the volume and the flow rate are important. Presently it is not possible to define specific volume requirements for various developmental stages of most species. It is always better to have a larger volume system than anticipated, first because large-volume systems are more biologically stable, and second because there is a better chance that each individual cephalopod will receive its minimum volume of water for life functions. Estimates of water volume/animal can be empirically derived only and will come with refinement of culture technology. For example, Forsythe and Hanlon (1980, 1981) were able to rear 56 *O. joubini* to sexual maturity (mean wet weight 14 g each at 23 weeks) in a 300 l closed system. This works out to roughly 5.4 l of water per octopus, or 0.38 l of water per g of octopus. These figures depend entirely upon the filtration system employed and certainly the minimum amount of water needed per *O. joubini* is less than this. Behavioural parameters concerning aggression and territoriality in some species of cephalopods will determine the volume of water/animal, in addition to filtration capacity of the system.

Both natural and artificial sea water are acceptable media for nearly all aspects of cephalopod cultures. The vast majority of work has been done with natural sea water, but much recent work has shown that artificial sea salts are at least adequate, if not superior in some ways. At The Marine Biomedical Institute in Galveston, Hanlon and his co-workers have maintained or reared ten species of cephalopods in artificial sea water, and workers elsewhere have had similar success. While much definitive analysis remains to be done on the efficacy of artificial sea salt composition, especially with respect to replenishment of trace elemenents, it is sufficiently safe at this time to state that it is a suitable medium.

B. TANK SYSTEMS

The essential requirements of a seawater system are that it deliver adequate clean water to every individual and that it provide sufficient horizontal and vertical space to accommodate the feeding, locomotory and other behavioural habits of the species. Theoretically the system should be a facsimile of the animal's natural environment, but in practice this is not feasible, and in fact cephalopods often are sufficiently adaptable that they will live and grow in relatively crude imitations of their habitat.

One of the first considerations in culture work is whether to use an open or closed seawater system, but this will probably be a straightforward decision based upon the researcher's access to natural sea water. It becomes a purely technical and economical consideration, because from the biological point of view the animal needs only water of high quality, irrespective of its delivery system. Open systems are proven, reliable and convenient, but they require a coastal location with high water quality, and they offer little or no control over temperature and salinity fluctuations, disease organisms, turbidity and pollutants. Closed systems provide a stable, controllable and reproducible marine environment and, with the use of artificial sea water, can be operated in any locale. But they require fairly high initial cost and more care in maintaining a good biological balance.

Tables 1 and 2 are a compilation of cephalopod species maintained, reared or cultured in open or closed systems. It is noteworthy that most of the closed system work is recent, and this partially reflects an increase in the understanding and implementation of the closed system approach used by many large inland public aquaria. One of the earliest successful culture experiments with *Sepia officinalis* was carried out in the closed system of the Berlin Aquarium (Schröder, 1966), and there are several public aquaria worldwide that commonly maintain *Nautilus*, *Sepia*, and *Octopus* for public viewing.

Filtration design and efficiency are critical elements in open or closed systems. Submerged filters composed of sand, gravel (usually crushed oyster shell, dolomite, or 'lavalite'

TABLE 1

Open Seawater System Rearing or Maintenance of Cephalopods. This is a partial literature review with representative citations for each species listed in alphabetical order. Asterisk indicates species with benthic young.

Subclass NAUTILOIDEA (nautilus)	
Nautilus macromphalus	Bidder, 1962; Cousteau, 1971; Haven, 1972; Martin *et al.*, 1978
Subclass COLEOIDEA	
Order Sepioidea (cuttlefishes)	
Family Sepiidae	
**Sepia esculenta*	Choe, 1966a,b
**Sepia subaculeata*	Choe and Oshima, 1963
**Sepia maindroni*	
**Sepia latimanus*	Inoha, 1971
**Sepia officinalis*	Boletzky, 1974b and 1979b; Dendton & Gilpin-Brown, 1973; Féral, 1977, 1978; Pascual, 1978; Richard, 1966, 1975; Yim & Boucaud-Camou, 1980
**Sepia lycidas*	Fukuoka Buzen Station, 1968
Family Sepiolidae	
**Euprymna berryi*	Choe, 1966a,b
**Sepiola rondeleti*	Boletzky *et al.*, 1971; Boletzky, 1974a and 1975c
**Sepiola robusta*	
**Sepiola affinis*	
**Sepiola ligulata*	
**Sepietta neglecta*	
**Sepietta obscura*	
**Sepietta oweniana*	Summers & Bergström, 1981
**Rossia macrosoma*	Boletzky and Boletzky, 1973
**Rossia pacifica*	Brocco, 1970
Family Idiosepiidae	
Idiosepius pygmaeus paradoxus	Natsukari, 1970
Order Teuthoidea (squids)	
(Suborder Myopsida)	
Family Loliginidae	
Sepioteuthis sepioidea	Arnold, 1965; LaRoe, 1970 and 1971
Sepioteuthis lessoniana	Choe, 1966a,b; Choe & Oshima, 1963; Inoha & Sezoko 1967; Matsumoto, 1975; Saso, 1979
Loligo vulgaris	Bidder, 1950; Boletzky, 1971, 1974a and 1979b; Neill, 1971; Neill & Cullen, 1974; Tardent, 1962
Loligo pealei	Arnold, 1962; Drew, 1911; Summers & McMahon, 1970 and 1974; Summers *et al.*, 1974
Loligo opalescens	Fields, 1965; Hurley, 1978
Loligo plei (= *Doryteuthis plei*)	LaRoe, 1970 and 1971; Roper, 1965
Doryteuthis bleekeri	Soichi, 1976
(Suborder Oegopsida)	
Family Ommastrephidae	
Illex illecebrosus	Amaratunga *et al.*, 1979; Boucher-Rodoni, 1975; Bradbury & Aldrich, 1969; O'Dor *et al.*, 1977, 1980; Rowe & Mangold, 1975
Todarodes pacificus	Flores *et al.*, 1976 and 1977; Mikulich & Kozak, 1971; Soichi, 1976
Family Enoploteuthidae	Young & Roper, 1977
Order Octopoda (octopuses)	
(Suborder Incirrata)	
Family Argonautidae	
Argonauta argo	Boletzky, in press c, Lacaze-Duthiers, 1892; Naef, 1923; Young, 1960; Zeiller & Compton, 1970
Family Octopodidae	
**Octopus joubini*	Boletzky & Boletzky, 1969; Opresko & Thomas, 1975; Thomas & Opresko, 1973
**Octopus briareus*	Borer, 1971; Hanlon, 1975 and 1977; Messenger, 1963; Wolterding, 1971
**Octopus maya*	Van Heukelem, 1976 and 1977; Walker *et al.*, 1970
Octopus cyanea	Van Heukelem, 1973 and 1976; Wells & Wells, 1970
Octopus defilippi	Grimpe, 1928

Octopus vulgaris	Altman & Nixon, 1970; Itami *et al.*, 1963; Mangold & Boletzky, 1973; Nixon, 1966
Octopus bimaculatus	Ambrose, 1981
Octopus macropus	Voss & Phillips, 1957
Octopus salutii	Mangold-Wirz *et al.*, 1976
Octopus tetricus	Joll, 1976 and 1977
Octopus dofleini	Gabe, 1975; Hartwick *et al.*, 1981; Marliave, 1981
**Hapalochlaena maculosa*	Tranter & Augustine, 1973
Pteroctopus tetracirrhus	Boletzky, 1976, 1981
Eledone cirrhosa	Mangold & Boucher-Rodoni, 1973
**Eledone moschata*	Boletzky, 1975b
**Bathypolypus arcticus*	Macalaster, 1976

Table 2

Closed Seawater System Rearing or Maintenance of Cephalopods. This is a partial literature review with representative citations for each species listed in alphabetical order. Asterisk indicates species with benthic young.

Subclass NAUTILOIDEA (nautilus)	
Nautilus macromphalus	Hamada *et al.*, 1980; Mikami *et al.*, 1980
Subclass COLEOIDEA	
Order Sepioidea (cuttlefishes)	
Family Sepiidae	
**Sepiella inermis*	Tang & Khoo, 1974
**Sepia officinialis*	Schröder, 1966; Overath, 1975; Zahn, 1979
Family Sepiolidae	
**Euprymna scolopes*	Arnold *et al.*, 1972
Order Teuthoidea (squids)	
(Suborder Myopsida)	
Family Loliginidae	
Loligo pealei	Brinley and Mullins, 1964; Hanlon *et al.*, 1978 and in prep.; Hulet *et al.*, 1979; Yang *et al.*, 1980a
Loligo opalescens	Hanlon *et al.*, 1979; Hurley, 1976; Yang *et al.*, 1980b, 1983; Hixon *et al.*, in prep.
Loligo plei (= *Doryteuthis plei*)	Hanlon, 1978; Hanlon *et al.*, 1978 and in prep.; Hulet *et al.*, 1979
Doryteuthis bleekeri	Matsumoto, 1976; Matsumoto & Shimada, 1980
Lolliguncula brevis	Hanlon *et al.*, 1978 and in prep.; Hulet *et al.*, 1979 and 1980
(Suborder Oegopsida)	
Family Ommastrephidae	
Ommastrephes sloani pacificus (= *Todarodes pacificus*)	Hamabe, 1963
Order Octopoda (octopuses)	
(Suborder Incirrata)	
Family Octopodidae	
**Octopus joubini*	Bradley, 1974; Forsythe, 1981; Forsythe & Hanlon, 1980 and 1981; Mather, 1972
**Octopus briareus*	Hanlon, 1975 and 1977
**Octopus maya*	Solis, 1967
**Octopus australis*	Tait, 1980
Octopus vulgaris	Itami *et al.*, 1963; Hirayama, 1966; Taki, 1941; Vevers, 1962
Octopus defilippi	Hanlon *et al.*, 1980
Octopus macropus	Taki, 1941
Octopus ocellatus	Taki, 1941; Yamauchi & Takeda, 1964
Octopus burryi	Hanlon & Hixon, 1980
Octopus rubescens	Warren *et al.*, 1974
Hapalochlaena lunulata	Overath & Boletzky, 1974
Eledone cirrhosa	Boyle & Knobloch, 1982

(Overath, 1979), or trickling filters are commonly used to provide filtration in aquaculture systems (see Antonie, 1976; Hirayama, 1974; Spotte, 1979; Wheaton, 1977). Spotte (1979) defines filtration as four processes: biological and mechanical filtration, physical adsorption, and ultraviolet light disinfection. In most open systems only mechanical filtration is used in the form of a settling tank or a sand, gravel or polyester cartridge filter to remove particulate matter and nektonic organisms from incoming water. All four filtration processes are important in closed systems. Biological filtration is accomplished by nitrifying bacteria living in the sand, gravel or biodisc substrates; these bacteria oxidize toxic ammonia to nitrite and then to less toxic nitrate. Mechanical filtration occurs in the sand or gravel filter or in auxiliary filters containing polyester filter fiber and activated carbon. Physical adsorption is accomplished with the activated carbon and with foam fractionators ('protein skimmers', Spotte, 1979); they remove dissolved organics and surface-active organics, respectively. Biological conditioning (when the system is first built) and maintenance are the keys to successful closed systems, and care always must be taken to not exceed the biological carrying capacity of the system. All tank systems should be made of inert materials so that no metal comes in contact with water.

Tank size depends upon the species, but we can make two generalizations: benthic cephalopods can be kept in small tanks, and nektonic, actively swimming cephalopods require large tanks. Benthic cephalopods include most of the sepioids and all the octopodids (cf. Tables 1 and 2) and most of these can be kept in an assortment of tank configurations and sizes. Generally it is advisable to keep small animals in rather small tanks or small compartments screened off from the rest of a large tank. This allows the researcher to keep track of small individuals, to control cannibalism from larger individuals, and to provide sufficiently high food density. Of course excessive crowding must be avoided. According to the animals' habits, the bottom of the tank may be covered with sand or gravel. Many benthic cephalopods (sepioids in particular) take cover in the sand during daytime. Among the nektonic squids, some, like the loliginid squid *Sepioteuthis sepioidea,* orient to the bottom substrates (LaRoe, 1971). For young benthic octopodids, shelters should be available to allow individuals to separate from one another. All tanks must be covered with tightly fitting lids or screens, especially when they hold octopuses or have a high water level. Squids and cuttlefishes do not crawl out of their tanks like octopuses do, but they may jet 'overboard' when frightened.

Larger round tanks are best suited for pelagic cephalopods (e.g., teuthoid squids and micronektonic young of teuthoids and some octopods) because the absence of corners avoids dead spots in water circulation and eliminates the possibility of animals crowding into corners. Also, it is desirable with pelagic organisms that both the cephalopods and their food organisms be distributed as evenly as possible, especially during the very young stages. Evenly distributed illumination from overhead and gentle, uniform flow of water help achieve this (cf. Blaxter, 1968).

C. HATCHING CONDITIONS

Eggs must be handled carefully during collection, and in particular temperature must be maintained within the limits of temperature adaptation of the species involved. This range of adaptation differs among species. The only general rule that can be given is that the eggs of most species can live and develop normally at temperatures around 15 to 18°C. for cold-water species this corresponds to the upper limit of their adaptative range, while for warm-water species it represents the lower limit. Even within the range of natural temperature adaptation, a quick rise of the temperature can be harmful for the embryo, especially at early developmental stages (Marthy, 1972).

Physical parameters measured at the site of capture of juvenile or adult cephalopods do not necessarily fall within the tolerance range of embryonic development. Thus low salinities may be tolerable to adults, but will kill their developing embryos.

If sufficient numbers of newly-laid eggs are available, parallel developmental series kept at different temperatures will provide the neces-

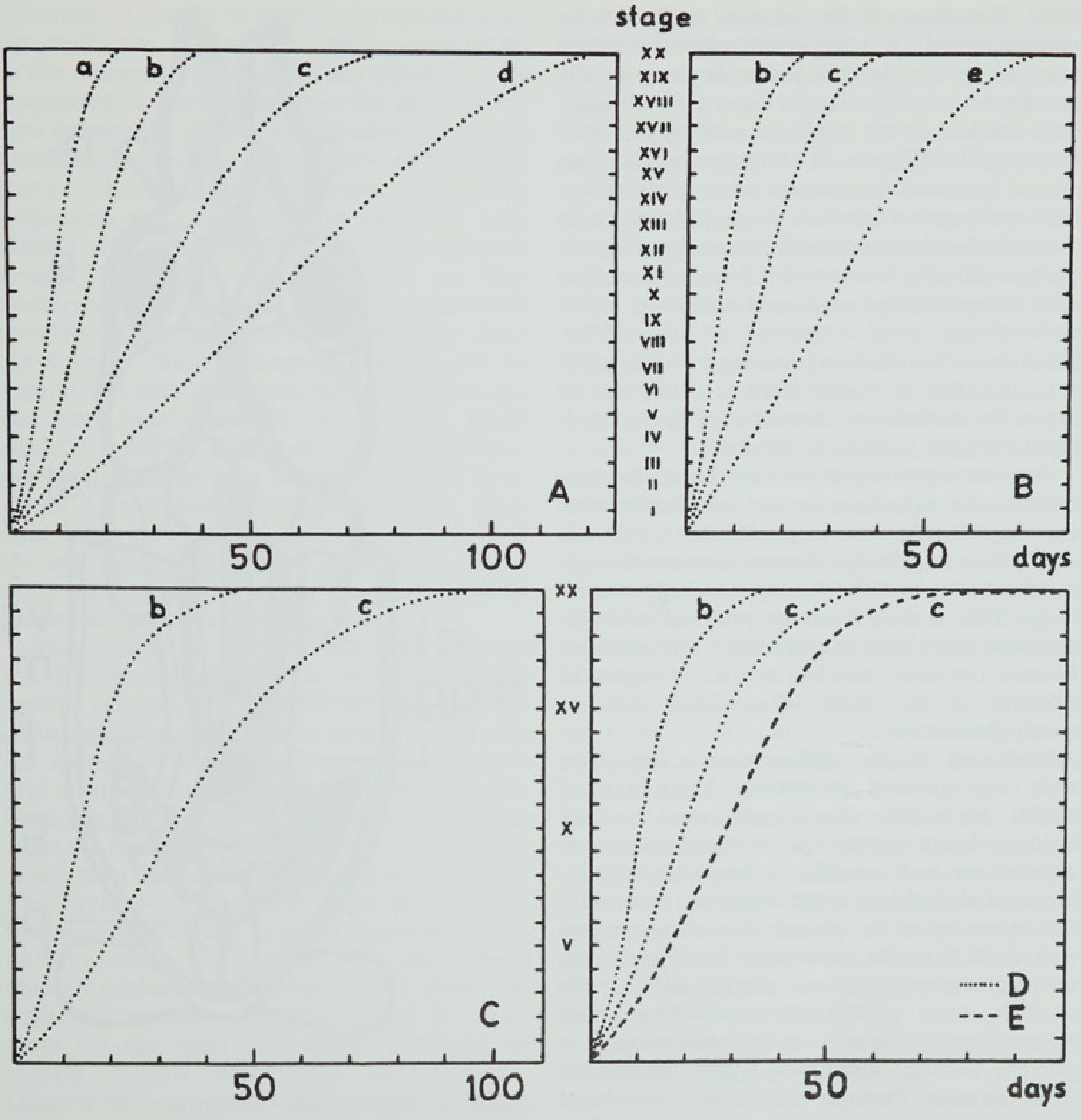

Figure 1. Rates of embryonic development (maxima) at different temperatures in *Octopus vulgaris* (A), *Loligo vulgaris* (B), *Sepia officinalis* (C), *Sepiola robusta* (D), *Rossia macrosoma* (E). a = 25°C, b = 20°C, c = 15°C, d = 13°C, e = 10°C. Stages according to NAEF (1923). (From Boletzky, 1974a).

sary information on temperature adaptation. Concurrently, developmental plots may be drawn by recording at regular intervals the embryonic stages reached at the different temperatures; this allows one to program hatching in later experiments, simply by speeding or slowing embryonic development with higher or lower temperatures (without sudden changes!).

Figure 1 is an example of stage/time plots for the embryonic development of different species. Hatching never can be programmed very precisely. A normal variation of several days must be expected for the total time of development. Hatching can be triggered artificially by various stimuli, but this is not advisable unless one can be certain that the embryos are fully developed; in particular the outer yolk sac must have reached a very small size and contain little or no yolk (Figure 2). Premature hatching always increases the chances of early mortality. Embryos become increasingly excitable towards the end of embryonic development, but they are maintained at a low activity level by the effect of a tranquillizing compound contained in the perivitellinic fluid (Marthy *et al.*, 1976). Mechanical stimulation (shaking of the eggs) or a sudden rise in temperature are sufficient to lower the excitability threshold of the animals and to trigger premature hatching.

Optimum conditions for embryonic development in the aquarium are not necessarily ideal for the postembryonic stage. If these conditions differ, one must bridge the gap between the egg-raising system and the rearing system for hatchlings. This is only a minor problem with the eggs and hatchlings of cuttlefishes and sepiolids because the newly-hatched animals settle on the bottom of the tank where they can be manipulated easily.

Screening of the outflow pipe is important with the actively swimming hatchlings of squids. Air bubbles should not be used in a tank holding squid hatchlings, because the small animals are easily caught in the stream of bubbles and air bubbles often adhere to their skin. Air stones must be placed in a compartment walled off from the main tank. In all instances, screens, especially those placed around the outflow, must allow slow water flow at all times. The mesh size must be small enough to prevent animals (including food organisms) from passing through the screen, yet large enough to allow the water to flow freely. The total surface area of the screen should be large. Uneven mesh distribution should be avoided, as the water flow through larger openings may be higher than the hatchlings can counteract by jetting. All screens should be cleaned frequently, because micro-fouling alters the flow characteristics. Clogging of mesh results in a rise of water level, which in turn raises the flow speed in the upper 'clean' part of the screen.

One of the safest methods to ensure normal

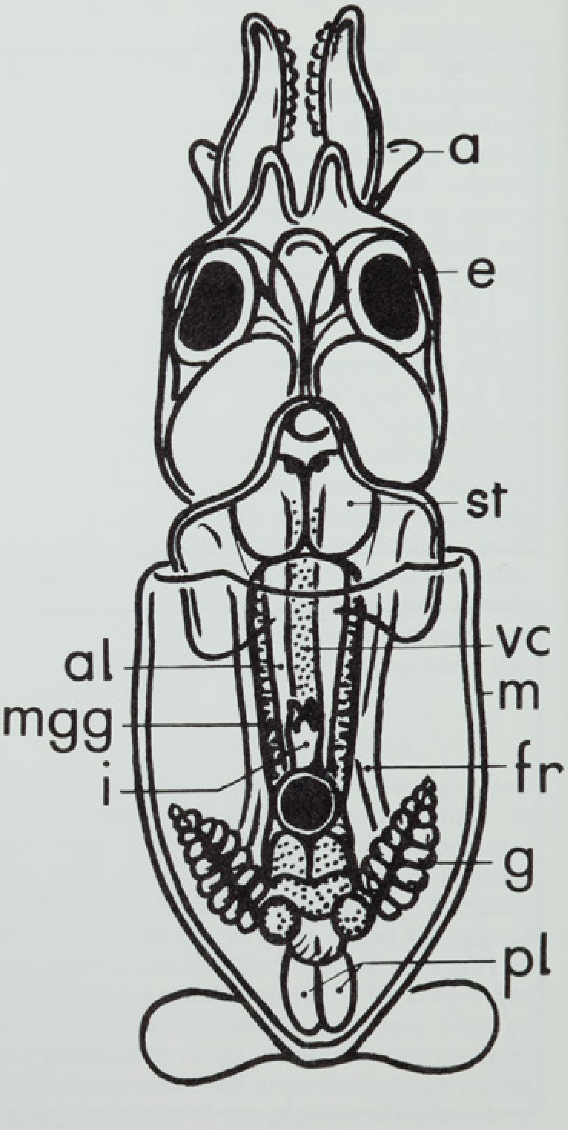

Figure 2. Semi-schematic presentation of a newly-hatched *Loligo vulgaris* in ventral view. The outer yolk sac amidst the arms has disappeared, whereas the inner yolk sac is still sizable. Its anterior lobe (a) lies between the two large lobes of the midgut gland (mgg). The posterior lobes (pl) of the inner yolk sac reach to the posterior end of the visceral complex. Other organs are the intestine (i), the gills (g), the funnel retractors (fr), and the vena cephalica (vc), all lying within the mantle (m). Dorsally to the funnel lie the statocysts (st). In front of the large optic lobes and on either side of the buccal mass lie the eyes (e). The arm crown comprises the two long tentacles and the shorter arms (a). (From Boletzky, 1975a.)

hatching for squids, in addition to optimal rearing conditions, is to suspend egg capsules singly in the rearing tank. Egg clusters should not be suspended as a whole, because the gentle water flow (ensure the absence of air bubbles!) may be insufficient to ensure oxygenation of the inner parts of the egg mass. Furthermore, separately suspended egg capsules allow optimum conditions for hatching, because the animals emerge into open water as soon as they penetrate the surface of the gelatinous envelopes. The process of penetrating these envelopes is 'fully automatic', because the integumental ciliature drives the animal through the 'bore hole' made by the hatching gland (Boletzky, 1979c). As squids tend to hatch during nighttime, hatching can be delayed to some extent by constant lighting of the tank. High light levels have caused excessive algal growth on egg clusters of *Loligo opalescens* (Yang, pers. comm., 1982); therefore it is advisable to maintain lighting at low intensity.

Most octopuses 'brood' their eggs and this necessitates slightly different techniques. If the mother octopus does care for the eggs, the bulk of the egg mass by all means should be left with the animal to ensure the natural oxygenation and cleaning functions. The swimming hatchlings can be collected by channelling the water from the (unscreened) overflow of the brooding tank into a large holding tank placed next to it. The overflow of the latter must be screened. This method also can be used for species having bottom-living hatchlings, but the young animals settled in the brooding tank should be collected regularly. Samples should be taken from the egg mass long before hatching, to closely follow embryonic development. Development can be speeded up by increasing temperature so that preliminary rearing trials can be run before the bulk of hatchlings arrives. Normal hatching continues over several days or weeks, according to the length of time during which the eggs have been laid.

All octopus eggs taken from the egg mass are endangered by fouling, because the unprotected chorion very quickly becomes colonized by microorganisms. To prevent this, the eggs should be kept in very clean sea water. An effective method to keep small-sized eggs is to spread them out in small numbers in Petri dishes in a few millimetres of filtered sea water, which must be changed daily. The low water level permits rapid oxygen diffusion. Large octopus eggs do not always develop under these conditions, probably because the large yolk mass settles in the chorion, which may impede the epibolic growth of the early blastodisc. These eggs should therefore be kept floating, e.g. in a funnel (of inert material) with a gentle water jet or stream of air bubbles rising from the funnel tube. The hatching mechanism of octopuses functions independently of the egg-care of the mother animal (Boletzky, 1966).

Although newly-hatched animals start to feed actively only hours or days after hatching, they always do so before their yolk reserves in the internal yolk sac are completely consumed (Boletzky, 1975a). Living prey organisms therefore should be present as early as possible. Prey organisms should be of a size no larger than the size of the hatchling. Indeed, this size relationship should be adhered to throughout rearing.

Adverse effects of confinement in rather small tanks can be alleviated for actively swimming animals, especially squids, by allowing them to locate visually the boundaries of their artificial environment at all times. Total darkness at night must be avoided; a dim source of artificial light is sufficient for their vision. However, sudden exposure to bright lights without a transition time after the period of dim light must be avoided, since it often produces a 'panic' reaction that can result in the animals injuring themselves.

The correct choice of tank systems and of food organisms is essential for the success of a rearing project. It is stressed here that the hatchlings must be placed as early as possible in the artificial environment in which they must live in subsequent months. The substrate chosen for the bottom of the rearing tank must satisfy the behavioural patterns of the animal as well as the experimental requirements, especially the necessity of keeping track of the reared animals and of the food organisms.

The change from the protected microenvironment of the egg-case to the open water exposes the animal to many dangers even in the absence of predators. Very close observation of early rearing conditions by the experimentor is essential in limiting hazards.

D. DISEASES, PARASITES AND PREVENTION

Very little is known about diseases in cephalopods (Hochberg, this volume). Presently there are only few reported cases of diseases or parasites which have seriously affected the maintenance of cephalopods (cf. Polglase, 1980).

In squids, fin damage from abrasion (Boletzky, 1974c) and subsequent bacterial, fungus or protozoan infections (Leibowitz *et al.*, 1977; Hulet *et al.*, 1979; Hochberg, pers. comm.) cause difficulty in carrying out forward attack movements on prey, so that starvation and infection soon lead to death. Prevention of fin damage is the only known remedial action (see also Marthy, 1974a,b).

In octopuses, Forsythe and Hanlon (unpublished data) have noted significant mortality from bacterial infections of the mantle skin during a large-scale pilot culture of *Octopus joubini* in closed systems. Nifurpirinol and tetracycline treatments in separate aquaria showed signs of alleviating the condition; Poupard (1978) stated that these antibacterial agents may have little adverse effect on beneficial nitrifying bacteria in filter beds, and therefore they hold promise for future treatment of skin damage. Yang *et al.* (1980b; in press) quarantine and, in some instances, prophylactically treat food organisms fed to reared squids with antibacterial agents such as chloramphenicol, erythromycin and tetracycline; they also treat crustacean food organisms such as mysidacean and palaemonid shrimp with quinicrine to eliminate protozoan ectoparasites. Future work should evaluate the effectiveness of antiparasitic agents such as quinacrine, which is used by Yang *et al.* (1980b) to treat food organisms fed to reared squids.

In laboratory culture, attention must be focused on bacterial and viral infections, especially those precipitated by overcrowding. Little is known about viruses in either squids (Devauchelle & Vago, 1971) or octopuses (Rungger *et al.*, 1971). Fungi have been reported to cause fatal lesions in the octopus *Eledone cirrhosa* (Polglase, 1980). There are numerous reports of parasitic infestations in wild-caught cephalopods (see reviews; Dollfus, 1958; and Hochberg, this volume). Hochberg (this volume) reviews the parasites of cephalopods and discusses potential parasite problems in culture.

Ultraviolet light or ozone often are used for disinfection of culture water, but their application and effectiveness in different culture designs are controversial. Spotte (1979) provided a recent synopsis of both methods. A great deal more directed research on their usefulness in controlling pathogens in marine systems must be done before they can be recommended for cephalopod culture.

Diets of Cephalopods

A. THE NATURAL DIETS OF CEPHALOPODS

The dominant prey organisms of cephalopods are crustaceans, other molluscs and fishes. Actively moving prey are located visually in most species, pursued and—if they are unable to escape—seized with the tentacles or arms. The relative size of the prey may be very large, sometimes similar to the size of the cephalopod predator. Large prey generally is reduced to pieces by the strong beaks; these pieces are grasped by the radula and swallowed. It has been observed also that very large prey sometimes may be swallowed whole (Bidder, 1950; see also Bidder, 1966 for records of food by various authors, and Boucaud-Camou and Boucher-Rodoni, 1982).

The stomach contents of a cephalopod may yield very precise information on the animal's natural diet, but often the stomach of freshly caught animals either is empty or contains material that is not easily identified. In samples obtained by trawling or dredging, the animals taken together with cephalopods may be considered potential prey, but unless they are recognized in the stomach contents of the cephalopods one cannot be certain. Also, it cannot be excluded that some abnormal predation occurs in a trawl net during the course of a tow.

In bottom dwelling octopodids, the exoskeletons and shells of crustaceans and molluscs often are found as 'middens' that allow identification of the food animals, provided it can be established that the remains were actually eaten by the octopus. Analysis, however, may be misleading because smaller crustacean parts often are washed away by currents.

Direct observations of cephalopod predation in the sea, generally by divers, largely are restricted to a few species of cuttlefishes, loliginid squids, and octopuses (cf. Lane, 1960; Altman, 1967; Hochberg & Couch, 1971; Hanlon, 1975; Hanlon & Hixon, 1980).

B. DIETS FOR CEPHALOPODS IN EXPERIMENTAL WORK

Many bottom-living cephalopods, in which energy consumption for locomotory activity may be very low, can survive for days or even weeks without food. For certain experimental purposes, this tolerance to starvation is most helpful, but for long-term maintenance a minimum supply of food is necessary.

According to Grimpe (1928) cephalopods that survive in the aquarium feed almost exclusively on crustaceans, and all of them show clear preference for living prey. Grimpe (1928) summarized knowledge of the diets of cephalopods up until that time, but recent work has shown that cephalopod diets are more diverse. The following sections update his summary.

The problems of food density in cephalopod culture also have been approached by Grimpe (1928) who stressed the 'voraciousness' of most cephalopods, but he made it clear that precise figures on optimal food intake were not available. Borer (1971) found that food intake in *Octopus briareus* and *O. bimaculoides* increased in proportion to the number of prey (crabs) offered daily and decreased following a reduction in prey size. In contrast, food density is much more difficult to define with nektonic cephalopods that have to be given greater tank space; these problems have been discussed by Yang *et al.* (1980a,b; 1982; see also Hirtle *et al.*, 1981).

1. Subclass **NAUTILOIDEA**
    i. Order NAUTILOIDEA
        a. Family NAUTILIDAE

Nautilus spp.

Willey (1902) summarized his experience with the feeding habits of the Pearly Nautilus. He stated that stomach contents indicated a crustacean diet under natural conditions, and added that 'any kind of animal bait will tempt *Nautilus*, and after a full meal the crop is found to be gorged to repletion'.

Bidder (1962) described the feeding of *Nautilus macromphalus* and *N. pompilius* in aquaria. In these observations of animals that survived for up to 8 weeks in captivity, pieces of fishes or crabs were fed to the animals.

Cousteau (1971) reported on a *Nautilus* from New Caledonia that lived for two months in the Monaco Aquarium, feeding on sardines. More recently, *N. macromphalus* has been regularly on display in Monaco (see also Packard *et al.*, 1980, Hamada *et al.*, 1980, and Ward, in press).

Haven (1972) maintained *Nautilus pompilius* in holding cages set at different depths in the sea and in aquaria. The animals were fed live and dead crabs and fishes, and pieces of chicken. At least part of the natural diet of *Nautilus pompilius* was found to consist of small crabs (ca. 1 cm carapace width). Haven suggested that this species is a bottom feeder and that possibly in addition to feeding on small crustaceans, it is a scavenger.

Ward and Wicksten (1980) analysed the stomach contents of *Nautilus macromphalus* in New Caledonia and found hermit crabs (*Aniculus aniculus*) to be the most important prey, followed by small brachyuran crabs. Fish and lobster (*Panulirus*) fragments also were found, and on several occasions *N. macromphalus* was observed in the natural habitat ingesting portions of newly molted lobster exuviae (*P. longipes*).

Mikami *et al.* (1980) used pieces of jack mackerel (*Trachurus japonicus*) and shrimp (*Pandalus borealis*) as food for *N. macromphalus* in the Yomiuri-Land Marine Aquarium (Tokyo). They also noted that the animals could not capture live fish (*Abudefduf assimilis*), crabs (*Hemigrapsus sanguineus*) or annelids, which are all fast-moving prey.

Carlson (1977) stated in 'The Chambered Nautilus Newsletter' that *N. pompilius* shipped from Fiji to the Waikiki Aquarium (University of Hawaii) were 'fed one fresh shrimp or chunk of fresh tuna every other day (occasionally every day), but they will not eat twice a day'.

2. Subclass **COLEOIDEA**

i. Order SEPIOIDEA

The Sepioidea or cuttlefishes are one of the two groups of decapodous cephalopods. The sepioids generally live at moderate depths and in close relation to the sea bottom. There are only two pelagic forms among them: *Spirula* with its coiled chambered shell, and the sepiolid *Heteroteuthis*. All the others spend most of their time on the sea bottom, and many hide in sandy and muddy substrates during day-light hours and thus remain quiescent for long periods.

Whereas *Spirula* and *Heteroteuthis* never have been kept in aquaria for more than a few days, some of the common benthic or nektobenthic species of *Sepia* and of several sepiolids have been reared from hatching to the adult stage.

a. Family SEPIIDAE

Sepia officinalis

Najai and Ktari (1974) analysed the stomach contents of more than 500 individuals of *S. officinalis* from the Tunisian coast. They identified the following food items: crustaceans (*Penaeus* sp. and other decapods; *Sphaeroma*, *Cymodocea* and other isopods; copepods; and ostracods), bony fishes, molluscs (octopod and decapod cephalopods, lamellibranchs, gastropods, and pteropods); a few worms (polychaetes and nemerteans); and algae (in two stomachs).

In a study of the feeding behaviour of newly hatched *S. officinalis*, Wells (1958) showed that young animals of this species regularly attack and eat mysids (*Mysis* sp.). These observations have been confirmed by others. In addition to mysids (*Praunus* sp.), very young cuttlefish can be fed on small prawns (*Leander* spp., *Crangon* spp.) and on amphipods (*Gammarus* spp.), as reported by Schröder (1966). This author cultured *S. officinalis* through two consecutive generations in the Berlin Aquarium, where the half-grown and adult animals fed on fishes and crabs (*Carcinus* sp.).

Messenger (1968) analysed the visual attack of *Sepia*, on prawns and crabs in particular. Additional observations are reported on young cuttlefishes feeding on fish fry (*Mugil* sp.), and on adults eating mantid shrimps (*Squilla* sp.) and smaller *Sepia*.

Neill and Cullen (1974) used young mullet (*Mugil* spp.) in experiments on the hunting behaviour of cuttlefishes. They found that attacks were more successful with single prey animals than with schooling prey, and they described the sequence of actions during an attack. Their observations complement those of Messenger (1968).

Richard (1966, 1975) cultured *S. officinalis* for experimental purposes in a marine laboratory. His observations indicated that very young animals accepted amphipods (*Marinogammarus marinus*, *M. stoerensis*, *Gammarus zaddachi*) and that optimum growth in juvenile and adult animals was obtained with a varied diet including prawns (*Crangon vulgaris*, *Palaemonetes varians*, *Palaemon serratus*), crabs (*Carcinus maenas*, *macropipus holsatus*) and fishes (*Gobius minutus*, *Cottus bubalis*, *Pholis gunellus*, sole, herring). Richard (1971) also suggested that newly hatched *Sepia* might be fed brine shrimp (*Artemia*) which can be obtained easily by mass culture. However, the growth rates obtained with these clearly were lower than with natural diets such as mysids and palaemonid or crangonid prawns (Pascual, 1978; Boletzky, 1979b).

Overath (1975) fed *Daphnia* to newly hatched *Sepia* and after two weeks, small *Crangon* sp. and *Astacus leptodactylus*. More recently Féral (1977, 1978) reared *Sepia officinalis* with the following diets; hatchlings with mysids (*Paramysis nouveli*, *Praunus flexosus*) and adult *Artemia salina* until they attained a length of about 5 cm. Larger cuttlefishes, 5 to 10 cm long, were fed crustaceans (*Crangon crangon*, *palaemon serratus*, *Orchestia marina* and young *Carcinus maenas*) and fishes (*Pomatochistus microps*, young *Mugil auratus* and *Onus mustellus*). For still larger animals, the prey offered were crabs (*Carcinus maenas*), large prawns (*Palaemon serratus*) and various species of fishes (*Gobius paganellus*, *Blennius* sp., *Ammodytes lanceolatus*, *Onos mustellus*, *Mugil auratus*).

Yim (1978, see also Yim & Boucaud-Camou, 1980) used natural zooplankton to feed very young cuttlefish, up to ten days old, and *Mysis* or very small *Crangon crangon* thereafter.

Pascual (1978) cultured *Sepia officinalis* through three generations feeding young animals on various diets composed of *Diamysis bahirensis*, *Mesodopsis slabberi*, *Palaemonetes varians*, and *Artemia salina*. Larger animals were given *Palaemonetes*, *Carcinus maenas*, *Engraulis encrasicholus*, *Atherina presbiter*, *Sardina pilchardus* and *Mugil auratus*.

Unless they are underfed or actually starving, cuttlefishes generally take live prey only, or else dead prey that is artificially kept in motion. Such prey may elicit attack and seizure by the cuttlefish even above the water surface (Boletzky, 1972). The upper size limit of a type of prey that will be attacked by a cuttlefish varies among individuals, and also it may depend on the momentary motivation for feeding. As a general rule, the total length of a fish or prawn should not be greater than the total length of the cuttlefish; the carapace width of a crab should correspond to not more than one half of the dorsal mantle length of the cuttlefish (cf. Boletzky, 1974a). There is no definite lower size limit for prey. Very hungry *Sepia* will attack very small prey, small mysids for example, which usually they are unable to seize with their tentacles when half-grown or adult.

Underfed *S. officinalis* may survive for many months (Boletzky, 1974b, 1979b), and with a regular minimum supply of food their growth rate can be kept extremely low (ca. $\frac{1}{10}$ of normal linear growth) from hatching to an age of one year or more. The minimum food requirements can be recognized from the buoyancy of the animals; starving animals generally float at the surface and are unable to remain on the bottom if they have been successful in descending by jet propulsion. After feeding they soon attain neutral buoyancy (cf., Denton & Gilpin-Brown, 1973). To facilitate their attack on moving prey, one may place starved cuttlefish in a tank with a very low water level, so that they float just above the bottom, or the prey may be presented at the water surface (e.g., suspended on a thread).

Among the earliest signs of starvation is the appearance of a longitudinal dark stripe on the dorsal side of the mantle, caused by the concentration of chromatophores resulting from skin contraction. The life cycle is summarized by Boletzky (in press, a).

Sepia lycidas

In a report of the Fukuoka Buzen Fisheries Experimental Station (1968), young animals within 12 hours of hatching attacked and ate various shrimps 5-12 mm long (*Metapenaeus joyneri*, *Palaemon pacificus*, *Crangon* sp., *Leander* sp.). Frozen food also was accepted (shrimps, fishes, clams, pelletized food), but only live shrimps, especially *Crangon* sp., yielded good results, with an average daily food ingestion of 0.1 g per individual in the first weeks after hatching. Larger juveniles were transferred to pond cages and fed larger *Crangon* sp., *Palaemon* sp., and later gobies and sliced fish.

Sepia latimanus

Inoha (1971) reported that eggs were laid in corals of the genus *Millepora*. The hatchlings had a dorsal mantle length about twice as large (13.5-15.8 mm) as in *Sepia officinalis*. They attacked and ate *Palaemon* sp. and other shrimps, whereas fast moving fish larvae (mullet, *Apogon lineatus*, *Chromis notata*) were able to escape.

Sepia esculenta, *S. subaculeata*, *Sepiella maindroni*

Oshima and Choe (1961), Choe and Oshima (1963), and Choe (1966b) reared these species of cuttlefishes in the laboratory from hatching to an age of four months. They used living *Neomysis japonica* as food for the young animals. In the older ones, the living prey were replaced by 'minced fish meat or salted mysis-shrimp placed on the bottom of the tank'. Choe (1966b) noted a lower growth rate in animals fed on dead food as compared to those fed on live prey. In a short-term experiment on the feeding rates of the three species of cuttlefishes, Choe also used *Leander serrifer*.

Eugusa (pers. comm.) wrote that 'a large-scale experiment on the culture of *Sepia* *subaculeata* was done with considerable success by the Fukuoka Prefectural Fisheries Experimental Station.' The young cuttlefishes started to feed 12 hours after hatching, living shrimp larvae 5-12 mm long being the best food; frozen larvae were seized in mid-water (not on the bottom!). However, for cuttlefishes ten days old, live prey could be replaced (entirely) by frozen shrimp, and 20 days after hatching, the young *Sepia* accepted fish meat.

Sepiella inermis

Tang and Khoo (1974) studied prey selection (type and size of prey) in this small species of cuttlefish. Prey organisms used in their experiments were fish (*Poecilia reticulata*), prawns (*Acetes* sp.), and crabs (*Dotilla* sp.); they 'corresponded quite closely to the type and size of prey consumed by *Sepiella inermis* in the natural environment'.

b. Family SEPIOLIDAE

Rossia macrosoma

This fairly large species of the sepiolid subfamily Rossiinae has been reared in the laboratory by Boletzky and Boletzky (1973) from hatching to the age of eight months. The animals were fed live prawns (*Leander serratus*) from hatching onward. The maximum length of the prawns presented was roughly twice the mantle length of *Rossia*. Mysids were rarely captured by the young animals. Crabs, even very small individuals, never were taken.

Rossia pacifica

This species rests in shallow depressions in shrimp beds and 80% of its diet consists of shrimps, although crabs, mysids, small fishes and cephalopods also are eaten (Brocco, 1970; Hochberg & Fields, 1980).

Euprymna berryi

Choe and Oshima (1963) and Choe (1966b) briefly reported on the laboratory rearing of this small species of subfamily Sepiolinae. The hatchlings were reared to the age of about two months with live mysids.

Euprymna scolopes

Arnold *et al.* (1972) used adult *Leander debilis* as food for adult animals of this species. Occasionally small *Gambusia affinis* were offered. Young animals hatched in the laboratory were fed on larval and adult *Anisomysis* sp., adult *Artemia salina*, and occasionally on newly-hatched *Octopus cyanea*. They were reared to the age of nearly seven months. The life cycle is reviewed by Singley (in press).

Sepiola spp. and *Sepietta* spp.

Boletzky *et al.* (1971) reared four species of *Sepiola* (*S. rondeleti*, *S. robusta*, *S. affinis*, *S. ligulata*) and two species of *Sepietta* (*S. obscura*, *S. neglecta*) from hatching to the adult stage (see also Boletzky, 1974a, 1975c). All the young animals were fed on mysids (*Leptomysis mediterranea*); older juveniles and adults were fed small *Leander* spp. In the area of Banyuls-sur-Mer (western Mediterranean) *Sepiola robusta* is caught regularly at depths of a few metres on a sandy bottom (in which it hides during daylight hours), together with the crangonid prawn *Philocheras* spp. (Boletzky, in press, b). A recent series of experiments has shown that sepiolids as well as young *Sepia officinalis* can be fed exclusively *Philocheras* if this prey is available in sufficient numbers (personal observations).

Summers and Bergström (1981, and pers. comm.) cultured *Sepietta oweniana* to the second generation in open seawater systems in Sweden. The large benthic hatchlings (5 mm ML) fed 'mixed, shallow-benthic arthropods which were sorted only by straining out those things which would not pass a 2 mm sieve'. they would not eat brine shrimp or fishes. At three months, they showed a preference for the mysids *Praunus flexuosus* and *P. inermis*, but also would accept the shrimps *Palaemon elegans*, *Thoralus cranchi* and *Crangon crangon*. Growth on this diet averaged 4 mm per month to maturity. Stomach contents of 515 wild-caught specimens showed that 7.2% had food in the stomach and that 80% of the remains were shrimps and euphausiids. Bergström and Summers (in press) reviewed the life cycle of *S. oweniana*.

ii. Order **TEUTHOIDEA**

The majority of the squids, which form the largest taxonomic group of the recent cephalopods (in terms of the number of families and genera), are pelagic animals that live in coastal and offshore waters. Among the oegopsid squids only two ommastrephids that live at least part of the year in rather shallow water have been used for long-term laboratory investigations. The only squid species that have been reared from hatching in the laboratory so far belong to the Loliginidae, which generally live close to shore. However, these animals are nektonic, as are all squids, and although they live close to the bottom, apparently they do not remain quiescent even for short periods under natural conditions. The high energy requirement of this continually active mode of life necessitates a high food intake in growing squids, with daily rates at least around 50% and occasionally higher than 100% of the predator's own weight (cf. LaRoe, 1971).

a. Family LOLIGINIDAE

Sepioteuthis lessoniana

Choe and Oshima (1963) reared this species from hatching to the age of 45 days on a diet of live mysids (*Neomysis japonica*), obtaining a daily increase of the squid's body weight between 7 and nearly 11% (Choe, 1966b).

Inoha and Sezoko (1967) fed larvae of *Macrobrachium* to young *Sepioteuthis*. Saso (1979) reared this species to the age of 170 days on a diet of fish larvae (*Atherina bleekeri*), small anchovies (*Engraulis* sp.), and later on larger *Atherina bleekeri* and *A. japonica*. Matsumoto (1975) fed horse mackerel and anchovy to wild-caught *S. lessoniana* (30-60 g) held in cages in the open sea and obtained a tenfold weight increase in about two months.

Sepioteuthis sepioidea

LaRoe (1970, 1971) reared this species from hatching to sexual maturity at nearly five months of age. The young animals were fed on coral reef mysids (*Mysidium columbiae*, *M. integrum* and *Heteromysis actinea*) and juvenile or larval fishes (*Gambusia* sp., *Poecilia* sp.). A variety of other prey were tried but were not eaten regularly by the young squids (e.g. copepods, including some large *Acartia* sp., chaetognaths, pelagic polychaetes, *Artemia salina*, zoea and megalopa stages of various crabs and other crustacean larvae, amphipods, very young crabs and shrimps).

Larger squids were fed primarily on fishes (anchovies, *Anchoa* sp.; mollies, *Poecilia* spp.; mojarras, *Gerres* sp.) and penaeid or palaemonid shrimps (cf. Arnold, 1965, who used pilchards and other small fishes). LaRoe notes that 'each of the foods found was only suitable for a definite size range. The squids would not attack prey that were too large or too small. Between the 21st and 26th day they ceased to attack mysids; by this time they were about twice as long in total length (ML about 1 to 1½ times longer) as mysids'.

Loligo vulgaris

In contrast to *Sepioteuthis*, the eggs of this species are small, and the hatchlings have a mantle length of about 3 mm, which is about half of that in newly-hatched *Sepioteuthis* (ca. 5 mm in *S. sepioidea*, 6-7 mm in *S. lessoniana*). Consequently the upper size limit of suitable prey is considerably smaller than with young *Sepioteuthis*.

Bidder, in an appendix to the paper by Portmann and Bidder (1928), reported on experiments aimed at the laboratory culture of hatchlings of *Loligo vulgaris*. The only positive indication of prey capture in the newly hatched squid was found with the copepod *Temora longicornis*, whereas captured oyster veligers were dropped 'as if in disgust'.

Boletzky (1971, 1974a, 1979a) fed hatchlings of *L. vulgaris* with young *Leptomysis mediterranea*, the telson and uropods ('tail fan') of which had been cut off in order to slow down the escape movement of this prey. This diet was supplemented by half-grown *Artemia salina* and crustacean larvae.

Larger juveniles and adults captured from the sea were used in an experimental study of the digestive mechanism by Bidder (1950). The experimental animals were fed small dead fish and pieces of fish, which they captured in midwater. Bidder observed that 'once food had fallen on the bottom, it was rarely taken again. Pieces of food suspended on threads in midwater were always ignored. The most successful method was to balance food on a loop of wire, fixed into the end of a long piece of glass tubing, so that neither operator nor tool was visible to the squid, and to let the food fall in as gently as possible'. Bidder also used *L. forbesi*, *Alloteuthis media* and *A. subulata*, in this study.

Tardent (1962) reported that young *L. vulgaris* (4-10 cm in mantle length) caught with night lights were kept regularly in the Naples Aquarium for periods up to two months. The squids were fed with pieces of sardines and live shrimps (*Lysmata* sp., *Leander* sp.). In contrast to the observations of Bidder (1950), Tardent found that 'food is as readily picked up from the bottom or walls of the tank as from the water surface', and he concluded that *L. vulgaris* 'seems to have much closer relations to the bottom than one might think'. Neill and Cullen (1974) studied the hunting behaviour of *L. vulgaris* using live fish (*Atherina* sp.) as prey. Worms (in press) reviewed the life cycle.

Loligo opalescens

The earliest attempts to rear the hatchlings of *Loligo opalescens* were made by Fields (1965). The food offered included newly hatched larvae of the copepod *Tigriopus fulvus* and of *Artemia salina*, motile cells of different algae, the diatom *Nitzschia closterium minutissima*, and fine planktonic material. The young squids were not observed to feed, and all died within ten days of hatching.

Hurley (1976) was successful in rearing *L. opalescens* to a maximum age of 100 days on a diet of *Artemia* nauplii and adults. The hatchlings, which are similar in size to those of *L. vulgaris* (mantle length 2.7 mm) readily attacked the nauplii (length 0.7 mm) and small adults of *Artemia salina* (5 mm long), copepods (1 mm long) and larval fishes (4 mm long). In an experiment with squids aged 49 days, a great number of larvae of the chub mackerel, *Scomber japonicus*, were presented to animals that had been feeding on adult *Artemia* of comparable size. The number of the fish larvae presented was about equal to the number of *Artemia* (of similar size) present in the tank. The squid attacked the fish larvae much more frequently than the *Artemia*, but only few attacks on the former were successful. In contrast to what LaRoe (1971) observed in *Sepioteuthis sepioidea*, Hurley found that young *L. opalescens* 'must be considered as predators on a wide range of prey types and prey sizes'. This author also cited a personal communication of McGowan, saying that young *Loligo opalescens* successfully attack the mysid *Metamysidopsis elongata*.

Hanlon *et al.* (1979) reared the hatchlings of *L. opalescens* to a mantle length of 17.3 mm in 79 days principally on a diet of copepods. The hatchlings vigorously attacked the large, slow-moving, white colored copepod *Labidocera aestiva* (3.0 to 3.5 mm long). Three weeks later at a mantle length of 5 to 6 mm the squids also ate the larger blue copepod *Anomalocera ornata* (5.0 to 5.5 mm long). Young squids of 6 to 9 mm ML also readily attacked and ate the clear copepods *Eucalanus hyalinus* (6.0 to 6.5 mm long). *Artemia* nauplii and adults were eaten at times of low copepod availability, but squids that were fed exclusively on brine shrimp (*Artemia*) did not survive beyond ten days. Squids did not feed on barnacle nauplii (*Balanus* spp. 0.2 to 0.5 mm). Squids showed a clear preference for copepods, and the growth rates obtained on this diet were slightly higher than reported by Hurley (1976). Mortality was attributed to fluctuating food availability and, in later stages, to fin damage.

Yang *et al.* (1980b, 1983), based on the results of Hanlon *et al.* (1979), used large-scale closed systems to rear the hatchlings to near sexual maturity at a mantle length of 77 mm after 233 days. The diet consisted of copepods, other crustaceans and fishes. During the first 70 days the squids readily attacked and ate the copepods *Acartia tonsa* (0.8 to 1.2 mm), *Labidocera aestiva* (1.5 to 2.5 mm) and *Anomalocera ornata* (2.0 to 3.0 mm). During the same period, squids were fed *Artemia* nauplii and adults (0.3 to 4.0 mm) as a supplementary food source, and they were seen to attack and eat chaetognaths. From days 60 to 130 the young squids (5 to 25 mm ML) were fed the myses and postlarvae of the pink shrimp *Penaeus duorarum* (2.5 to 6.0 mm) and the mysid shrimp *Mysidopsis almyra* (2 to 10 mm). Beginning at day 100 the growing squids were fed an assortment of shrimps and fishes including the grass shrimp *Palaemonetes pugio* (1.5 to 25 mm) and the estuarine fishes *Fundulus similis* (8 to 35 mm), *Menidia beryllina*, *Adeinia xenica*, *Fundulus grandis*, *Cyprinodon variegatus*, *Gambusia affinis* and *Mugil* spp. (all

15 to 70 mm). Growth on this diet was 1.69 per cent per day and mortality was attributed to starvation and fin damage.

Hixon and his co-workers (in prep.) have cultured *L. opalescens* through to sexual maturation and egg laying. The techniques, foods and tank systems were similar to those described above, except that food was made available constantly and at higher densities. Growth rate was nearly double the previous experiments of Yang (1980b, in press). Egg laying occurred on day 184 in a female approximately 85 mm ML. For the first time the reared squids showed cannibalism, which coincides with observations of natural populations off the coast of California. Adult feeding dynamics of *L. opalescens* have been studied by Karpov and Cailliet (1978).

Hochberg and Fields (1980) noted that adults fed on euphausiids, mysids, fishes, benthic polychaete worms and their own young. Loukashkin (1976) analyzed stomach contents of 1000 adult *L. opalescens* and found that, among the 33% of stomachs with food, 42% had crustacean remains, 20% fish remains and 14% polychaete worms and miscellaneous material. The pelagic red crab *Pleuroncodes planipes* has been observed to be eaten by *L. opalescens* (Siger, pers. comm.). A review of the live cycle of this squid species is given by Hixon (in press).

Loligo pealei

The small hatchlings of this species (1.6 mm ML) are similar in size and morphology to those of *L. plei* (McConathy *et al.*, 1980). Chanley (unpublished report, 1976) fed them egg yolk and minced mussel meat with maximal survival of 13 days. Haefner (1959) indicated from stomach content analyses of *L. pealei* in Chesapeake Bay that young squids prefer a diet of shrimps, and larger squids prefer fishes.

The only success in rearing the hatchlings has been by Yang *et al.* (1980a) who reared one squid to 3.3 mm ML in 40 days. The general methodology and tank design were similar to that in Hanlon *et al.* (1979). They fed on very small copepods (*Acartia tonsa*, *Labidocera aestiva* and others). Very small rotifers (*Brachionus pliciatilis*), marine cladocerans (*Diphanosoma* sp.) and *Artemia* nauplii were not readily taken.

Adult *L. pealei* have been maintained for periods of varying length up to 28 days by Drew (1911), Arnold (1962), Summers and McMahon (1970, 1974), and Summers *et al.* (1974) using the estuarine fish *Fundulus* as food. Hanlon *et al.* (1978 and in prep.) maintained this species up to 71 days on a fish and shrimp diet similar to that described for *L. plei*.

Whitaker (1978) studied the biology of *L. pealei* and *L. plei* on the southeastern coast of the United States. Dominant prey were fishes, followed by crustaceans and squids. A small proportion of stomach contents also contained chaetognaths and some miscellaneous items (see also Vinogradov & Noskov, 1979). Vovk and Khvichiyia (1980) analyzed feeding in juvenile *L. pealei* and found that main food objects were young fishes, copepods, squids, chaetognaths, euphausiids and other shrimps. The change from mesoplanktonic to macroplanktonic food was observed at a size of about 8 cm ML, and to the adult type of feeding between 12 and 16 cm ML. Macy (1982) found that, overall, crustaceans were more frequently consumed than either fishes or squids. However, there was a general trend for squids less than 15 mm ML to consume more crustaceans, while those over 15 mm ML consumed more fishes. Summers (in press) reviewed the life cycle of *L. pealei*.

Loligo plei (= *Doryteuthis plei*)

The small hatchlings of this species are only 1.5 mm ML (Hanlon *et al.*, 1979 Figure 1; McConathy *et al.*, 1980), and they have not been reared yet. Hanlon (1978) tried rearing them in small aquaria on *Artemia* nauplii, rotifers (*Brachionis pliciatus*) and small copepods but none survived beyond three days. In a separate experiment, young wild-caught juveniles 12 to 22 mm ML fed vigorously for several days on postlarval white shrimp (*Penaeus setiferus*) until the shrimp supply ran out (Hanlon *et al.*, 1979).

Larger juveniles and adults (32-285 mm ML) fed vigorously and grew well on shrimps (*Palaemonetes pugio* and *Penaeus* spp.) and an assortment of estuarine fishes including the sailfin molly *Poecilia latipinna*, the sandtrout

Leiostomus xanthurus and all the fishes listed above for *L. opalescens*. Survival on these diets has been relatively high (mean 19 days, maximal 84 days) and growth has been fast (up to 73 mm ML per month) (Hanlon *et al.*, 1978 and in prep.). The field study by Whitaker (1978) on feeding in this species is mentioned above (*L. pealei*).

Doryteuthis bleekeri

Soichi (1976) kept this species for 67 days in a public aquarium. Matsumoto (1976) maintained adults of this species for up to three weeks in an aquarium, feeding them slices of raw tuna and occasionally living goldfish. In later experiments, Matsumoto and Shimada (1980) achieved survival for ten squids of 43-60 days by feeding them thawed pieces of frozen sardines and live goldfish (*Carassius auratus*).

Lolliguncula brevis

This small species is peculiar in its preference for low salinities (Hulet *et al.*, 1979, 1980; Hendrix *et al.*, 1981), which in nature brings it into contact with all the estuarine food organisms listed above that are used to maintain and grow *Loligo opalescens*, *L. plei* and *L. pealei*. No attempts have been made to rear the hatchlings, but on this shrimp and fish diet juveniles and adults (27 to 91 mm ML) survive for comparatively long periods (mean 37 days, maximum 124 days) and grow quickly (mean 10 mm ML/month) (Hanlon *et al.*, 1978 and in prep.).

Lolliguncula panamensis

Squires and Barragan (1979) recorded the stomach contents of this species from trawl samples. They found that 81% of squids with food in their stomachs had pelagic fish remains such as engraulids (*Cetengraulis* spp.) and clupeids (*Opisthonema* spp.). Another 15% had crustacean remains such as the shrimps *Xiphopenaeus riveti* and others.

b. Family OMMASTREPHIDAE

Illex illecebrosus

Bradbury and Aldrich (1969) fed *Illex* on dead capelin (*Mallotus villosus*) suspended on a thread. These authors noted that 'not only will individuals feed, but they will fight for the capelin suspended in their midst'.

Boucher-Rodoni (1975) also used *Mallotus villosus* as food for *Illex* in a study of digestion, but the head, tail and viscera of the fishes were removed before its presentation to the squid.

O'Dor *et al.* (1977) maintained *Illex illecebrosus* in a large tank for 82 days. The squid first fed on live *Fundulus* sp., later on frozen *Fundulus* and on pieces of frozen mackerel, which they captured in midwater. The only male of the group apparently was attacked early in the experiment; it was found dead and half eaten. There was no cannibalism among the females, which became fully mature (see also Amaratunga *et al.*, 1979). In later maintenance and growth studies, O'Dor *et al.* (1980, see also O'Dor, in press) found that *Illex illecebrosus* readily fed upon shrimp (*Crangon* sp.) and a wide variety of small live fishes including capelin *Mallotus villosus*, herring *Clupea harengus*, mackerel *Scomber scombrus*, smelt *Osmerus mordax*, salmon smelts *Salmo salar* and *Fundulus* sp. Vinogradov and Noskov (1979) found that crustaceans were dominant among the prey of *Illex illecebrosus.*

Only very recently have egg masses and hatchlings of known identity been spawned in the laboratory, but all died within eight days and no rearing attempts were made (O'Dor and Durward, 1978).

In view of the small size of the eggs, similar to that of *Illex coindetii* (cf. Boletzky *et al.*, 1973), and the consequently small size of the hatchlings, which are characterized by the fusion of their tentacles ('rhynchoteuthion' stage), one can presume that the newly hatched *Illex* feed on rather small planktonic organisms. It is inconceivable, however, that the 'proboscis' formed by the fused tentacles acts as a pipette, as suggested by Abel (1916). Probably in functional terms the transitory fusion of the tentacles corresponds to the 'press-button' mechanism of the tentacular suckers in adult squid (cf. Boletzky, 1974c). As the fused tentacles have sizable suckers at their tips, it would seem likely that prey of considerable size (in relation to the *Illex* hatchling) are seized with them.

Todarodes pacificus

Mikulich and Kozak (1971) maintained juveniles and adults of this species in aquaria for periods up to 35 days. Flores *et al.* (1976) found that adult squids could be kept alive for ten days without food, and that they accepted pieces of shrimp and sardine fillet as a regular diet (Flores *et al.*, 1977), with a resulting survival of up to 50 days. Soichi (1976) kept *Todarodes pacificus* for up to 59 days in the aquarium and fed them juvenile mullet and sliced anchovy. Hatchlings of this species have been obtained from egg masses spawned in the laboratory (Hamabe, 1963), but they have not been reared so far. They are very small, similar to the *Illex* hatchlings (cf. above). Records of natural foods of *T. pacificus* have been reviewed by Clarke (1966), the life cycle by Okutani (in press).

Dosidicus gigas

This voracious, active predator seems to prey on nearly any prey available. All feeding information comes from field studies. Fitch (1968) reported that, in the size range of 9 to 50 cm ML, small individuals fed mostly on crustaceans, medium sized squids fed on pelagic fishes (families Engraulidae, Myctophidae, Scorpaenidae, and Embiotocidae), and large squids fed on smaller squids (see also Clarke, 1966).

Nesis (1970) reported that *D. gigas* off Chile and Peru fed upon myctophids (70.2%), squids (13.3%), plankton (7.9%), saury (1.2%) and other unidentifiable foods (7.4%). Sato (1976) reported that *D. gigas* off Baja California fed primarily on the pelagic red crab *Pleuroncodes planipes* but also on myctophid, engraulid and carangid fishes and large quantities of unidentified larvae.

Erhardt *et al.* (MS. presented at work-shop) reported that, in the Gulf of California, *D. gigas* diet consists mainly of sardines (*S. sagax caeruleus*), mackerel (*Scomber japonicus*) and pelagic red crabs (*Pleuroncodes planipes*). From May to July the preferred diet is post-larval penaeid shrimp. Some squids greater than 65 cm ML have been captured with more than 500 g of shrimp larvae in their stomachs! In areas of intense commercial fishing with night lights and jigs, the *D. gigas* feed mainly on their own species.

Hochberg and Fields (1980) stated that *D. gigas* feeds on numerous fishes (anchovies, grunions, skippers, myctophids) and molluscs (pteropods, heteropods, cephalopods). Although *D. gigas* never has been maintained in captivity, it seems possible to keep small individuals in an aquarium. This species is particularly interesting for its very large giant axons. A review of its live cycle is given by Nesis (in press).

Ommastrephes spp.

Clarke (1966) gives a few indications of the stomach contents of *O. pteropus* (fishes, crustaceans, squid hooks) and *O. caroli* (fish and squid remains).

Hixon *et al.* (1980) analysed caecum and stomach contents of *O. pteropus*. Of the filled guts, some contained crustacean carapace remains; these belong to the smaller individuals. Larger animals appear to prey primarily on fishes and on other squids.

Nigmatullin and Pinchukov (1976) found mainly fish and squid remains in the stomachs of *O. bartrami*. This species was more recently analysed by Araya (this volume) who found stomach contents to be mostly fish remains: lantern fishes, sardines, larvae of mackerel and sauries. Squids represented only 18-30% of contents: *Watasenia scintillans*, *Onychoteuthis borealijaponica*, and cannibalised *Ommastrephes*. Planktonic crustaceans (2-18% of contents) were more abundant in young squid as compared to adults; identified crustaceans were members of the Euphausiacea, and *Parathemisto* sp. Consequently Araya (this volume) considered *O. bartrami* as predominantly piscivorous.

iii. Order **OCTOPODA**

a. Family ARGONAUTIDAE

Argonauta argo

This seems to be the only species among the pelagic Incirrata in which feeding has been observed in an aquarium. Lacaze-Duthiers (1892) described a female *Argonauta* which he kept for two weeks in the aquarium of Banyuls-sur-Mer (western Mediterranean). It was fed small living fishes, which it seized very quickly when they came into contact with one of the arms. Young (1960) described feeding experiments using pieces of fish, and Zeiller and Compton (1970) fed an animal brine shrimp and small fishes.

More recently, Boletzky (in press c) kept a female *Argonauta* for one week in a laboratory tank and fed it small crangonid prawns (*Philocheras* sp.) touched to the arms or the mouth, and pieces of shrimp and crab (*Carcinus mediterraneus*); especially portions of crab gonad were touched to the mouth. The animal swallowed these very rapidly using its radula to draw the food in.

b. Family OCTOPODIDAE

All the other laboratory experiments with octopods in which feeding was observed have been made with different species of the benthic octopodid family. In general it is comparatively easy to have the adults feeding on living or dead prey such as crabs, shrimps, bivalves or fishes, and even young octopuses can be raised on a diet of crab meat. In those species, however, that have very small eggs in relation to the size of the adults, the small young hatched from these eggs live for some time in the plankton. Of these, apparently only the hatchlings of *Octopus vulgaris* and *O. ocellatus* in Japan have been reared to the settling stage.

The following species accounts are arranged alphabetically into two groups: the first group includes species with small eggs and small nektonic hatchlings; the second group includes species with large eggs and benthic hatchlings.

Group 1—Small eggs, nektonic hatchlings

Eledone cirrhosa

The hatchlings of this species probably live in the plankton for some time, although they have been found to settle for short periods on hard substrates (Boletzky, 1977). They were fed on half-grown *Artemia*, but did not survive for more than a few days.

Benthic young and adult animals have been maintained in aquaria for many months on a diet of live *Carcinus maenas* (Mangold & Boucher-Rodoni, 1973). Boyle and Knobloch (1981) studied hole-boring by *Eledone cirrhosa* in decapod crustacean carapaces and fed them the crabs *Carcinus maenas*, *Macropipus holsatus*, *M. depurator*, *M. puber*, *Cancer pagurus*, *Corystes cassi velaunus*, *Hyas araneus* and *Pagurus bernhardus*, the shrimp *Crangon vulgaris* and the lobsters *Nephrops norvegicus* and *Homarus vulgaris* (see also Boyle, 1981).

Boyle (in press) summarized the life cycle and reported that *Eledone cirrhosa* also eats eels and probably other fishes as well.

Boyle and Knobloch (1982) studied the growth of juveniles and adults (6 g to 1217 g) fed on a diet of crustaceans, primarily the crabs *Carcinus maenas*, *Macropipus depurator* and *M. holsatus*. Growth on this diet was comparable to other species of octopuses.

Sanchez (1981) described the stomach contents of 171 *E. cirrhosa* caught by trawl in the western Mediterranean Sea. She found that their diet was primarily crustaceans (the shrimp *Alpheus glaber*, the crabs *Gonoplax* sp., *Medeus conchii* and other brachyurans) but also included polychaetes and fishes.

Octopus bimaculatus

Ambrose (1981) observed predation in the field and laboratory and found that *O. bimaculatus* consumed more than 50 prey species from three phyla. Although crabs were clearly preferred, gastropods accounted for 90% of the diet because of the availability in the natural habitat, even though they were the least preferred prey. Shrimps, lobsters, bivalves, chitons and fishes were also consumed, but to a lesser degree. Food preference was determined to be: crabs $\gg$ hermit crabs $>$ bivalves $=$ less motile grazers (e.g. the abalone, *Haliotus* sp.) $\gg$ snails. In summary, this octopus is an opportunistic predator that feeds on a wide size range of organisms.

Octopus burryi

Hanlon and Hixon (1980) fed adult (31 mm ML) and juvenile (13 and 15 mm ML) *O. burryi* the calico crab *Hepatus* sp., the fiddler crab *Uca* sp. and the shore crab *Sesarma* sp. and all were readily eaten. In recent unpublished work Forsythe *et al.* (unpublished data) caught two juveniles in the plankton during night light stations in the Gulf of Mexico and reared one to maturity on a mixed diet of crabs (xanthid mud crabs *Panopeus* sp., hermit crabs *Clibanarius* sp. and fiddler crabs *Uca* sp.) and shrimp *Palaemonetes pugio*. Subsequently a large female (107 mm ML) was caught by trawl; it laid eggs in the laboratory. Forsythe (unpublished data) attempted to rear the small nektonic hatchlings (1.7 mm ML) in a closed seawater system on live wild-caught copepods, principally *Acartia* and *Labidocera*. The hatchlings fed aggressively, but none lived beyond two weeks and no growth was observed.

Octopus cyanea

Van Heukelem (1976) attempted to rear the nektonic hatchlings of this species, which are similar in size to those of *Octopus vulgaris*. The longest survival was 21 days with hatchlings that were fed combined diets of *Macrobrachium* and *Artemia* larvae. Van Heukelem reported that the newly hatched animals 'began feeding within a few hours of hatching on any appropriate sized crustacean offered. *Artemia* of various sizes from nauplii to adult were attacked and eaten readily as were adult mysids, copepods, and *Lucifer* sp.' (cf. Dew, 1959).

Wells and Wells (1970) fed newly settled (benthic) young of *O. cyanea* 'tiny pieces of fresh bivalve and hermit crab abdomen from the end of a fine wire moved close to the home' of the octopuses. First attacks on small grapsid crabs were observed in the second week. In later weeks the young animals were fed different crabs (grapsids, portunids, xanthids, *Ocypode*), the sand crab *Emerita*, the amphipod *Corophium*, alpheid shrimps and small bivalves (*Ctena bella*, *Macoma* and *Pingua* spp.). Attempts to feed the octopuses on *Littorina scabra* were only partially successful and rather suggested that littorinids are only eaten in the absence of more tasteful food.

Live crabs were used as food for young and adult *O. cyanea* by Yarnall (1969), Boucher-Rodoni (1973) and Van Heukelem (1973, 1976). Van Heukelem (1966) found that xanthid crabs were the principal food of the species on Coconut Island Reef (Hawaii), but he concluded that 'food habits probably depend more on what crabs are abundant in the area rather than selection by the octopus, as the sand-burrowing portunids and *Calappa* were found at lairs surrounded by hard substratum'. Van Heukelem's analysis of crop and stomach contents in animals from a different location revealed, in addition to crab remains, stomatopods, alpheid shrimps, an isopod and fish bones. One animal was captured with a small, paralyzed moray eel in its arms. The life cycle of *O. cyanea* has been reviewed by Van Heukelem (in press).

Octopus defilippi

Grimpe (1928) kept this species in aquaria for several weeks and even months at the Naples Zoological Station. He fed them small crabs of the genus *Pisa* and noted that the octopuses could not readily kill larger crabs. Grimpe further noted that this species survived for short periods on dead shrimp and brachyuran crabs.

Hanlon *et al.* (1980) twice reared wild-caught 'Macrotritopus larvae' to adult *O. defilippi* (from 10 to 90 mm ML in 150 days) on a diet of live fiddler crabs (*Uca* sp.).

Octopus dofleini

This species, known as the giant octopus of the Northwest American coast, has been maintained for long periods in several public aquaria. Gabe (1975) fed adult animals frozen herring (*Clupea* sp.) and large living *Cancer magister* crabs. The nektonic young, hatched in the laboratory, were fed various foods, but accepted only fish fry (*Hemilepidotus hemilepidotus*) and adult *Artemia*. Because of technical problems with the aquarium system, the hatchlings did not survive long.

Marliave (1981) reared the hatchlings to 87 days using nauplii and adults of *Artemia salina*, frozen krill (*Euphausia pacifica*), larval cottid fishes (*Hemilepidotus hemilepidotus*) and trout micropellets. Krill was the preferred food. Marliave (1981) hypothesized that the hatchlings cling to the air-water interface to feed on neuston for the first month in the plankton.

In a field study of adult *O. dofleini*, Hartwick *et al.* (1978) found that they feed almost exclusively on crabs, bivalves and gastropods. Crabs were *Cancer*, gastropods included the moon snail *Polinices lewisii* and the abalone *Haliotis kamchatkana*, and the bivalves included *Chlamys hastata*, *Clinocardium nuttalii*, *Gari californica*, *Hinnites giganteus*, *Humilaria kennerleyi*, *Macoma* sp., *Protothaca staminea*, *Saxidomus giganteus*, *Semele rubropicta*, *Glycymeris subobsoleta*, *Modiolus rectus*, *Mya truncata*, *Mytilus californianus*, *Solen sicarius*, *Tresus* sp., and the brachiopod *Terebratalia* sp.

Hartwick *et al.* (1981) found that octopus reared in the laboratory or in boxes suspended in the sea fed on live kelp crabs *Pugettia producta* and fillets of dead hake, *Merluccias productus*, in addition to the organisms listed in the previous paragraph (see also Hartwick, in press).

Hochberg and Fields (1980) stated that this species feeds 'on crustaceans (shrimps and crabs), molluscs (scallops, clams, abalones, moon snails, and small octopuses), and fishes (rockfishes, flatfishes, and sculpins).'

Octopus macropus

Taki (1941) reported that *O. variabilis typicus*, which 'is quite allied to *O. macropus*' (and probably falls under synonymy of this species) 'does not feed on living shrimp, stomatopods and crabs, but the bivalve flesh is occasionally eaten', but he noted that fragments of prawn or fish (Gobiidae) were often found in the crop of this species, while pieces of polychaetes were more rarely found.

Voss and Phillips (1957) reported a female *O. macropus* that lived for nearly five months in an aquarium. Feeding was not observed directly, but apparently the animal fed at night on shrimp (*Penaeus* sp.) and small crabs (*Callinectes* sp.) that were regularly supplied.

Hochberg an Couch (1971) noted that this species feeds predominantly on hermit crabs near reefs, and Hanlon *et al.* (1980) noted this species feeding on crabs in a coral rubble area near St. Croix, U.S. Virgin Islands.

Octopus ocellatus

Taki (1941) kept adults in closed seawater systems and fed them the isopod *Lygia exotica* or the bivalve *Venerupis philippinarum*. Yamauchi and Takeda (1964) reared the hatchlings up to 160 g in 229 days. The large, nektonic young (10 mm ML) fed on larval shrimp as well as small (0.2-0.3 g) pieces of dead shrimp meat or *Taper* sp. clam meat until settling on day 10. Until day 70 they were fed minced *Taper* sp. meat. Thereafter (greater than 30 g wet body weight) they ate live *Taper* sp. clams at a feeding rate of about 20 to 30% body weight per day.

Octopus rubescens

Warren *et al.* (1974) used the crab *Hemigrapsus oregonensis* as prey for *Octopus rubescens* in a behavioural study. These authors stated that 'the small animals can be maintained with ease in the laboratory for at least six months, on a diet of 15 to 20 medium-sized rock crabs (shell width 10 to 12 mm; weight 0.2 to 0.5g) per week'.

Hochberg and Fields (1980) report that the adults feed mainly on crustaceans, molluscs and fishes. In the field, small crabs and hermit crabs seem to be preferred. In the laboratory they have been known to drill and eat a variety of gastropods.

Octopus salutii

The hatchlings of this species are much larger (5.2 mm) than those of *O. vulgaris* (2.2 mm), but they have similar body proportions and they are nektonic (Mangold *et al.*, 1976). They feed not only in midwater on small pieces of crab muscle and hepatic gland (as do the hatchlings of *O. vulgaris*), but also on pieces of crab placed on the bottom of the tank (Boletzky, unpubl. obser.). But, these hatchlings have not been reared beyond the first week from hatching. Benthic young and adult animals have been maintained in the laboratory for several months with living *Carcinus maenas* as food (Mangold *et al.*, 1976).

Octopus tetricus

Joll (1976, in press) fed the small nektonic hatchlings of this species on a mixed diet of live *Artemia* nauplii and commercial rice powder preparation ('Farex'); the longest survival was 21 days. Juvenile and adult animals captured from the sea were fed on live crabs (*Portunus pelagicus*), rock lobsters (*Panulirus cygnus*), and mussels (*Mytilus edulis*). In a growth study (Joll, 1977), the octopuses were fed live crabs of *Portunus pelagicus*, *Nectocarcinus integrifrons*, *Leptograpsus variegatus*, and *Plagusia chabrus*.

Octopus vulgaris

Itami *et al.* (1963) reared the nektonic hatchlings of this species to settling and beyond. The newly hatched octopuses, which had a dorsal mantle length of about 2.2 mm, were fed zoea larvae of *Palaemon serrifer* (2-4 mm long), which had been cultured in the laboratory on a diet of *Artemia* nauplii, also added to the octopus tank. In an earlier experiment, the same authors used larvae of *Upogebia maior*

(5-6 mm long) as food for octopus hatchlings, and they reared these to a total length of 6 to 7 mm ML.

When the young octopuses grew to a total length of 6 to 7 mm ML, the early larvae of *Palaemon serrifer* were found to be too small to be caught by the octopuses. At this stage, larger larvae of *Palaemon serrifer* were fed (within 20 days these were reared, using *Artemia* nauplii, to the post-larval stage which has a length of 7 mm ML). When the octopuses approached the 'settling stage', they would sometimes sit on the bottom or the wall of the tank, attaching themselves to the substrate with their suckers, and occasionally they attacked dead food on the bottom. These periods of occasional settling became longer, but the animals still fed primarily in midwater. Definitive settling (which of course does not exclude occasional swimming) occurred between days 33 and 40 of rearing (at temperatures between 22 and nearly 27°C) when the octopuses had attained a dorsal mantle length of about 5 to 6 mm (total length 10 to 13 mm). They were then fed on small pieces (3-4 mm) of ovaries, testes and hepatic glands of the crab *Charybdis japonica.* Three or four days after settling, they were fed on small shrimps and young crabs (*Gaetice depressus*) that had a carapace width of 5 to 7 mm. A young octopus with a total length of 30 mm ML would eat four or five young crabs per day. These octopuses were reared to the age of 90 days.

High mortalities occurred when food was lacking for a few days. Such periods may be bridged with an 'emergency' supply of half-grown and adult *Artemia* that can easily be cultured (cf. Mangold & Boletzky, 1973; Boletzky, 1974a). Young octopuses only a few days after hatching already 'attack' and eat small pieces of crab muscle and gonad that sink from the water surface. Using this feeding method alone, hatchlings have been raised over two weeks, during which time the animals increased considerably in size. In a comparative experiment this food was found to be more readily attacked in midwater than living shrimp larvae of suitable size. Comparatively large pieces of crab muscle (white) or gonad (yellow) sinking from the surface often were attacked by several young octopuses, which generally continued to ingest parts of this food after it had touched the bottom. Octopuses were rarely seen to feed on partly stripped crab legs suspended in midwater. Dark pieces (e.g. of crab gill) never were attacked (Boletzky, unpublished observations).

A large number of different food animals have been successfully used in laboratory work with juvenile and adult *O. vulgaris*. However, if shore crabs such as *Carcinus maenas*, probably the most widely used food for octopus, are available in sufficient numbers and suitable sizes (i.e. carapace width generally not larger than one half of the octopus' mantle length), there is no need for other food items (cf. Nixon, 1969). In the study of the behaviour of *O. vulgaris* in its natural habitat, *Altman* (1967) found 'a wide range of food species, mainly crabs and lamellibranchs', of which she listed four and six species, respectively, together with two gastropod species. The mechanism of hole boring during feeding on molluscan prey has been reviewed by Wodinsky (1969, 1973), with a list of all the mollusc species that have been reported to have holes presumably bored by *Octopus*. The mechanism of hole-boring has been elucidated by Nixon (1979, 1980). Mandibular movements in feeding were analysed by Boyle *et al.* (1979).

Hochberg and Couch (1971) observed *O. vulgaris* on a reef in the U.S. Virgin Islands feeding on the bivalves *Glycymeris decussata*, *G. pectinata*, *Laevicardium laevigatum*, *Arcopagia fausta*, *Artigona rigida* and *Anadara notabilis*, and also on the gastropod *Strombus gigas*, *S. costatus* and *Conus* sp.

Guerra (1978) analyzed the stomach contents of 100 wild-caught *O. vulgaris* (5 to 22 cm ML) in the western Mediterranena Sea. He found that 80% of the diet consisted of crustaceans, 12% of fishes and 8% of cephalopods. In shallow water of 15 to 25 m deep in *Posidonia* sea grass beds, the crustacean diet was 68% shrimps and 32% crabs, while in deeper water of 30 to 80 m the diet was 67% crabs and 33% shrimps. Crustaceans in the diet included: amphipods; the stomatopod *Squilla mantis*; the palaemonid *Palaemon* sp.; the penaeids *Penaeus kerathurus* and *Solenocera membranacea*; the crangonids *Crangon crangon*, *Pontocaris catafracta* and *Philocheras* sp.; and the other shrimps *Pandalina brevirostris*, *Alpheus* sp. and *processa* sp. Brachyuran crab species included *Dromia personata*, *Ethusa mascarone*, *Dorippe lanata*, *Calappa granulata*, *Macropipus* sp., *M. corrugatus*, *M. depurator*, *Carcinus mediterraneus*, *Goneplax rhomoides*, *Pisa nodipes*, *P. armata*, *Inachus* sp. and *Pachygrapsus* sp. Anomuran crab species included *Anapagurus laevis*, *Anapagurus* sp., *Galathea* sp. and *Pisida longicornis*. Cephalopod prey included *Loligo vulgaris*, *Sepia* sp. and *Octopus* sp. Fish remains included *Cepola rubescens*, *Uranoscopus* sp., and unidentified clupeids.

Nigmatullin and Ostapenko (1976) analyzed the diet of 2 025 *O. vulgaris* from the northwestern coast of Africa and found predominantly crustaceans (53.6%), followed by fishes (25.5%), molluscs (9.5%), and other *O. vulgaris* (7.5%).

The preference for a crab diet, already noted by Taki (1941), is again emphasised by Altman and Nixon (1970; see also for reference list on feeding behaviour). These authors also noted that an all fish diet, often used as standard reward in behaviour experiments, causes a colour change of the digestive gland from the normal orange colour to an olive-green colour that is never observed in animals freshly captured from the sea. It may finally be noted that attempts to substitute other food items for the natural prey of *Octopus* have been made long ago. Vlés (1914) found that octopuses readily accepted chicken eggs, fresh ones as well as hard-boiled rotten eggs!

Octopus vulgaris is regularly kept in certain inland aquaria (cf. Vevers, 1962). It is one of the most widely used cephalopods for experimental studies (Wells, 1978). Mangold (in press a) reviewed the life cycle.

Pteroctopus tetracirrhus

Boletzky (1976) maintained subadult and adult animals of this species over periods of four to nearly five months in aquaria. The octopuses were fed mainly *Carcinus maenas* (claws removed), and occasionally *Leander serratus*, *Lysmata seticaudata* and *Nephrops norvegicus* (see also Boletzky, 1981).

Group 2 – Large eggs, benthic hatchlings

In contrast to the preceding species, the hatchlings of the following octopods are fairly large relative to the adult size, and they remain benthic from hatching onwards. The feeding habits of the hatchlings are similar to those of the adults, and it is not surprising that rearing them from hatching is easier than rearing nektonic young to the stage where they change to a benthic mode of life.

Bathypolypus arcticus

Macalaster (1976) maintained two animals in the laboratory over several months. They accepted a wide variety of prey species, the most common of which were polychaete worms, amphipods (*Gammarus* spp.) and other small crustaceans.

The analysis of stomach contents in 450 specimens captured in the Newfoundland area revealed that the following groups were represented in the diet of *Bathypolypus arcticus*: ophiurids, crustaceans, polychaetes, bivalves, gastropods, foraminifers, sipunculids and cumaceans. Macalaster concluded that '*B. arctictus* is probably not selective, but opportunistic in its choice of prey'. O'Dor and Macalaster (in press) reviewed the life cycle.

Eledone moschata

Boletzky (1975b) reared the large benthic hatchlings of this species to the adult stage. During the first two months, the young animals were fed small pieces of shrimp (*Leander* spp.) and crab (*Carcinus maenas*). Later on they regularly fed on small living crabs (generally *Carcinus maenas*). The young animals usually pounce upon living and dead prey, but they also accept food that is touched to them or that is simply placed on the bottom of the tank. More recently, feeding experiments have shown that young *E. moschata* are able to capture the small crangonid *Philocheras* spp., although often many attacks are necessary as this prey may escape by very rapid leaps.

In another rearing experiment (Boletzky, unpublished data), *E. moschata* was reared entirely on pieces of fresh crab. Growth was slower with this diet. In the earlier experiment (Boletzky, 1975b) the males were not sexually mature at the age of one year, whereas the females were spawning at ten months of age. In the later experiment, where growth was slower, the smallest males became sexually mature together with the females, larger males one to two months later. Finally a batch of animals was severely underfed from hatching onward, and under these conditions the females became mature *after* the males (see also Mangold, this volume and Mangold, in press b).

Hapalochlaena maculosa
(=*Octopus maculosus*)

In contrast to the somewhat larger species of blue-ringed octopus, *H. lunulata*, which has small eggs (3.5 mm long) and hatchlings (2.3 mm ML) and first lives in the plankton (Overath & Boletzky, 1974), the eggs (6-7 mm) and hatchlings (3.5-4.0 mm ML) of *H. maculosa* are large relative to the adult and live on the bottom. These large young have been cultured by Tranter and Augustine (1973), who found that the hatchlings 'showed little interest in food until about one week after hatching, by which time the more vigorous ones were beginning to attack and eat the less vigorous ones. They then began to accept pieces of crab meat and soon welcomed such rations daily'. Live crabs (*Chasmognathus laevis*, *Sesarma erythrodactyla*, *Heloecius cardiformis*) were attacked and eaten only by octopuses at least four weeks old: 'At first they would attack only crabs smaller than themselves, but later, particularly when they were hungry, they would kill and devour larger ones'.

Octopus australis

Tait (1980) found that this species readily ate the live grapsid and portunid crabs *Paragrapsus quadridentatus*, *Cyclograpsus audounii*, *C. granulatus* and *Carcinus maenas* in the laboratory. His analyses of stomach contents of wild-caught specimens indicated that crustacea, predominantly isopods, constitute most of the diet. Other crustacean remains represented the Amphipoda, Tanaidaea, Mysidaea and Cumacea. Molluscan remains included bivalves, gastropods and octopods. A few stomachs had polychaete worm remains.

Octopus bimaculoides

Hochberg and Fields (1980) reviewed the existing literature on this species and they stated that the adults feed on molluscs, crustaceans and occasionally fishes. In the rocky intertidal zone it feeds on various limpets (*Collisella* sp. and *Notoacmea* spp.), the black abalone *Haliotis crachecrodii*, the snails *Olivella biplicata*, *Tegula funebralis* and *T. gallina*, the clam *Protothaca staminea* and several hermit crabs of the genus *Pagurus*. In mud flat regions it feeds on the bivalves *Chione undatella*, *Mytilus edulis*, *Leptopecten monotimerus*, and *Argopecten aequisulcatus* and it sometimes captures the small blennies *Hypsoblennius gilberti* and *H. gentilis*. In subtidal waters it feeds on the abalones *Haliotis rufescens*, *H. fulgens* and *H. corrugata*, the snails *Kelletia kelletii*, *Astraea undosa* and *Norrisia norrisi*, and the hermit crab *Paguristes ulreyi*. They state that under laboratory conditions this octopus will eat almost any shelled mollusc.

Borer (1970) analysed food intake in *O. bimaculoides* using shore crabs, *Pachygrapsus crassipes*, as food.

Octopus briareus

Messenger (1963) fed the comparatively large hatchlings of *O. briareus* on pieces of freshly killed shrimp touched to them and on live crustaceans of small size (less than 10 mm in length), namely *Latreutes fucorum*, *Leander* sp., *Hippolyte* sp. and some unidentified amphipods, and on young and adult *Artemia*. Messenger observed that 'the animals always seized the prey with a few arms and anchored themselves with the remainder. They never swept down on the prey like adult octopuses and indeed many feedings were the result not of an attack by the octopus, but of the prey accidentally entangling itself with some of the arms'.

Wolterding (1971) fed the hatchlings of *O. briareus* on disarticulated legs of adult fiddler crabs (*Uca pugilator*). These legs were placed at the end of a long glass needle 'and lowered toward the octopus, which grabbed the food and drew it off the needle'. Wolterding noted that 'after two weeks, young *O. briareus* begin to feed on very small *Uca pugilator*, amphipods and majids'. Leg segments of adult *U. pugilator* were given along with the live food for two more weeks. Larger animals were presented with about 65 species of polychaetes, echinoderms, crustaceans and fish. Some were actively attacked but not eaten, while others were not attacked but were eaten when coming into contact with the octopus. Cannibalism occurred on other *O. briareus* as well as on *O. joubini*.

The following species were found to be eaten (being or not being actively attacked): polychaetes: *Hermodice carunculata*, *Onuphia magna* (without tube), *Chaetopterus variopedatus* (with tube); crustaceans: *Leander tenuicornis*, *Tozeuma carolinense*, *Hippolyte* sp., *Penaeus duorarum*, *Synalpheus brevicarpus*, *Alpheus formosus*, *Panulirus argus*, *Gonodactylus* sp., *Portunus* spp., *Callinectes sapidus*, *C. ornatus*, *Aratus pisonii*, *Grapsus grapsus*, *Pachygrapsus transversus*, *Cardisoma guanhumi*, *Gecarcinus lateralis*, *Calappa flammea*, *Mennippe mercenaria*, *Panopeus herbstii*, *Sesarma cinereum*, *Ocypode albicans*, *Libinia erinacea*, *Mithrax hispidus*, *Stenorhynchus seticornis*, *Macrocoeloma*, sp., *Emerita talpoida*, *Coenobita clypeatus*, *Clibinarius tricolor*, *C. vittatus*, *Dardanaus venosus*, *Petrochirus digenes*; fishes: *Scorpaena brasiliensis*, *Opsanus beta*, *Acanthostracion quadricornis*, *Hippocampus erectus*, *Trachinotus carolinus*.

Wolterding noted that 'all crabs up to a size equal to that of the octopus were actively attacked'. Echinoderms were not eaten by *O. briareus*. The only molluscs eaten were other octopuses, as mentioned above; neither gastropods nor bivalves were eaten.

Borer (1971) used the fiddler crab, *Uca pugilator*, as food in all experiments except one on the control of food intake in *Octopus briareus*. In one experiment, stone and mud crabs (*Panopeus herbstii*, *Eriphia gonagra*, and *Micropanope nuttingi*) were used in addition to fiddler crabs.

In a study of growth in *O. briareus*, Hanlon (1975) fed some hatchlings on very small live *Uca pugilator* (3-8 mm carapace width) and others on crab legs and pieces of shrimp that were placed with fine forceps into the arms of the octopus hatchlings. Hanlon found that 'one small shrimp *Penaeus duorarum* (60 mm long) is adequate for feeding 150 hatchlings'. *Artemia* was used only as a supplementary food source. Larger octopuses were also fed on blue crabs (*Callinectes*) and on shrimp (*Penaeus duorarum*, *P. aztecus*, *P. brasiliensis*) (see also Hanlon, 1977).

In recent experiments Forsythe and Hanlon (unpublished data) reared this species primarily on live shrimps but also on crabs and fishes *Fundulus similis*, *Mugil cephalus* and *Menidia berylline*. The methods and prey organisms were identical to those used earlier (Forsythe & Hanlon, 1981) and the growth rates on a shrimp diet were comparable to those obtained on a crab diet. At the Dallas Aquarium, *O. briareus* has been fed live freshwater crayfish (*Cambarus* sp.). Hanlon (in press, b) reviewed the life cycle.

Octopus joubini

This species, like the preceding one, has eggs very large (8 mm long) in relation to the adult, and the hatchlings are benthic and can be reared rather easily. Most workers fed them a diet of crab legs and/or small crabs of the genus *Uca* (Boletzky & Boletzky, 1969; Thomas & Opresko, 1973; Opresko & Thomas, 1975; Forsythe & Hanlon, 1980, 1981; Forsythe, 1981).

Several other prey organisms have been used. Bradley (1974) used crab meat and small living shore crabs of *Carcinus maenas*. Mather (1972, 1980) investigated the predatory behaviour and feeding of *O. joubini* using *Uca pugilator*, the hermit crab *Pagurus pollicaris* and the gastropod *Nassarius vibex* as prey. She found that the shells of the snails that had been eaten showed no sign of drilling (cf. Wodinsky, 1969, 1973). Thomas and Opresko (1973) noted that gammarids, caprellids and various other amphipods as well as isopods were rejected by the young octopuses, as generally were *Artemia*. Forsythe and Hanlon (1980) reared *O. joubini* primarily on *Uca* spp. and xanthid mud crabs, but found that small penaeid shrimp *Penaeus* spp., palaemonid shrimp *Palaemonetes pugio* and mysid shrimp *Mysidopsis almyra* were accepted though less preferred by the octopuses. They also found that the small marine amphipod *Orchestia grillis* was accepted readily by octopus hatchlings and 'seems to be as acceptable a live food as small crabs'. They found that dead food such as crab, fish or shrimp meat was accepted only reluctantly, but could be used to maintain adult octopuses temporarily if no live food were available.

In the most recent experiments (Forsythe & Hanlon, 1981) *O. joubini* was reared to sexual maturity on a diet composed exclusively of live mysidacean and caridean shrimps (*Mysidopsis almyra* and *Palaemonetes pugio*). Survival and growth rates were comparable to previous rearing studies that used live decapod crabs (Forsythe, 1981) and showed that the more easily collected and available shrimps were reliable food alternatives for rearing *O. joubini.*

This species has been reared several times in inland aquaria (Bradley, 1974; Overath, pers. comm., 1975; Forsythe & Hanlon, 1980). The life cycle is reviewed by Hanlon (in press a).

Octopus maya

Solis (1967) reared the large benthic hatchlings of this species to the age of 76 days, using mainly small crustaceans as food.

Van Heukelem (1976, 1977) fed the hatchlings of *Octopus maya* bits of frozen crab meat and viscera, frozen shrimp (*Heterocarpus ensifer*), frozen *Artemia*, live *Artemia* nauplii, juvenile and adult *Artemia* reared on yeast and phytoplankton, live gammarid and caprellid amphipods, isopods, and a variety of zooplankton. Feeding on frozen food resulted in slower growth and higher cannibalism than feeding on living prey. Larger animals, weighing more than 10 g, were fed xanthid crabs. Octopuses weighing more than 500 g were fed primarily on the crab *Podothalmus vigil* but were given *Portunus sanguinolentus* or *Thalamita cranata* when supplies of *P. vigil* were insufficient. Two to four month old octopuses accepted gastropods (*Littorina* sp. and *Cypraea caputserpentis*) and clams (*Tapes* sp.), but they would not eat these molluscs if living crustaceans were present. This octopus species was cultured through four generations. Van Heukelem (in press) reviewed the life cycle of *O. maya*.

C. ARTIFICIAL DIETS AND CEPHALOPOD MASS CULTURE

The earliest successful attempts to rear cephalopods opened a new line of aquacultural prospects. In the summary of his report 'On the Growth, Feeding Rates and the Efficiency of Food Conversion for Cuttlefishes and Squids', Choe (1966b) concluded that 'four to five months are thought to be enough for their growing into a fair commercial size'.

However, fifteen years later, neither cuttlefishes nor squids have made their breakthrough in aquaculture. In 1977, Egusa (pers. comm.) described the situation in Japan as follows: '*Octopus vulgaris* is the only cephalopod commercially reared in Japan. Its annual production of reared animals has been about 50 tons in recent years (about 100 tons 1967-1971). The main foods are horse mackerel, saury, and other trash fish, whose food conversion factors are said to be 2.5 to 5.0. No work has been done on artificial foods for this octopod. There are only two reports on the experimental culture of *O. vulgaris* hatchlings (Itami *et al.*, 1963) and of *O. ocellatus* (Yamauchi & Takeda, 1964). In these experiments live crustaceans, molluscs, and fishes were used as foods, no attempt being done on artificial diets. Ever since no scientific report has been published on the culture of octopods'. He concludes: 'Cephalopod young are very selective feeders, requiring live animals of suitable size, and a great difficulty lies inevitably in obtaining food animals in large quantities needed for the mass culture of cephalopod larvae. The success of the mass culture seems to depend entirely on the development of synthetic food'.

Van Heukelem (1976) suggested that 'of all cephalopods raised in captivity to date, *O. maya* appears to be the best candidate for mariculture', and he emphasised that 'difficulties to be overcome before large scale, economical production could be achieved include development of a cheap, easily storable food. I have no doubt that this could be achieved in a short time by an experienced fish culturist with a good background in nutrition and a fair amount of insight'. Indeed the essential dietary constituents will have to be determined and made available in an acceptable form, e.g., enough copper must be included because cephalopods depend on it for their haemocyanin synthesis (cf. Ghiretti & Violante, 1964).

In view of the increasing demand for cephalopods on the markets of Oriental and Latin countries (Voss, 1973, 1974), the development of a standard 'pellet food' for octopods, with the corresponding method of presentation, would seem to be an urgent goal. But although the raw material for such food would be available, in large quantities from fish and shrimp processing plants and canneries, transformation of this raw material into cheap storable food for octopods still awaits realization.

Discussion

A tabular presentation of culture data clearly shows that many more cephalopod species have been maintained or reared in captivity (20 genera, 52 species; Tables 1 and 2) than have actually been cultured through whole generations (7 genera, 11 species; Table 3). The large majority of those species that have been cultured in the laboratory are benthic, only one is nektonic (*Loligo opalescens*). Culture of cephalopods through the life cycle must therefore be regarded as being in the early stages of development, particularly as compared to the advanced culture development of finfishes, shelled molluscs or penaeid and palaemonid shrimps. The review of diets indicates that cephalopods are carnivores that feed on a wide size range and variety of life food organisms, primarily crustaceans, shelled molluscs, fishes and other cephalopods.

Clearly many cephalopods are adaptable, to some degree at least, to maintenance and rearing work. The relatively small proportion of cephalopods that has been kept in the laboratory (i.e. approximately 52 species of more than 700 in the Class Cephalopoda) is mostly a reflection of the lack of work on cephalopods. Certainly many more are amenable to maintenance or rearing, especially the benthic sepioids and octopuses. Several active pelagic squids of commercial importance have been maintained or reared for months, as shown by the recent works on *Todarodes* (Flores *et al.*, 1976, 1977), *Illex* (O'Dor *et al.*, 1980) and *Loligo* (Hanlon *et al.*, 1980 and in prep.; Hixon, 1980). It is encouraging that even delicate midwater squids such as *Abraliopsis* sp., *Pyroteuthis addolux*, *Heteroteuthis hawaiiensis*, and very strong pelagic swimmers such as *Symplectoteuthis oualaniensis* can be captured and maintained in captivity at least for hours or days (Young and Roper, 1977; Young *et al.*, 1979a,b). These achievements set the stage for improvement of techniques that satisfy the four basic requirements of successful maintenance, rearing or culture work:

(1) atraumatic collection and transport of live embryos, juveniles, or adults at the outset of culture
(2) high quality sea water
(3) sufficient tank space to accommodate the benthic or nektonic mode of life as well as distinctive behavioural traits
(4) appropriate type and quantity of live food

Future prospects for culture (*sensu stricto*) are more limited than those of maintenance and rearing, but recent substantial advances indicate good future potential. Culture of species with large, benthic young (e.g. *Sepia officinalis*, *Octopus maya*) is an established, straightforward enterprise (cf. Table 3), and those basic techniques are surely applicable to other species. Studies on *Octopus vulgaris* by Itami *et al.* (1963) and on *Loligo opalescens* by Yang *et al.* (1980b, in press) provide the essential techniques for species that have nektonic young, but they also highlight the fact that such studies are labor intensive, expensive and time consuming. Food is by far the problem of overwhelming importance, and this aspect of culture must be addressed vigorously in order to refine and simplify techniques.

The following sections briefly sum up the data in this review and our suggestions for future investigation. We begin by stating the most obvious gaps in our knowledge, then continue with the desirable attributes of candidate species and the theoretical and practical limitations of studying them, and we conclude by stressing the importance of rapid exchange of information among cephalopod biologists.

A. GAPS IN OUR KNOWLEDGE

Clearly one of the most crucial conditions for successful culture work is the healthy state of the animals at the outset of an experiment. If the experiment is begun by collecting juvenile or adult cephalopods in the sea, atraumatic

TABLE 3

Cephalopod species that have been cultured at least to the first filial generation in the laboratory.

Order	Family	Species	Mode of life of young animals	Mean mantle length at hatching (mm)	Approximate adult size at reproduction (mm ML)	Maximum time in culture (days)	Number of generations	Type of seawater system	Reference
Sepioidea	Sepiidae	Sepia officinalis	benthic	8.0	70 - 250	420	2	closed	Schröder, 1966
		" "	"	"	"	500	"several"	open	Richard, 1966, 1971, 1975
		" "	"	"	"	730	1	open	Boletzky, 1979b
		" "	"	"	"	609	3	open	Pascual, 1978
		" "	"	"	"	1,800	5	open	Zahn, 1979; pers. comm. 1981
	Sepiolidae	Sepiola affinis	benthic	3.2	20	250	1	open	Boletzky, et al., 1971; Boletzky, 1975c
		Sepiola robusta	"	2.2	20	220	1	open	
		Sepiola rondeleti	"	3.7	20	150	1	open	
		Sepietta oweniana	"	~ 5.0	30 - 40	~ 300	1	open	Summers & Bergstrom, 1981
Teuthoidea	Loliginidae	Loligo opalescens	nektonic	2.7	85	233	1	closed	Yang et al., 1980, 1982; Hixon et al. (in prep)
Octopoda	Octopodidae	Octopus briareus	benthic	7.0	90	500	1	open	Wolterding, 1971, 1981
		Octopus joubini	benthic	3.3	25	510	4	open	Thomas & Opresko, 1973; Opresko & Thomas, 1975
		Octopus joubini	benthic	5.0	30	240	2	closed	Forsythe & Hanlon, 1980, 1981; Forsythe, 1981
		Octopus maya	benthic	7.0	100	1,100	4	open	Van Heukelem, 1976, 1977
		Eledone moschata	benthic	10.0	100	380	1	open	Boletzky, 1975b
		Hapalochlaena maculosa	benthic	4.0	35	360	2	open	Tranter & Augustine, 1973

procedures of capture and transport are particularly important. Although certain generalizations may be possible for some cephalopods, species-specific characteristics of behaviour must be taken into account for the choice of collection methods. For example, not all squid species react similarly to specific capture methods (seine, night light, dipnet, jig), and the method of greatest consistency and effectiveness will have to be determined. Transport requirements also must be defined precisely for each species. The advantages and drawbacks of anaesthesia during transport are largely unexplored.

One of the greatest gaps in our knowledge of cephalopod life history concerns the early juvenile phase of nektonic species. What are the optimum conditions for survival and growth of hatchlings and juveniles in captivity, especially as related to water movement, light conditions, food types and food densities? The types of food attractive to young nektonic cephalopods are live copepods, larval crustaceans and larval fishes that have an erratic swimming motion. The sizes of food that hatchlings and juveniles attack range widely from less than ⅓ to more than double the mantle length of the cephalopod, but it remains to be determined which types and sizes of food organisms meet the behavioural and nutritional requirements of different cephalopods. Probably the optimum density of food organisms is a function of the type of food offered; indeed finding the density that promotes optimal feeding with a given prey type is of particular importance. Certain types of live prey may not be favorable to cephalopod growth at all. Unfortunately this is true with the most easily cultured food organism, the brine shrimp *Artemia* spp. A possible alternative to be investigated is the palaemonid shrimps that can be cultured through their life cycle, so that larvae, juveniles and adults can be used as prey suitable for all growth stages of cephalopod predators (cf. Itami *et al.*, 1963).

For larger juveniles and adults, substitution of natural prey by an artificial food ration is conceivable, but the entire complex of features required to make such food acceptable to a cephalopod predator remains to be studied (e.g. size, texture, taste, visual stimuli, including outline and movement of the 'prey'). On the positive side there exists the possibility of behaviourally conditioning the cephalopod predators to feed on artificial foods (cf. Boletzky, 1972).

Sensory and reproductive physiology must be studied from the viewpoint of maintaining, rearing or culturing cephalopods in an artificial, confined environment. Aspects of social behaviour, particularly territoriality, intraspecific aggression and cannibalism, are serious restraints in keeping some species in captivity. Aspects of sexual maturation can be important limitations in the culture of many species, especially regulating factors and behavioural and physiological changes that accompany them. Since laboratory conditions are poor representations of the natural environment, study should be directed at determining the appropriate 'sensory input' (cf. Blaxter 1970) necessary for normal behavioural and physiological development.

The problems of parasites and diseases in cephalopod culture are only beginning to be recognized. They may become of major importance when large-scale or intensive culture is undertaken, and methods of prophylaxis must be developed.

Finally, there is a significant dearth of information on the habits and the commercial and scientific value of most of the 700 or more species of cephalopods that are known to exist. Many of them undoubtedly hold future promise as being useful and important to man, and no one should ever be discouraged from making preliminary observations of these species under laboratory conditions.

B. CANDIDATE SPECIES AND LIMITATIONS

The choice of species depends largely upon the purpose of the investigation. Commercially important species will be studied in the context of fisheries biology, or the species will be chosen to provide experimental material such as squid giant axons. If possible, initial work should be set up with species that are easily available from local stocks.

Each of the following attributes of a candidate species should be carefully reviewed: (1) egg size and resulting size of hatchlings, (2) mode of life of hatchling, especially of octopuses (does it correspond to the adult mode?), (3) numbers of offspring per female, (4) food requirements, (5) growth rates, (6) time to sexual maturation, (7) activity and behaviour, and possibly (8) tolerance to operative techniques. Whenever such information is not available from the literature, personal consultation with those who have observed or studied the species is advisable. Fishermen often are a particularly good source of information on general aspects of occurrence and life history.

In addition to the aforementioned theoretical limitations of choosing a species, there are practical limitations to consider. In most cases, very large facilities are too expensive, so that maintenance or culture of very large species become prohibitive. For many purposes in basic and applied research, small species are useful models, but they cannot always answer the questions relating specifically to larger species.

For a given animal size, difficulties are always greater with actively swimming animals than with the bottom-living species. This applies in particular to density limitations. Bottom-living cephalopods need minimum horizontal areas that have been estimated at ten times the body surface area in cuttlefishes (Richard, 1975) or more generally as $(5 \times \mathrm{ML})^2$ for most benthic cephalopods that are not territorial (Boletzky, 1974a). Water depth is less important for benthic animals, whereas actively swimming cephalopods generally need greater water depths in addition to horizontally wider space.

Apart from space requirements, adult size of animals has its implications in the time scale of rearing and culture work. Small species like *Octopus joubini* and *Sepiola* spp. are sexually mature four to five months after hatching. According to the length of embryonic development, which varies with temperature, the entire reproductive cycle of these species covers only six to eight months. With very large species, the minimum duration of one reproductive cycle is always more than one year, sometimes two years or more. Even medium-sized cephalopods like *Eledone moschata* have a reproductive cycle covering more than one year, especially when they have very large eggs that need several months for embryonic development. For a review of cephalopod life cycles consult Boyle (in press).

These aspects have to be taken into account when a rearing or culture program is planned, because for a given volume of culture space, the 'output' per unit time decreases drastically with increasing adult size of the animals. Adult size as such can be kept in limits to a certain extent. Indeed food intake often decreases under culture conditions, either for lack of an optimal choice of food organisms or for other reasons like disturbance of normal activity cycles or general sensory deprivation. Experiments with *Eledone moschata*, reported in this article, and with *Sepia officinalis* (Boletzky, 1979b) show that 'dwarfed' individuals can live and behave normally, reach sexual maturity and reproduce. These results have important practical and theoretical consequences. On the practical side, they show that rather large species like *Sepia officinalis* need not attain the normal adult size to be useful as experimental animals, for example in physiological or behavioural long-term experimentation. On the theoretical side, they draw attention to the considerable physiological flexibility of many cephalopods that are able to adapt to highly artificial conditions. We do not know if cultivation increases behavioral or morphological variation, which in turn may dramatically affect their suitability as experimental animals.

C. INFORMATION FLOW

In spite of modern communication systems, exchange of information often is slow. Considerable time can be lost in 'trial and error' approaches to culture, when in some instances the technology already exists and need only be communicated to the experimentor. The present review attempts to present the state of the art as it appears to us in 1981/82. More recent information in culture, especially unpublished data and suggestions, would have been helpful in updating this review, and we solicit such information for the future. Written information should periodically be complemented by personal contacts between the people actually involved in one or several of the very many aspects related to cephalopod culture. The first

International Workshop on the Biology and Resource Potential of Cephalopods held in Melbourne and Queenscliff in March 1981 provided an excellent example of using personal contact to provide interdisciplinary coverage of the particular problems of Australian squid fisheries.

To learn the complex interrelationships of cephalopods in their natural environment it is necessary to maintain information feedback between the fisheries biologist (with his broad approach) and the culturist (with his reductionist approach). For example, age determination, which can be provided by laboratory culture, is one of the key problems in all attempts to describe the dynamics of a natural population. The possible use of periodic structures such as 'growth rings' of statoliths was discussed at this workshop first from the practical viewpoint of routine aging of specimens sampled in fishery biology, and second under the more fundamental aspect of cyclic processes in growth. Culture work is necessary to provide detailed insight into cephalopod life cycles; conversely, fisheries investigation provides stimulating insights into spatial and numerical dimensions of population dynamics that cannot be reconstructed under culture conditions.

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