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Types of Development and Sexual System Functioning of Cephalopods -

Approach to Creation of General Scale for Maturity Stages

by

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ABSTRACT

Principal types of sexual system structure and functioning
have been defined in cephalopods based on our own and leterary data -
one type in males and three types in females. Types are an order
specific character in females. Peculiarities of reproductive system
and possible ways of sexual system evolution within the cephalopod
orders were considered. It has been found that different living
forms of one and same order solve the problem of reproduction on
the same morphofunctional basis, this evidently attributed to rela-
tive youth of principal recent groups. General scale of seven maturi-
ty stages for cephalopod males and females has been developed by
major types of sexual systems, each stage having visually distinct
characters and being supplemented with histological picture of the
gonad state. Main advantages of this scale for maturity stages
are in that both ecological and evolutionary analysis of different
types of reproductive strategies within the cephalopod class is
enabled by the use of this scale.

INTRODUCTION

Periodization of sexual system development is the most impor-
tant tool for investigation of animal reproductive biology at
individual, intrapopulational, interpopulational and interspecific
level. Information on sexual system anatomy of females and males
of cephalopods many species has generally been done when being
described for the first time (review: Nesis, 1982 and others).
Sexual system development and functioning have been studied in

considerably poorer way, existing a detailed description only for
a dozen of the most numerous commercial species, such as Illex
illecebrosus (Ommastrephidae) (Durward et al., 1979; Burukovsky
et al., 1984 and others), Loligo opalescens (Loliginidae) (Fields,
1965; Grieb, Beeman, 1978 and others) and some other species.

There have been created a lot of various scales for cephalapods
maturity stages by present time (review: Juanico, 1983). As main
criteria for a division into stages it has been selected as a rule
some kind of characters' combination, for instance, the most deve-
loped oocytes in females' ovaries (Mangold, 1963), or visual
characters of gonads and accessory glands (Lipinsky, 1979). The fol-
lowing terminology is used to characterize cephalopods maturity rate:
juvenile, immature, maturing, mature and spent, different authors
implying different meaning (Juanico, 1983). It is a matter of diffi-
culty to take one's bearings in such papers. There are few complex
scales for maturity stages including visual, meristic and weight
characters. They are created for Illex illecebrosus (Burukovsky
et al., 1984; Nigmatullin et al., 1984) and Sthenoteuthis pteropus
(burukovsky et al., 1977; Zuev et al., 1985). The authors point
out that processes of development of gonads and accessory glands
are specified for each species, and it is necessary, thefore, to
develop a proper maturity stage scale for each species. It is natu-
rally that with this approach a comparison of sexual system develop-
ment in different species is rather complicated. This implies a
problem of complex universal scale creating for cephalopods stages
of maturity which could describe and make a diagnosis for all
the stages of sexual system development both in females, and males.
Each stage of a general scale must possess clear, visually distin -
guishable characters, and be supplemented with a histological
picture of gonad state. I don't agree with Juanico (Juanico, 1983)
in that maturity scales for the same species can differ depending
on the tasks of investigation. It is required to use a simplified
version of the eleborate scale for field analyses, otherwise the
material continuity is lost.

Besides complexity, the following is agreed in this paper when
developing the scale. Firstly, the scale has to be objective one,
being described by the same maturity stages the similar processes

of sexual system development and functioning of females and males. Secondly, the whole scale must be developed in such a way that it could be possible with this to study and compare the realization of cephalopods reproductive strategy of different types created in the course of evolution.

Actually, there are practically no comprehensive papers describing reproductive strategy (only for octopus- Boletzky, 1981), in spite of great diversity of literature on structure and functioning of cephalopods reproductive system (review: Wells, Wells, 1977; Arnold, Williams-Arnold, 1977 et al.,). The main purpose of this paper is the generalization and typization of structure, development and functioning of reproductive system in ontogenesis, and in the case of such typization possibility, elaboration on its basis of the model maturity stages general scale both for females and males of cephalopods.

MATERIAL AND METHODS

Literature data referred to in corresponding chapters of the paper were in the main used as the material. Besides, many problems related to the development of maturity stages general scale were considered when applying biological analysis to several thousands of nectonic squids from Ommastrephidae family: Illex illecebrosus (juveniles mainly), Dosidicus gigas and Sthenoteuthis pteropus (all the stages). Moreover, there were used the results of investigations by V.V.Laptikhovsky of oocyte state in the ovaries of 47 individuals of cephalopods 14 species: Octopus vulgaris (3 spec.), Argonauta argo (1 spec.), Tremoctopus violaceus (4 spec.), Sepia bertheloti (3 spec.), Sepiella ornata (1 spec.), Abraliopsis atlantica (8 spec.), Pterygioteuthis gemmata (7 spec.), Onychoteuthis banksi (2 spec.), Illex argentinus (13 spec.), Todaropsis eblanae (1 spe.), Ornithoteuthis antillarum (1 spec.), Gonatus fabricii (3 spec.), Octopoteuthis sicula (1 spec.), Histioteuthis reversa (2 spec.). There were determined dimensions, presence or absence of nucleolii in nuclii, and in most cases, degree of follicle formation.

SEXUAL SYSTEM STRUCTURE OF CEPHALOPODS

Cephalopods are short-cyclic and monocyclic (with the excep-

tion of nautilus) animals of sexuality with a sexual system of
complicated structure. In the most general aspect, sexual system
of males and females consists of a gonad (testis and ovary) which
is in the sexual sector of coelome in the posterior body part, two
or one isolated gonoducts and a complex of accessory glands which
participate in different secreta production and enhance mainly
maximum conservation of mature sexual cells.

Brief description of main types of sexual system structure
in cephalopods is given below (scheme of fig. 1).

Females

Octopus. Sexual system is of the most simple type. The gonad
is of the oval shape. Double tubular oviducts, with oviducal glands
set on them as a ring in finger, are appended to sexual coelome
(review: Wells, Wells, 1977).

Cuttlefish. Sexual system is of more complicated type than
in octopus. The gonad is of a semi-spherical shape. Oviducts are
in pairs, non-curved. Accessory glands are of three kinds. Oviducal
glands, in contrast to those of octopus, are displaced into the dis-
tal end of oviduct in such a way that eggs liberated from the ovi-
ducts pass through the cavity of these glands. Apart from the
oviducal glands there are nidamental ones which are usually of
the oval shape. Besides, there exist additional nidamental glands
function of which is mysterious (Nesis, 1982).

Squids. There observe a vast diversity in sexual system struc-
ture. As a rule, the gonad is of conic shape. Either one oviduct
is developed (subfamily Pyroteuthinae: suborder Myopsida), or both
of them are developed (the rest of the representatives of Oegopsida
suborder). Oviducts are strongly curved tubes with small entrance
of funnel shape. Three types of accessory glands are present in
Myopsida suborder (oviducal, nidamental and additional nidamental),
being presented in Oegopsida suborder two types (oviducal and
nidamental). In squids of Enoploteuthinae subfamily with the absence
of nidamental glands oviducal ones are well developed.

Males

Sexual system of cephalopod males is rather uniformly struc-
tured in the representatives of all the principal groups. The testis

is unpaired of rounded (in octopus) or conic (in cuttlefish and squid) shape. Spermaduct is usually unpaired and curved. In its proximal part it is enlarged (ampulla). Spermatoduct turns into spermatophoric gland owing to the activity of which a complex structure is formed, being characteristic of cephalopod males. This is spermatophore. Spermatophoric gland is connected through spermatophoric duct to Needham sac (spermatophore dipository). Distal part of Needham sac is musclized and transformed into a special appendage (penis). In males of certain species sexual system is paired, e.g. in Histioteuthis hoylei, Selenoteuthis scintillans and Oregonioteuthis springeri (Nesis, 1982). In general, sexual system in males is of considerably more complicated structure than that in females, which mainly signifies greater numbers of accessory glands participating in spermatophore formation.

CEPHALOPOD SEXUAL SYSTEM DEVELOPMENT

Cephalopod sexual system development is of a number of successive stages, namely (terminology by Burukovsky et al., 1977; Nigmatullin, Sabirov, 1987):

1. Juvenile. Gonad formation, differentiation of germinative epithelium derivatives inside it, and auxiliary glands formation take place.

2. Physiological maturation. Processes of formation of mature sexual cells take place in the gonad, i.e. oogenesis and spermiogenesis. Auxiliary glands grow and their sectors are formed in this stage.

3. Physiological maturity. Expelling of mature sexual cells out of gonad to sexual coelome.

4. Functional maturation. Preparation of mature sexual products to a form with which it becomes possible their deposition (spawning) into the environment. In females this is a formation of mature eggs additional membranes, i.e. the third and the fourth ones (if they do exist), a process of eggs movement into the organs where the spawning will take place from. In males this is a formation of substances which inactivate the sperm, a formation of spermatophores providing the sperm transport to a female without losses.

5. Functional maturity. Organism is completely ready for spawning, being sexual products apt to be spawned.

In the most simple case, which is spawning of mature sexual cells into the water without preliminary treatment of accessary glands secreta (in Patella primitive mussels), organism is ready for spawning in the third stage, i.e. the stage of physiological maturity is at the same time the stage of functional maturity for their sexual system. In highly organized forms (higher Gastropoda, Cephalopoda) mature sexual cells undergo a number of processes (formation of egg additional membranes in females and that of spermatophores in males) before they are expelled out of organism.

In monocyclic animals what overwhelming majority of actually existing cephalopods, probably with the exception of Nautilus and octopus of Cirrata suborder belong to (Nesis, 1985), sexual system undergo through initial three stages once, through the fourth and the fifth stage either once (momentary spawning), or several times (pulsatory spawning - a term by R.N.Burukovsky).

Let us consider the features of development and functioning of cephalopod sexual system in two initial stages (before mature sexual cells expelling).

Juvenile stage and functional maturing

Embryonal rudiment of gonad in octopus is at first double, then it becomes the only one (Wells, Wells, 1977), being unpaired in cuttlefish and squids from the very beginning (Lemaire, 1972; Floroni, 1978). Differentiation inside the gonad, at any rate in Sepia, begins on the day of hatching (Lemaire, Richard, 1971) under the effect of optical glands secretion (Richard, 1970) when rapid meiosis initiation transforms gonial cells into oocytes and spermatocytes.

Oogenesis in different cephalopod species is rather of the same type (Arnold, Williams-Arnold, 1977). Oocyte in the course of its development undergoes successive stages of initial and simple follicle developed, complex follicle and vitellogenesis which ends in follicle expelling and ovulation. With their similarity apparent, the stages are evidently not identical. Thus, the most important time interval of nucleolii decomposition and R-RNA penetration in oocyte cytoplasm is observed in different species with different follicle condition. In Lolliguncula brevis, Alloteuthis subulata,

Loligo opalescens, Octopus tehuelchus and Dosidicus gigas this
this takes place during the intercalation (Cowden, 1968; Bottke,
1974; Knipe, Beeman, 1978; Pujals, 1986; Michel et al., 1986),
disappearing nucleolii in Illex argentinus still before the formation
of follicular epithelium folds (Shuldt, 1979). Examination of oocy-
tes in different developmental stages by V.V.Laptikhovsky strongly
suggests different time intervals of nucleolii disappearance, i.e.
they cannot be visually distinguishable before the simple follicle
formation in Octopoteuthis sicula and Sepia bertheloti or after-
wards in Abraliopsis atlantica. In Argonauta argo and Pterygioteu-
this gemmata, in the stage of simple developed follicle nucleolii
start decomposing and acquire a characteristic blot shape observed
in I.argentinus (Shuldt, 1979). In Octopus vulgaris nucleolii
keep inalterable to the moment of complex follicle formation and,
probably, disappear just before vitellogenesis initiation. Nucle-
olii are visible in this species during the follicular folds forma-
tion up to the moment when vitelus accumulation start impedes clear
distinguishing of nucleus.

Spermiogenesis takes also place in a various manner in diffe-
rent cephalopods. In Loligo opalescens primery spermatocytes have
not been observed neither in mature individuals, nor in maturing (?)
ones (Grieb, Beeman, 1978). Even in mature squids of I.argentinus
there exist in the gonad not only primary spermatocytes, but, pro-
bably, gonial cells also (Shuldt, 1979). In the same manuer, pre-
meiotic oocytes have been revealed in all the developmental stages
of the gonad in S.pteropus (Burukovsky et al., 1977), and have not
been noted in immature individuals of I.illecebrosus (Burukovsky
et al., 1984).

Mechanisms which regulate gonad and accessery glands develop-
ment have not been fully studied yet. In octopus gonad develops
in the process of protoplasmatic growth of oocytes independently
of optical gland activity in the stage of physiological matura-
tion (Buckley, 1976). At the same time, gonoducts evidently develop
autonomously too: in castrate juvenile octopus oviducts and sperma-
tophoric glands develop normally (Taki, 1945; Wells,Wells, 1977).
Castration of adult octopus males can either cause degeneration
of SOC (Taki, 1945) or not (Callan, 1940). In latter case spermato-

phoric gland was also removed, only Needham sac and penis being intact.

In the stage of physiological maturity functioning of gonad and accessory glands starts being synchronous. Preliminary start of accessory glands takes place shortly before general expelling of mature sexual products, i.e. a formation of preliminary spermatophores takes place in spermatophoric gland (without seminal receptacles) (Laptikhovsky, Nigmatullin, 1987), oviductal glands of cuttefish can produce quite formed egg capsules without eggs (Boletzky, 1975).

Physiological maturity, functional maturation and maturity.

Females

Octopus. The most simple type of sexual system functioning is observed. In the simplest case accumulation of mature eggs is not observed in the coelome, entering the eggs immediately after ovulation one by one the oviducts where they start to be covered with a thick membrane formed by secret of oviductal glands. Such a kind of sexual system functioning is observed in the most primitive octopus of Cirrata suborder (Aldred et al., 1982; Boletzky, 1979). Short-term accumulation of eggs in the coelome and one-momentary spawning take practically place in each octopus of Incirrata suborder, probably with the exception of Octopus zonatus for which the repeated spawning has been observed (Rodaniche, 1984).

Cuttlefish. Accumulation of mature eggs as in octopus takes place in the sexual coelome and partially in the proximal sectors of oviducts which are concave wide funnel.

Squids. Accumalation of mature eggs occurs in the oviducts, where portions of mature eggs are formed for spawning. Spawning is either one-momentary (Todarodes - Hamabe, 1962), or takes place several times due to empting and successive accumulation of a new portion of eggs in oviducts (Thysanoteuthis - Arkhipkin et al., 1983), Berryteuthis magister (Reznik, 1983).

Problem of accessory glands homology in octopus females is to be paid a special attention to.

It is known that in gastropods different by their origin

glands take part in formation of egg laying. Egg laying mucous secret is formed by pallial, pedal and hypobranchial glands in different representatives of this class. Besides, in mollusks laying their eggs in rigid capsules there also exist capsular and proteic glands in a complex of pallial glands. These glands differ in their origin, in the functional and hystological way (Chukhlin, 1984). Oviductal glands by their functions in octopus (secreting adhesive cement) differ from those of cuttlefish and squid (excreting light mucous secret which forms the third membrane of egg). Nidamental glands in squid and cuttlefish also differ in a considerable extent both by their form, and by secret excreted, i.e. in cuttlefish it is a secret of the fourth membrane of egg thick capsules, being mucus of egg laying in squids. Probably, these glands are not homological formations.

Both octopus and cuttlefish lay dawn eggs one by one and if they lay dawn several eggs one after another at the same time, the laying all the same consists of a group of individual eggs, each of them being covered either with the third membrane, or with the third and with the fourth (thick) membranes which are in the shetler under the protection of a female (in octopus) or not (in cuttlefish).

Practically, in all squids (with the exception of evidently smaller Enoploteuthidae - Young, Harman, 1985) egg laying is a "real" one and is of a quite complex structure. When spawning, squid female dips eggs in the third membrane into secret of nidamental glands (Hamabe, 1962 and others). Mucous egg laying is inedible for predators, and under its protection embryos freely develop. Squid egg laying are, as a rule, formed (Hamabe, 1962; Sanzo, 1929; Sabirov et al., 1987), being specific egg size and number in each laying; they evidently vary in an insignificant extent. Thus, it is necessary to synchronize the processes of mature eggs accumulation and accessory glands functioning for these egg laying being formed. Continious asynchronity of gonad development is caracteristic of squid (Burukovsky et al., 1977; Arnold, Williams-Arnold, 1977). This means that being accumulated eggs in the coelome as in octopus and cuttlefish, trere won't exist distinct markers for determination of egg portion size

necessary for one egg laying, or all the egg reserve in gonad had to be layed down at one moment (as it has been observed in most of octopus). Possibly, benthopelagic and nectobenthonic ancestors of squids possessed such spawning type, i.e.. laying down of all the reserve of real absolute egg fecundity existing in the sexual coelome at one moment with a formation of mucous egg laying. However, it is more profitable for monocyclic animals with a short life span which encounter in the environment of unstable conditions that real absolute fecundity be realized by portions for at least some part of posterity may have an opportunity of living under the favourable conditions for their development. Against the background of a continious asynchronity of gonad development accumulation of mature egg portion in oviducts is the most simple resolution of this problem. Secondary accumulation of eggs in oviducts is also confirmed by the fact that the eggs being slipped out of the follicle pass into the oviducts as in case of spawning up to the place of their falling into the oviductul glands, and only then start being accumulated, stretching the oviduct from its distal end towards its proximal end. Having finished egg accumulation in oviducts, oviductal and nidamental glands "swell" and start secreting, taking place spawning of mature eggs and egg laying formation. The main reason for egg accumulation in oviducts of squid females was evidently the necessity of spawning by portions which had to be realized against the background of continious asynchronity of gonad development and existence of nidamental glands excreting mucous secret for egg laying formation. In this connection, spawning by portions with the accumulation of a part of real absolute fecundity in oviducts is evidently of more primitive character than momentary spawning in those squids which accumulate all the reserve of real absolute fecundity in oviducts.

Males

On maturing of sexual cells, i.e. spermatozoons, and their slipping off the testis ampullas, their accumulation in the sexual coelome does not take place, passing those immediately to the spermatuct. There is a whole complex of accessory glands. Secret of some of them at first inactivates sperm, and then under the

effect of others spermial mass which has reached the spermaduct
gets clothed with different secrets, being formed at last a sperma-
tophore the main function of which is passing the sperm inside
it to a female without losses (Drew, 1919). In a superstructural
formation of spermaduct, i.e. in Needham sac, accumulation of
spermatophores usually occurs, each of them being similar to eggs
layed in females. Thus, in cephalopod males accumulation of "sperm
thrown out" takes place in Needham sac, being further transfered
a portion of such sperm thrown out to a female. In most primitive
cephalopods living at present, i.e. octopus of Cirrata suborder,
there are no spermatophores formed, forming in their spermaducts
only spermatic packets which are formations where spermatozoons are
situated with their tails towards the centre and their heads to-
wards the periphery (Aldred et al., 1984). In octopus of Argonau-
toidea superfamily (fig. 1) one spermatophore is formed in sexual
viae. This spermatophore "bursts" in Needham sack and its content
is somehow pumped into spermatic reservoir of specialized arm
(hectocotylus) which comes off when copulating and creeps into
the female mantle cavity (Nesis, 1982).

It is noteworthy to point out that in primitive mollusks
(Monoplacophora and others) sexual system of males is organized
and functions as a type similar to that of octopus females when
sperm accumulation occurs in the sexual coelome and its coming
out into the spermaduct is connected with spawning. In primitive
prozobranchial mollusks (Littorina) sexual system of males functi-
ons in such a way as in squid females, taking place accumulation
of mature sperm in the enlarged part of gonoduct, i.e. spermatic
ampullas. In higher prozobranchial (Ptenoglossa) spermatozoons
are transfered by special formations, i.e. spermatozeugmae which
are able to move actively (Chukhchin, 1984). In cephalopod males,
as well as in some higher gastropods (pulmonary mollusks - Stylom-
matophora), spermatophore formation takes place in sexual viae
what is evedently parallelism in both groups of animals.

In higher gastropods sperm is transfered to the female cloaca
by a special copulative organ, i.e. penis which is either the body
wall protrusion, or the tentacle modified. In cephalopod males

"penis" is the distal part of Needham sac with slightly muscular
walls which does not serve for internal fecundation, but for sper-
matophore transfer. Such a transfer is realized either directly
to a female (in squids with a long penis - Onychoteutis), or in
most cases to hectocotylized sector of ventral arm (in squids
with rather short penis - Ommastrephidae and other). Thus, in strict
terms, distal part of Needham sac in cephalopods not always can be
called as "penis".

TYPES OF REPRODUCTIVE STRATEGY AND EVOLUTION OF SEXUAL
SYSTEM IN CEPHALOPODS

It can be observed by sexual system structure and features
of its functioning (first of all in females) how the formation of
living forms has been occurred during the evolutionary processes
in different cephalopod groups at different morphofunctional complex
of sexual system characters. Living form evolution of cephalopods
has been considered according to Nesis (1985) and characters of
r-and-K strategies have been studied as to cephalopods according
to Boletzky (1981). It has been very interesting to observe how
the representatives of all three orders of cephalopods living at
present were "fitting themselves" into the pelagic layers.

It is known that all the cephalopods living at present appeared
relatively not long ago, i.e. in Early Paleogene, starting the
blossoming of main orders in Neogene (Nesis, 1985). Division of
orders took place much earlier: in Upper Triassic-Early Jurassic
(Nesis, 1985). Evidently, in Mesozoic principal types of sexual
system structure were finally formed for all three orders (fig. 1),
preserving and remaining orderly specific the latter, in spite
of the fact that within orders many species in Neogene had made
different living forms (Nesis, 1985). During a short period
(Neogene-Antropogene) cephalopod mollusks having similar living
forms and belonging to different orders could not create similar
reproductive types, for instance, in pelagic octopus, cuttlefish
and squids different types of sexual system structure and functio-
ning are observed (fig. 2). On the other hand, forms living du-
ring long geological time which differ by their origin, but having
similar living forms, i.e. benthopelagic (nautilus from Devonian,
finned octopus from Jurassic) at different morphofunctional

complex of characters could resolve the same problem, namely: laying of eggs one by one down the bottom with a formation of thick skinny membrane (shell) which protects embryo from unfavorable environmental conditions and predators. Oviductal and nidamental glands take part in shell formation in nautilus, and only distal part of oviductal gland participates in octopus having fins (Aldred et al., 1984).

Octopus. On passing of octopus of Incirrata suborder to the benthonic mode of life their reproductive strategy type has considerably changed (as compared with their ancestors) (fig. 2). In all the species of these animals accumulation of either small quantity (in deep-water forms of Benthoctopus, Bentheledoe, or considerable quantity of eggs in the coelome occurs (some of Octopus, Eledone), then taking place a momentary spawning. Eggs are individually adherent by means of oviductal gland secret in the holes or in female arms (as in case of Hapalochlaena maculosa). Females usually protect eggs layed down (Boletzky, 1981). As a rule, females die after larvae hatching. In forms having small eggs indirect development with a pelagic larva is observed while forms with larger eggs are characterized by direct development with bottom juveniles. Thus, in octopus K-selection dominates, appearing r-selection component only in individuals with small eggs (Boletzky, 1981).

Let us consider in what way pelagic octopus and first of all holopelagic octopus developed from benthonic ones. Main character, i.e. protection of eggs layed down by a female is also observed with coming out into pelagic layers. Alloposidae females, in spite of their planktonic mode of life, evidently lay eggs down the bottom (Nesis, 1982). Females of epipelagic Tremoctopus violaceus, as well as of midwater octopus of Bolitanidae and Amphitretidae families bear eggs similar to H.maculosa in arms, but not over the bottom, as in this bottom octopus, and just in pelagic layers (Nesis, 1977). In Argonauta females to protect eggs born in arms there was developed a shell which is not homologous to that of nautilus, taht is a peculiar "cradle" of eggs (Boletzky, 1981). At last, development of eggs just in oviducts, i.e. oviviparity, is observed in epipelagic Ocythoe and midwater Vitrele-

donella. Thus, in octopus K-selection dominates, protecting females eggs layed down in themselves up to the moment of larvae hatching when coming out into pelagic layers.

Cuttlefish. Other than in octopus reproductive strategy type has been observed (fig. 2). Cuttlefish which are mainly nectobenthonic animals also accumulate eggs in sexual coelome similar to octopus, but their eggs before being layed down start being covered not only with secret of oviductal glands, but with thick secret of capsule nidamental glands too. Eggs are layed down one by one or in clusters like grape bunches to different kinds of shelters or to hard substrate and, as a rule, is not protected (Choe, 1966). Females of some species (Boletzky, 1983) cover eggs with ink or "rolled" them in sand for masking. Thus, eggs of cuttlefish are always heavier than water (owing to their thick shell) and that is why no one species of this order has become up to the moment holopelagic animals. Within the order a transition to benthonic mode of life has been observed (_Rossinae_, _Sepiolinae_, _Sepiadaridae_). Both micronectonic _Heteroteutis_ (Boletzky, 1978) and planctonic _Spirula_ "are forced" to lay down their eggs over the bottom and in any event be related with the shelf while distributing. Within the order there are both large-egged forms with bottom juveniles (_Sepiidae_, _Sepiadaridae_, _Sepiolidae_), and small-egged forms with pelagic larvae (_Idiosepiidae_, _Heteroteuthis_). Thus, in cuttlefish like in octopus K-selection principally dominates, however egg protection differs from that of octopus (being layed eggs mainly down shelters). Component of r-selection appears in small-egged forms.

Squid. The third type of reproductive strategy is cheracteristic of them (fig. 2). As it has been mentioned above, nidamental glands of squid excrete mucous secret which is usually of neutral boyancy and forms egg laying down. This reproductional type allowed for squids to develop practically every living form caracteristic of cephalopods and first of all to habit pelagic waters. In the forms of nectobenthonic organizational type (_Loligo_) females spawn nidamental gland secret into the water, and then driving themselves they thrust in this secret with their anterior part and lay eggs down inside (Hamabe, 1962). Minimum fecundity

has been observed in squids inhabiting the shelf, where there is more or less stable substrate for bottom laying of eggs down. A characteristic representative is Sepioteuthis in the mucous spawn of which only 2 to 6 eggs are contained, hided by female in secluded places (La Roe, 1971).

The fecundity of squids inhabiting the shelves is several hundreds to several thousands of eggs (Loligo). Maximum fecundity has been observed in squids which spawn in pelagic and pre-bottom waters. It is evidently related to the fact that the water column, unlike the ground is a more unstable environment, and far from eggs spawned get in favourable environmental conditions for their development. In this way several kinds of r-strategy (including elements of K-selection) have been realized in squids, i.e. embryonization and egg protection with mucus. The first one which is evidently the most primitive, initial, has been observed in squids with high potential fecundity and pulsatory spawning, that is Thysanoteuthis, Berryteuthis (Arkhipkin et al., 1983; Reznik, 1983). They have prolongated individual maturity period during which a female may spawn several tymes. The second kind of strategy has been noted in squids which are also of high potential fecundity, but of short maturity period and spawning (Todarodes, Illex and others) (Hamabe, 1962; Durward et al., 1980; O'Dor et. al., 1982 and others). In that case prolonged group spawning that is sometimes of all the year round character has been stated.

In squids of Enploteuthinae subfamily (the third species) which are of comparatively low fecundity (several hundreds- several thousand of eggs) an interesting feature have been noted, that is laying down of eggs one by one into water column (Shimamura, Fukatuki, 1957). In this case eggs are only covered with secret of oviductal glands, being absent nidamental glands. The problem of egg protection has been probably resolved in another way in species of this subfamily than in two previous cases: egg dispersion through the water column does not evidently allow for small nectonic and planktonic predators be specialized on their eating (hypothesis by F.E.Alekseev). Such a kind of r-strategy with small sizes of squids and short life span (half a year according to our data) has allowed for them to inhabit the niche of micronectonic and pelagic

predators in full, extent, their high abundance evidencing of this.
Accumulation of eggs in Enoploteuthinae occurs as in all squids,
in oviducts, that is why nidamental glands has been reduced, being
evidently of no need (eggs being layed down one by one).

Thus, their own main types of sexual system structure and
fuctioning (of females) are presently observed in all three orders
of cephalopod mollusks' class. In spite of the fact that different
living forms are characteristic of one order species, the problem
of reproduction is revolved by them on the same morphofunctional
basis. It is evidently related to a relative youth of principal
cephalopod groups which live at present. In ancient, archaic species
of benthopelagic mode of life (nautilus and finned octopus) similar
reproductional type has been developed on different basis. Cephalo-
pods of main orders which are of similar forms have their future.

GENERAL SCALE OF CEPHALOPOD MATURITY STAGES

It is possible to develop a general scale of maturity stages
for female and male sexual system of main cephalopod orders on
the basis of sexual system structure and features of its functio-
ning. Terminology by Burukovsky et al., (1977) is used when descri-
bing gonad development and maturity stages for sexual system.

At the I-II stages of sexual system development in males
and females similar processes take place, that is laying down and
differentiation of gonad and accessory glands, their growth and
final formation. Processes of oogenesis and spermiogenesis which
take place at this time in gonad naturally differ in great extent.
Besides, as it has been mentioned above, gametogenesis differs
insignificantly in different species, that is why it is necessary
to describe histological aspect of gonad development individually
for males and females at each stage of maturity. Therefore, it is
reasonable to differentiate between maturity stages at the stage
of physiological maturation by the degree of development of gonad
and accessory glands with the addition of maximum degree of sexual
cell development.

It is suggested to differentiate between maturity stages at
next stages basing on the fate of mature sexual cells, namely on

their movement and staying in different sections of sexual system
up to the moment of spawning (laying down of sexual products into
the environment).

At the stages of functional maturation and maturity functioning
of sexual system greately differs in males and females (see above),
i.e. sexual products spawned into the environment differ by their
origin (being individual eggs in octopus and sperm "layed down",
spermatophores in cephalopod males). Therefore, it seems to be
inexact when describing stages of functional maturation and maturity
in cephalopod males and females only by stages of maturity and attri-
buting functionally mature individuals to the V stage (as Zuev et
al., 1985 did). These processes are different by their complexity
and significance. Without any doubt, formation of spermatophores
did not take place in males of cephalopod ancestors, accumulating
sperm either directly in coelome, or in the enlarged parts of
spermaduct. The whole process of spermatophore formation followed
the anaboly tipe (aggregation of different glands to the spermaduct).
On the other hand, passing of mature sexual cells to different sec-
tors of sexual system can be divided into stages which are similar
from functional and evolutionary point of view both in males and
females.

Description of a general scale of maturity stages for cephalo-
pods is given below. In table 1 only distinctive features characteris-
tic of each stage which are necessary for its determination are
given   , below being given commentaries.

Five-degree scale of sex maturity stages for squids elaborated
by the AtlanTNIRO laboratory for commercial invertebrates study
(Burukovsky et al., 1977; Nigmatullin, Sabirov, 1987) is taken as
a principle. I believe, as the above-mentioned authors, that sexual
products which are at most advanced stages of their formation or
their moving on through the sexual system play the leading part in
maturity stage determination.

I. Juvenile stage. It corresponds to "0" stage of maturity.

It includes two substages:

Ia. Pre-differential stage. Rudiments of gonad and accessory
glands have already been formed, but their differentiation has not

taken place yet, and it is by no means impossible to determine
the sex. In Sepia this stage covers only a part of embryogenesis,
and in Loligo it is obviously observed its displacement to later
stages of animal development, starting their formation nidamental
glands in myopsids in post-embryonal period. In gonad only gonial
cells of two types are present at this stage, one of them being dis-
appeared before differentiation is possible (Lemaire, Richard, 1971).

Ib. Post-differential stage. It lasts from the moment when it
is possible to make a histological diagnosis of sex up to the moment
when it can be distinguished visually. At this stage either only
gonial cells, or gonial cells and pre-myotic oocytes and oocytes
of I-phase protoplasmatic growth are present in female gonad. It
is obviously necessary to consider as an exception presence of
oocytes at the stage of goblet shaped follicle development (Knipe,
Beeman, 1978) in juvenile Loligo opalescens gonads.

2. Physiological maturity.

I stage. "Differentiation and growth of accessory glands" make
it possible visual distinguishing of sex at this stage. Gonad is
of dull-grey filament shape. The most advanced oocytes are at the
I phase of protoplasmatic growth as in I.illecebrosus (Burukovsky
et al., 1984), Pterygioteuthis gemmata, Tremoctopus violaceus
(data by V.V.Laptikhovsky), or at the II phase of protoplasmatic
growth (primary follicle) as in S.pteropus (Burukovsky et al., 1977),
Gonatus fabricii.

II stage. "Gonad development and accessory gland growth".
Gonad is of semitransparent lamina form, being accessory glands of
dull-white colour; it is possible to distinguish between their
sectors. In I.illecebrosus at this stage active growth of SOC
(Nigmatullin et al., 1984) starts, being this delayed at the period
of sexual maturity. The most advanced oocytes in the gonad are at
primary follicle phase, as for instance, in I.illecebrosus (Buru-
kovsky et al., 1984), and Abraliopsis atlantica (author's data),
and in the beginning of simple follicle (of goblet shaped follicle)
phase, as in S. pteropus (Burukovsky et al., 1977), Octopoteuthis
sicula and Sepiella ornata (V.V.Laptikhovski, pers. com.).

III stage. "Gonad maturation and accessory gland final forma-

tion". Gonad is large and opaque. In females' ovaries granular structures are well visible. Three substages can be distiguished in females:

III-I. The most developed oocytes are at the phase of simple follicle formed.

III-2. The most advanced oocytes are at the phase of complex follicle (intercalary period).

III-3. The most advanced oocytes are at the phases of tropho-
plasmatic growth, but mature eggs have not appeared yet.

Duration of these stages is different in different species. Thus, in S.pteropus the main part of III stage falls into III-1 substage (Burukovsky et al., 1977), and in I.illecebrosus are frequent the individuals the most advanced oocytes of which are in the gonad at the phase of complex follicle of III_2-III_3 stages (Burukovsky et al., 1984). Sexual system in females of all the cephalopods passes through all three stages. Omitting or rare frequency of one or another substage means that it takes place in extremely short terms.

In males the process of formation and accumulation of spermatozoons in testis ampullae of gonad takes place, not being melted edges of gonad when cutting.

Accessory glands are opaque and, as a rule, of white colour, being their sectors completely formed and well developed.

3. Physiological maturity.

IY. stage. "Mature gonad". Mature sexual cells are expelled out of gonad into sexual coelome. In females ovulation and coming out of mature eggs into the coelome take place, being well distinguished the stage by presence of mature eggs on gonad surface and in the coelome. When carrying out histological analysis, empty follicles can be seen in the gonad. Sperm extrusion out of testis ampullae is observed in males, being "melted" edges of testis. At this stage accumulation of mature eggs in the coelome of octopus and cuttlefish females takes place.

4-5. Functional maturation and maturity.

Later on a period of functional maturation and maturity comes.

Expelling of mature sexual cells out of sexual coelome in cephalo-
pod males and females takes place in a different way. Various con-
ventional limits of transition from one sexual system sector to
another can be defined (fig. 1).

The first one is gonoduct origin, the second one is the locati-
on of gonoduct confluence with auxiliary gland ducts, the third
one is at the exit out of the zone of accessory gland activity and
the fourth one is at the exit out of gonoduct.

In octopus and cuttlefish females mature eggs pass through
every existing conventional limit when being spawned. In squid
females eggs pass through the first conventional limit before their
spawning, being observed free passage of mature eggs to the second
conventional limit after which their accumulation in oviducts takes
place. In males of cephalopod ancestors this phenomenon was obvious-
ly observed as well, however at present the second conventional li-
mit in males is also opened for immediate passage of mature sperma-
tozoons.

V stage. "Mature sexual cell passage into gonoducts". In squid
females accumulation of eggs in oviducts occurs at this stage.

VI stage. "Mature sexual cell passage into zone of activity
of accessory glands and sexual cell treatment with secret of these
glands". (In squid females it is observed when spawning). In males
after spermatophore treatment (their formation) accumalation of
them is also observed in an accessory ogran (Needham sac). However,
in Argonautoidea superfamily males sperm passes from the spermato-
phore blown up in Needham sac into hectocotylus cavity, and only
after this spawning "itself" takes place (transfer of heotocotylus
filled in with sperm to a female).

VII stage. "Individuals spent". Degeneration of sexual system
is observed after spawning season. Gonad is greatly reduced (as
compared to IV-VI stages). Traces of degeneration are noted: in fema-
les oocytes at trophoplasmatic growth stages are practically absent;
in males some white "islets" can be present against the dull-grey
background of testis degenerated. Accessory glands are usually
large, being their development as at V-VI stages, however their
consistency is not elastic, being soft and melting. Individuals,

as a rule, die at the end of stage.

Thus, octopus and cuttlefish females are functionally mature at the end of IV stage (after which spawning that includes V and VI stages takes place). Squid females are functionally mature in the middle of V stage (after accumulation of mature egg portion in oviducts). Cephalopod males (except <u>Argonautoidea</u> superfamily) are functionally mature at VI stage, and males of <u>Argonautoidea</u> super-family being functionally mature at VI_2 stage.

To my mind, general scale for maturity stages suggested allows describing the most different processes of development and functio-ning of cephalopod sexual system. Laying down of eggs one by one, as it is for instance observed in finned octopus, without their accumulation in gonad cavity can be described as follows: during the period of presence of several mature eggs in the coelome female is at IV stage of maturity, being at V stage when passing the egg into the oviduct during spawning, and so on.

Maturity stages must be divided into substages taking into account specifity of each cephalopod group. For instance, in squid females of <u>Ommastrephidae</u> family it is reasonable to single out V_1, V_2, and V_3 stages (Burukovsky et al., 1977).

It is necessary to note that an individual when spawning repe-atedly returns to the stage of lesser rank after being spawned. The same phenomenon can be observed in fish when after spawning their sexual system returns from V-VI stages to II-III ones (Pravdin, 1966).

Therefore, the course of development and sexual system functio-ning in cephalopod males and females is in general similar (table I). However, duration and especially significance of each stage (descri-bed by maturity stages) are far from being identical. As a definite ecological aspect of animal usually corresponds to each stage of sexual system maturation (Froerman, 1985), rare frequency of any stage means that we either cannot find animals at this maturity stage, or this stage is of very short duration and is not signifi-cant for reproductive strategy of this species. For instance, phy-siological maturity stage (IV stage) is of extreme importance for octopus and cuttlefish females (just at this stage accumulation of sexual products before spawning takes place) and is of minimum

significance and shorter duration for squid females which accumulate
their sexual products at V stage observed only when the above-menti-
oned animals spawn. Finally, in cephalopod males IV and V stages
are of short duration and of little importance for the ontogenesis
since males have to produce and accumulate large quantity of sperm
"layed down", i.e. spermatophores for spawning.

Main advantage of a general scale suggested for maturity stages
is in that its using allows for making both an ecological and
evolutionary analysis of ways for realization of reproductive
strategy of different types and species within cephalopod mollusks
class. Estimation of each stage duration will enable definition of
this process ecological significance for species under investigation
and more thorough study and comprehension of its life cycle.

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Table 1 Model of general scale of maturity stages for cephalopod mollusk males and females

Maturity stages	F e m a l e s		M a l e s	
	Octopus, cuttlefish	Squids	Octopus, cuttlefish, squids	Octopus of Argonautidae
1	2	3	4	5
0	I juvenile stage. Sex is not visually distinguishable. Gonad is of thin filament form in blood vessel of the sexual coelome.		The same	The same
I AG rudiment and gonad development	II stage. Physiological maturation. Accessory gland rudiments: oviductal gland rudiments are visible at the serual coelome sides. Gonad has an aspect of dull-grey filament. Oocytes are at the second phase of protoplasmatic growth.		Rudiment of SOC is visible in the sexual coelome covering.	
2 AG differentiation, further gonad development	It is possible differentiate between OG and NG (if there are). AG is of dull-white colour. Gonad is of semitransparent lamina shape of dull-white colour. Oocytes are at the phase of simple follicle.		It is possible to distinguish between SOC sectors. Gonad is of dull-white colour; at the end of stage it is possible that in testis ampullae first spermatozoons appear. AG are of dull-white colour.	
3 Gonad maturation and AG final formation	Gonad is large, opaque, being quite visible granular structure, Oocytes are at the phases of intercalary and trophoplasmatic growth. AG are completely formed and usually of white colour.		Gonad is large and usually of dull-white colour. Spermatozoons are forming and accumulating in testis ampullae, not being "melted" its edges when being cutted. AG are completely formed and usually of white colour.	
4 Mature gonad. Mature sexual cells appear in the coelome.	III stage. Physiological maturity. 4-1. First mature eggs appear. First mature eggs appear in the coelome. 4-2. Mature egg accumulation in the coelome.		Sperm extrusion out of testis ampullae, its edges being "melted" when cutting.	

Table 1 (Continued)

1	2	3	4	5
5 Transfer of mature sexual cells into gonoducts	When spawning	5.1. Passage into oviducts up to their distal edge. 5.2. Egg accumulation with normally function-ing gonad. 5.3. Egg accumulation with reducing gonad.	Transfer of sperm into the semiduct, but there are not spermatophores in the Needham sac (with spermial re-servoirs).	
6 Passage of mature sexual cells into zone of AUX G activity and their treat-ment with AUX G secret.	When spawning	When spawning	6.1. The first sperma-tophore formation in SOC sectors. 6.2. First spermatopho-res appear in the Needham sac. 6.3. SP portions are accumulated with normally functioning gonad. 6.4. SP portion is accumulated with reducing gonad.	6.1. The same topahore formation in 6.2. SP appea-rance in Needham sac. 6.3. Transition of sperm from the Needham sac into the hectocotylus cavity.
7 Gonads spent.	Gonads spent.	Gonads spent.	Gonads spent.	Gonads spent.

Note: Markers of each maturity stages are underlined, OG - oviductal glands, NG - nidamen-tal glands, SOC - spermatophoric organ complex, AUXG - auxiliary glands (see the text).
- IV stage (functional maturation)
- V stage (functional maturity).

MATURITY STAGES

IV V VI VII VIII

A

B

C

D

NEEDHAM
SAC

E

— 1   — 5
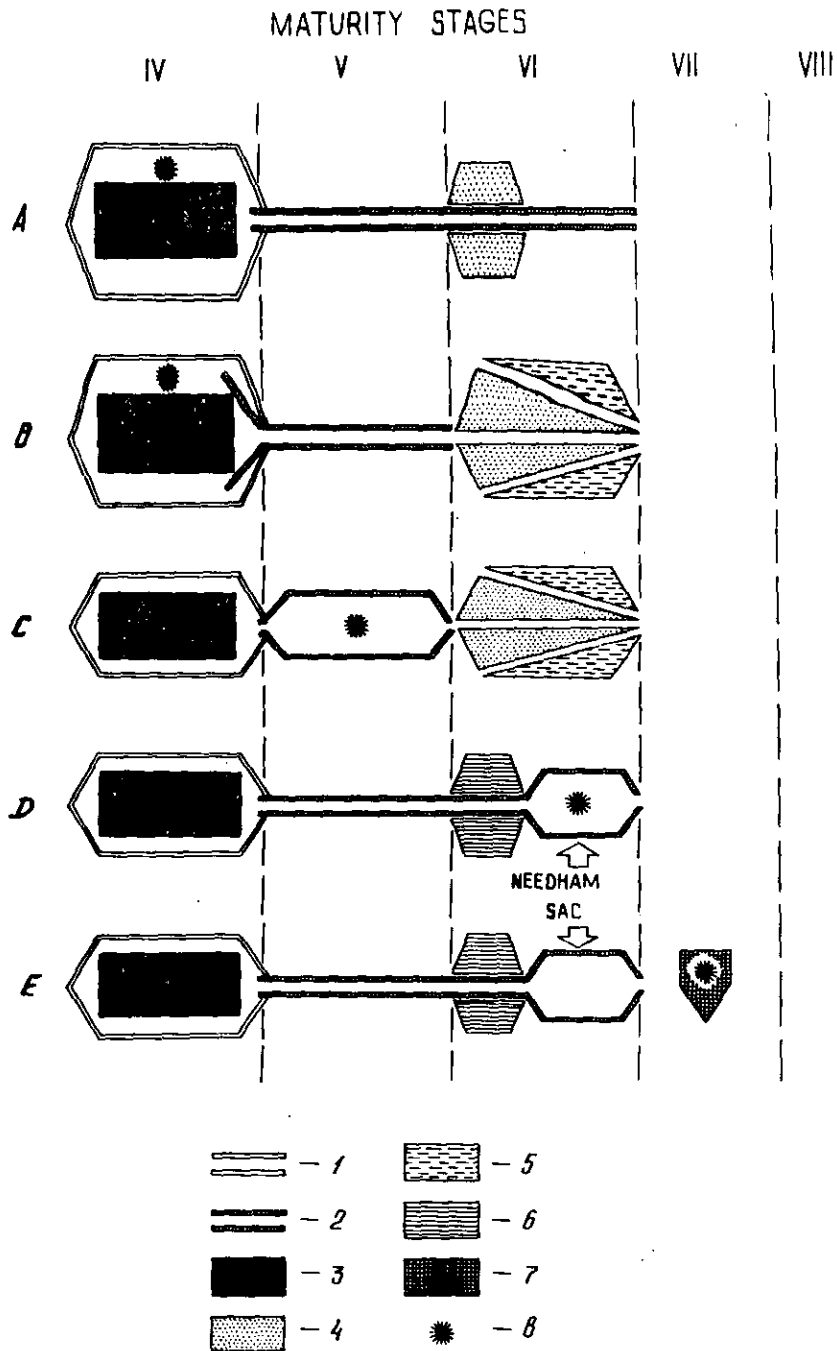— 2   — 6
— 3   — 7
— 4   — 8

Fig. 1. Scheme of sexual system structure in cephalopods:
octopus females (A), cuttlefish females (B), squid females (C), males
of all the orders (D) and Argonautidae males (E). Definitions:
Coelome coverings (1), gonoducts (2), gonad (3), accessory glands:
oviductal glands (4), nidamental glands (5), spermatophoric gland
(6), hectocotylus reservoir (7), site of sexual products accumulati-
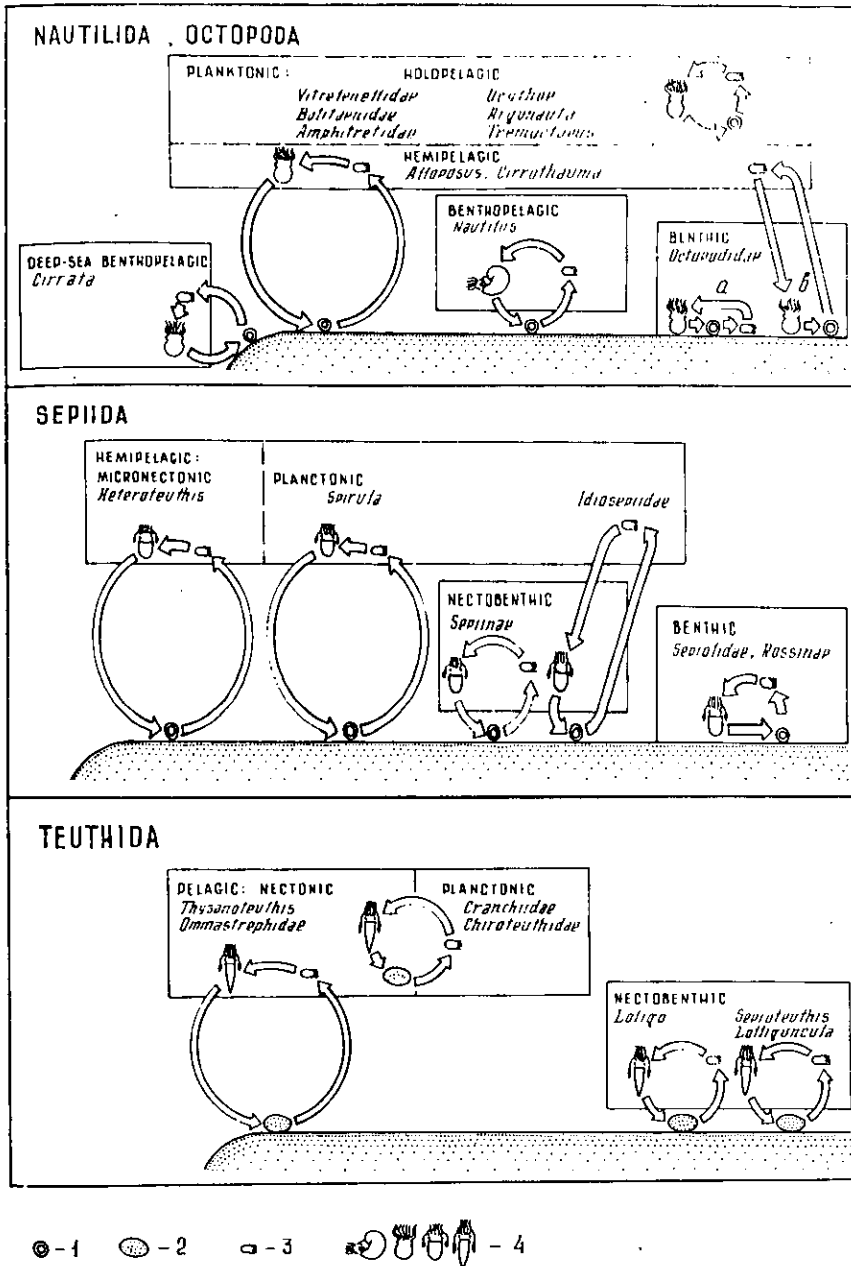on (8).

Fig. 2. Ontogenetic migrations (scheme of life cycles) in principal groups of cephalopods (by Nesis, 1985). D$_e$finitions: eggs (1), eggs layed down (2), larvae or early juveniles (3), adult individuals (4).