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RESULTS OF SOVIET INVESTIGATIONS OF THE DISTRIBUTION AND ECOLOGY OF PELAGIC SQUIDS (OEGOPSIDA) IN THE SOUTHERN OCEAN

Abstract

The USSR has carried out a long-term investigation of the distribution and ecology of pelagic squids (Oegopsida) in the Southern Ocean. In 1965-1977 a total of 326 squid specimens were collected at 124 stations with sampling by midwater nets. 125 specimens of that total were identified as Brachioteuthis riisei. In recent years (1978-1984) the collection was increased by two or three dozen specimens mostly identified as the little-studied Alluroteuthis antarcticus (family Neuleuthidae). 14 species of squid are considered to inhabit permanently the Southern Ocean. They belong to 9 families (13 genera). The pelagic squids are very seldom caught by fishing nets in Antarctic waters and data on squid beaks taken from sperm whale stomachs were also considered.

Up-to-date descriptions of all fourteen species are suggested. Where data are available the description includes geographical distribution, habitat, size, food diet and position of a species in a food web. Such description is also suggested for M. hamiltoni, the data on which come only from beaks found in sperm whale stomachs. All species are divided into three major groups in accordance with their habitats : tropico-subtropical, notal and Antarctic types.

In view of the absence of squid beaks in the bottom sediments in the Antarctic, two hypotheses are suggested : all squids migrate to the Antarctic in the summer seasons from the sub-tropical and notal areas, or the abundance of the true meso- and bathypelagic squida is very low.

It is proposed to concentrate future research on squids in the waters of high bioproductivity south of 60°S.

RESULTATS DES ETUDES SOVIETIQUES SUR LA REPARTITION ET L'ECOLOGIE DES CALMARS PELAGIQUES (OEGOPSIDA) DANS L'OCEAN AUSTRAL

Résumé

L'URSS a mené une étude à long term sur la répartition et l'écologie des calmars pélagiques (Oegopsida) dans l'océan Austral. En 1965-77, au total, 326 spécimens de calmars ont été prélevés à 124 stations par échantillonnage à l'aide de filets mésopélagiques. Sur ce total, 125 spécimens ont été identifiés comme étant de l'espèce Brachioteuthis riisei.

Au cours des dernières années (1978-1984), la collection s'est élargie par le prélèvement de deux ou trois douzaines de spécimens identifiés pour la plupart comme faisant partie de l'espèce peu étudiée Alluroteuthis antarcticus (famille des Neuleuthidae). 14 espèces de calmars habitent de manière permanente l'océan Austral. Ces espèces appartiennent à 9 familles (13 genres). Les calmars pélagiques ne sont que très rarement pris au filet dans les eaux antarctiques et les données provenant des becs de calmars trouvés dans les estomacs de cachalots ont également été étudiées.

Des descriptions très récentes de toutes ces quatorze espèces sont suggérées. Dans les cas où les données disponibles le permettent, la description comprend la répartition géographique, l'habitat, la taille, le régime alimentaire et la position de l'espèce dans la chaîne alimentaire. Une description semblable est également suggérée en ce qui concerne l'espèce M. hamiltoni, pour laquelle les données ne proviennent que des becs trouvés dans les estomacs de cachalots. Toutes les espèces sont réparties en trois groupes principaux selon leur habitat: type tropico-subtropical, type notal et type antarctique.

Etant donné l'absence de becs de calmars dans les sédiments de fond en Antarctique, deux hypothèses ont été avancées: tous les calmars émigrent en Antarctique au cours de la saison d'été, quittant les régions subtropicales et notales, ou bien l'abondance des calmars proprement méso- et bathypélagiques est très faible.

On propose de concentrer les futures recherches sur les calmars dans les eaux de haute bioproduktivité au sud de 60°S.

#### РЕЗУЛЬТАТЫ СОВЕТСКИХ ИССЛЕДОВАНИЙ ПО ВОПРОСАМ РАСПРОСТРАНЕНИЯ И ЭКОЛОГИИ ПЕЛАГИЧЕСКИХ КАЛЬМАРОВ (OEGOPSIDA) В ЮЖНОМ ОКЕАНЕ

##### Резюме

СССР была проведена долгосрочная программа исследований по вопросу распространения и экологии пелагических кальмаров (Oegopsida) в Южном океане. В 1965 -1977 г.г. было собрано в общей сложности 326 образцов кальмаров на 124 станциях при помощи среднеглубинных тралов. 125 образцов из общего числа было определено как принадлежащие к виду Brachioteuthis riisei. В недавнее время (1978-1984 г.г.) коллекция была пополнена двумя или тремя дюжинами образцов, определенных в большинстве случаев как принадлежащие к малоизученному виду Alluroteuthis antarcticus (семейство Neuleuthidae). Считается, что 14 видов кальмаров постоянно обитает в Южном океане. Они принадлежат к 9 семействам (13 родам). Пелагические кальмары очень редко вылавливаются рыболовными сетями в водах Антарктики; были рассмотрены также данные по клювам кальмаров, найденным в желудках кашалотов.

Предлагаются новейшие описания всех четырнадцати видов. При наличии соответствующих данных описания включают в себя географическое распределение, место обитания, размер, пищевой режим и положение вида в трофической цепи. Подобное описание также предлагается и для вида *M. hamiltoni*, данные по которому были получены только по клювам, найденным в желудках кашалотов. Все виды разделены на три основные группы в соответствии с их местом обитания: тропическо-субтропические, нотальные и антарктические.

Ввиду отсутствия клювов кальмаров в донных отложениях Антарктики предлагаются две гипотезы: все кальмары мигрируют в Антарктику во время летнего периода из субтропических и нотальных областей, либо численность подлинно мезо- и батипелагических кальмаров является весьма низкой.

Предлагается сосредоточить будущие исследования кальмаров в водах высокой биопродуктивности, к югу от 60° ю.ш.

#### RESULTADOS DE LAS INVESTIGACIONES SOVIETICAS SOBRE LA DISTRIBUCION Y ECOLOGIA DE LOS CALAMARES PELAGICOS (OEGOPSIDA) EN EL OCEANO AUSTRAL

##### Extracto

La URSS ha llevado a cabo investigaciones a largo plazo sobre la distribución y ecología de los calamares pelágicos (Oegopsida) en el Océano Austral. En 1965-1977 se recolectó un total de 326 especímenes de calamares en 124 estaciones con muestreos hechos por redes semipelágicas. De dicho total 125 especímenes se identificaron como *Brachioteuthis riisei*. Durante los últimos años (1978-1984) la colección se aumentó en dos o tres docenas de especímenes la mayoría de los cuales han sido identificados como los poco estudiados *Alluroteuthis antarcticus* (familia Neuleuthidae). Se considera que 14 especies de calamares habitan el Océano Austral permanentemente. Pertenecen a 9 familias (13 géneros). Los calamares pelágicos son capturados muy raras veces por redes pesqueras en las aguas antárticas y también se consideraron los datos sobre los picos de calamar obtenidos de los estómagos de ballenas enanas.

Se sugieren descripciones actualizadas todas estas 14 especies. Donde hay datos disponibles, la descripción incluye la distribución geográfica, habitat, tamaño, dieta

alimenticia, y la ubicación de la especie en la red alimenticia. Tal descripción también se sugiere para M. hamiltoni, los datos sobre los cuales sólo se obtuvieron de los picos hallados en estómagos de ballenas enanas. Todas las especies quedan divididas en tres grupos principales según sus habitats: tipos tropicales-subtropicales, notales y antárticos.

En vista de la abundancia de picos de calamar en los sedimentos de fondo de la Antártida, se sugieren dos hipótesis: todo calamar emigra a la Antártida en las temporadas de verano desde las áreas subtropicales y notales, o la abundancia del verdadero calamar mesopelágico y bathypelágico es muy baja.

Se propone concentrar las investigaciones futuras en los calamares de las aguas de alta bioproduktividad al sur de los 60°S.

Less is known of the squids of the Southern Ocean than all other groups of marine animals which usually occur in this vast region or migrate into Antarctic waters in warmer seasons. This gap in our knowledge of the group of Antarctic pelagic cephalopods seems to be due to the fact that they are rarely caught by fishing gear and the main material available for examination by specialists is represented by samples from the stomach contents of sperm whales taken in the Southern Ocean. The samples collected by such indirect methods consist primarily of beaks, sometimes fragments of bodies, or very rarely intact specimens of squid. Because of this, it is difficult not only to study the biology and ecology of squids, but even to identify species found in the stomachs of sperm whales.

A total of 326 specimens of Antarctic Squids were collected at 124 stations with midwater hauls in the Southern Ocean during studies carried out by the Soviet Union in the years 1965-1977. Of that total, 125 specimens from 42 stations were identified as Brachioteuthis ritsei (Filippova, Yukhov, 1979). In recent years (1978-1984), the collection was increased by two or three dozen specimens taken during Antarctic expeditions carried out by VNIRO and AZCherNIRO in certain areas of the Southern Ocean. Most specimens were identified as the little-studied Alluroteuthis antarcticus (family Neoteuthidae) and as a result the first description made by Odhner (1923) was completed and the identification description of the genus Alluroteuthis and family Neoteuthidae was changed (Filippova, Yukhov, 1982; 1983).

Although squids are not often found in the catches of pelagic fishing gear, the collected data provide a general idea of the spatial distribution of species in the Southern Ocean. In turn, the analysis of data on the distribution and feeding habits of the sperm whale, the principle consumer of squids, and material on spatial and quantitative distribution of major food species of squids (mesopelagic fish) indicate certain ecological characteristics of this group of nekton animals.

Pelagic squids from the sub-order Oegopsida are widely distributed in the Southern Ocean. As is already known, in contrast to the meridional distribution pattern of species of the sub-order Myopsida, representatives of Oegopsida are characterised by a latitudinal distribution pattern, their

habitats being confined to latitudinal climatic zones of the World Ocean (Zuev, Nesis, 1971). Analysis of the available data indicates that the group of oceanic squids in the Southern Ocean has the same pattern of distribution. This regularity in the distribution pattern of squids in the latitudinal climatic zones of the ocean is in full agreement with principles of zonation in the oceanographic and biological structure in the Southern Ocean and with principles of separation of two different natural latitudinal zones (Deacon, 1982; Lubimova, 1982; 1983; 1984).

The sub-order Oegopsida includes 23 families, 77-81 genera and 226 species. A considerable part of the species are warm-water cosmopolitans, 36% of all species occur in more than one ocean and 13% occur in more than two oceans. More than half of all species (120) are found in the Atlantic Ocean (Nesis, 1982). Latitudinally, complex species composition (over 60% of all species) is noted for the tropical and sub-tropical waters, whereas to the north and south of the equatorial zone, i.e. in the temperate and particularly in the sub-polar waters of the Northern and Southern Hemispheres, the species composition is much less diverse (Zuev, Nesis, 1971).

It is ascertained that the families Onychoteuthidae, Cranchiidae, Histioteuthidae are diversely represented in the equatorial zone (Akimushkin, 1963; Zuev, Nesis, 1971; Filippova, 1971; Nesis, 1973). These are the same families which compose the bulk of the species composition of squids occurring in the Southern Ocean. The diversity and richness of forms of oceanic squids in the tropical and sub-tropical waters undoubtedly indicate their warm-water origin and their subsequent dispersion from the equatorial zone into the boreal and notal zones in the geological ancient past.

Squids are known to be one of the most ancient groups among all existing groups of nekton animals. The fossil ancestors of squids, Belemnitidae, which differ from squids only in the specific gravity of their calcified skeletons, inhabited warm oceanic waters. Their fossilized skeletons are found in the Jurassic layer of Central Europe (Kabanov, 1967, 1983; Akimushkin, 1968). It is evident that the ancient origin and the cosmopolitan character of oceanic squids Oegopsida, are responsible for

their fairly wide distribution in the warm waters of the World Ocean, and for the penetration of some species into the productive areas of the temperate waters of the boreal and notal zones. At the same time, it is substantiated that the distribution of pelagic squids in the temperate waters is limited to some extent as their existence is closely associated with warm currents and their vertical distribution is dependent upon warm-water masses. Therefore, despite the diversity of Oegopsida forms in the Atlantic Ocean, it is shown that the Gulf Stream appears to be a mechanism responsible for such an elementary evolutionary factor as isolation of species in the temperate zone. The current is a natural barrier preventing the penetration of species inhabiting and spawning in the mesopelagic layer of the warm North Atlantic water mass<sup>1</sup>, beyond its northern boundary. Squids brought by Gulf Stream eddies into cool coastal waters of the Northwest Atlantic, die particularly in the winter-spring season (Froerman, 1983). Similar regularities in the distribution of oceanic squids in the system of warm currents (Kuroshio, East Australian Current, Alaska Current) are also known for the temperate zone of the Pacific in the Northern Hemisphere (Zuev, Nesis, 1971; Berzin, 1971).

No doubt, the same regularity of the distribution of squids Oegopsida should be found in the notal and Antarctic areas of the Southern Hemisphere. Therefore, the data on the feeding habits of sperm whales in the Southern Hemisphere summarised by Soviet researchers (Klumov, 1971), information on squid occurrences in the stomach samples of sperm whales and in fishing gear catches (Filippova, Yukhov, 1979) and on the different types of species habitats (Nesis, 1982), indicate a close association of squids from the Southern Ocean with the Antarctic Circumpolar Current waters (ACC). According to instrumental measurements of depths where sperm whales dive in search of squids (from 400 to 600 m on average ; Yukhov, 1982) and information on the depths of hauls where the most specimens were

<sup>1</sup> The North Central water mass is characterised by high salinity and temperature according to Sverdrup's Classification, 1942, cited by the Russian translation (1974, pp114-118) of the Encyclopedia of Oceanography, A. Gordon, New York, 1966.

caught in the Southern Ocean (Filippova, Yukhov, 1979; 1982) we may come to a definite conclusion that the permanent environment of squids in the Antarctic is the Antarctic Deep Warm Water Mass<sup>2</sup>. In view of this fact, the lack of epipelagic forms of oceanic squids in the Antarctic noted by all researchers does not seem to be accidental (Klumov, 1971; Zuev, Nesis, 1971; Filippova, Yukhov, 1979; Nesis, 1982). It is known that the upper 200 m layer in the Antarctic is held by the Antarctic Surface Cool Water Mass which is characterised by constant low salinity and low temperature (it may drop below zero in winter and in summer there is a residual layer of the sub-surface temperature minimum ; Makarov, 1956; Sarukhanyan, 1980).

The attachment of oceanic squids to warm currents and water masses seems to be a general feature in their distribution northwards and southwards from the equatorial zone of the World Ocean, and the main characteristic of their etology due to their warm-water origin. No doubt, this characteristic is formed in the process of long-term evolution in Oegopsida as adaptation to the conditions of the temperate and subpolar waters of the World Ocean. Recent paleogeographical, paleoclimatic and paleoceanographic data show that the penetration of oceanic warm-water squids into Antarctic waters probably took place in the early Tertiary period. According to the data (Verbitakij, Kvasov, 1980; Myagkov, 1980; Znachko-Yavorskiy, 1980; Zonenshain, 1980; Losev et al., 1980), the early Tertiary period (Paleocene and Eocene) was characterised by the existence of one mainland in the Southern Hemisphere consisting of the modern continents of South America, Australia and Antarctica. At that time, the continent was washed around by warm currents moving away from the equator, and temperate climatic conditions were prevailing in the Antarctic. However, in the early Oligocene when a deep-water strait was formed between Australia and Antarctica, the glaciation of the Antarctic continent started and was responsible for the predominance of cold currents there. Only

<sup>2</sup> The upper boundary of the Antarctic Deep Warm Water Mass is at the depth of 200m, the lower boundary is 3000-2000 m deep on average (Dencon, 1937; Sarukhanyan, 1980).



three of these equatorial currents remain. Such meridional currents existed in the Southeast Indian Ocean and Southwest Pacific up to the mid-Miocene. A warm current originated in the Atlantic, in the coastal water of South America, and penetrated into the Weddell Sea.

Thus the temperate climate in the Antarctic in the Paleocene and Eocene and the existence of three powerful equatorial currents moving south in the Pacific, Atlantic and Indian Ocean until the mid-Miocene, are likely to have attributed to the penetration and dispersal of the tropical and sub-tropical fauna (Oegopsida) in the Antarctic. Later, in late Miocene-early Pliocene, the Antarctic was separated from South America, resulting in complete isolation of the Antarctic continent and its rapid cooling, an increase in the volume of cool Antarctic waters and the formation of the ACC. The influx of warm water from the equator is confined to the Antarctic Deep Water Mass. This seems to have resulted in the adaptation of warm-water squids to the ACC waters and their association with the Antarctic Warm deep water. At the same time, it is quite evident that only a few species from the sub-order Oegopsida with very rich species composition (226 species), could adapt themselves to the Southern Ocean. The evidence is supported by the fact that the species composition of oceanic squids occurring in the notal and Antarctic areas is extremely poor (Nesis, 1982). Moreover, the most widely distributed species in the Southern Ocean are not typical for the Antarctic. As is known, endemism is not specific to the group of oceanic squids as a whole (Akimushkin, 1963). Nevertheless, some species are referred to as endemic Antarctic forms because they have never been found to the north of the Antarctic Convergence (Filippova, Yukhov, 1979).

Therefore, squids of the Southern Ocean belong to 9 families, 13 genera and 14 species (Table 1). Six families out of nine are monotypic and represented by one genus and one species each. The remaining three families include 1-3 genera and 203 species each; they are tropical or sub-tropical by origin: Crauchiidae (3 genera, 3 species), Onychoteuthidae (2 genera, 3 species) and Histioteuthidae (1 genus, 2 species). Among the former six families there are two cosmopolitan families (Brachioteuthidae and Bathyteuthidae), a tropical Neoteuthidae, a bipolar Gonatidae and two families (Psychroteuthidae and Batoteuthidae) which never occur in the Northern Hemisphere (Nesis, 1982).

Besides the abovementioned species, there are indications that such widely spread cosmopolitan forms as Architeuthis sp., Onychoteuthis banksii, Chiroteuthys veranyi, which permanently inhabit the tropical waters, can penetrate into the Southern Ocean. Their occurrence is known only from the stomach contents of sperm whales both in the Northern Hemisphere and in the sub-tropical and notal waters of the Southern Hemisphere. They are mainly bathypelagic species (Klumov, 1971; Zuev, Nesis, 1971; Nesis, 1982). Since they are not typical for the Southern Ocean they are not included in the list of species contained in Table 1.

Relying on the data summarised by Klumov (1971), Philippova and Yukhov (1979; 1982; 1983), the present analysis includes all materials used by them, data on the analysis of whale stomach contents, data on captures by midwater fishing gears, including data published in other countries and in the monographic review "World Ocean Cephalopods", Nesis (1982). Using all the material, the complex characteristics of each of 14 species occurring in the World Ocean are suggested. Meaonychoteuthis hamiltoni is considered separately as opinions on the distribution of the species in the Antarctic are controversial because they rest only on data on the analyses of stomach contents of sperm whales and are represented mainly by beaks (Klumov, Yukhov, 1975).

Moroteuthis ingens (Smith, 1881) is known to occur in the Southern Ocean according to data on the stomach contents of sperm whales and samples from midwater fishing gear collected at 37 stations between 40° and 55°S. It was encountered on the Patagonian shelf, off Southern Chile, the Falkland Islands, Prince Edward Island, Crozet, Kerguelen, New Zealand and once off South Georgia. It inhabits the bathypelagic layer and is characterised as a circumpolar notal species entering the Antarctic Convergence. The length of the mantle is up to 52 cm. Mesopelagic fish from the family Myctophidae and small-sized squids are found in the diet of some specimens.

Morotheuthis knipovitchi (Filippova, 1972) is known to occur in the Southern Ocean according to data on the stomach contents of sperm whales and from data on catches of midwater fishing gear. It was once found in the stomach of an Antarctic toothfish (Dissostichus mawsoni) withdrawn

from the stomach of a sperm whale. It was encountered at 18 stations between 45° and 55°S in the Indian Southern Ocean, between 55° and 65°S in the Atlantic Southern Ocean and some specimens are found at 4 stations in the vicinity of the South Polar Circle. It inhabits the mesopelagic and bathypelagic layers and is characterised as a circumpolar Antarctic species, but it also occurs north of the Antarctic Convergence. The length of the mantle is up to 45 cm. Mesopelagic fish from the family Myctophidae and small-sized squids are found in the diet of some specimens.

Kondakovia longimana (Filippova, 1972) is known to occur in the Southern Ocean according to data on the stomach contents of sperm whales and from midwater net samples collected at 28 stations, including 21 stations in the Pacific Southern Ocean from 56° to 68°S, some specimens in the Atlantic Southern Ocean are found at 60°S and in the waters of the Antarctic Convergence in the Indian Ocean. It inhabits the mesopelagic layer and can rise into the epipelagic layer. It is characterised as a circumpolar Antarctic species, which has not yet been encountered north of the Antarctic Convergence. The length of the mantle is 80-115 cm. Mesopelagic fish from the families Myctophidae and Paralepididae, small-sized squids and Antarctic krill are found in the diet of some specimens.

Galiteuthis glacialis (Chun, 1906) (synonyms G. aspera, Filippova, 1972, Crystalloteuthis glacialis (Chun, 1906) is known to occur in the Southern Ocean according to data on the stomach contents of sperm whales caught off Prince Edward and Crozet Islands and from midwater fishing gear catches at 4 stations in the Scotia Sea. It inhabits the meso- and bathypelagic layers and can rise into the lower epipelagic layer; it is characterised as a circumpolar Antarctic species, but is found also in the notal water north of the Antarctic Convergence. There are no data on the length of the mantle. Feeding habits are not known.

Taonius pavo (LeSueur, 1821) is known from the stomach contents of sperm whales in the Northern Hemisphere as a widely distributed form, but the evidence of its occurrence in the diet of sperm whales in the Southern Hemisphere still needs to be proven. It is characterised as a widely distributed but rare tropical-subtropical species. It is supposed to

penetrate into the notal waters, but it was not found in the Southern Ocean. It seems to occur in the mesopelagic layer. The length of the mantle is up to 40-45 cm. There are no data on the feeding habits.

Histioteuthis atlantica (Hoyle, 1885) and H. eltaninae (N. Voss, 1962) are species which are not typical for the south polar area of the World Ocean. Numerous representatives of the family Histioteuthidae in the sub-tropical and temperate waters occur in the diet of sperm whales. They are distributed everywhere except for the Arctic and Antarctic areas. They inhabit the meso- and bathy- pelagic layers and the abyssalpelagic layer as well. H. atlantica is characterised as a circumglobal south sub-tropical and notal species. It is supposed to be able to penetrate into the Antarctic Convergence, but no specimens have been found in the Southern Ocean. The length of the mantle is up to 20 cm. There are no data on the feeding habits. H. eltaninae is characterised as a circumglobal notal species. It is encountered off the Falkland Islands and New Zealand. Two specimens were observed in the Antarctic Convergence. The length of the mantle is up to 7 cm. There are no data on feeding habits.

Gonatus antarcticus (Lönnerberg, 1898) is known from the stomach contents of sperm whales in the Southern Hemisphere and some specimens were encountered in midwater fishing gear in the notal waters off the Falkland and Crozet Islands. It is distributed up to South Africa and North Peru, north of the Antarctic Convergence. It inhabits the meso- and bathy- pelagic layers and is characterised as a circumpolar notal species entering the Antarctic Convergence. The length of the mantle is up to 35 cm. There are no data on the feeding habits.

Alluroteuthis antarcticus (Odhner, 1923) is known from the stomach contents of sperm whales and midwater fishing gear catches at 34 stations in the Southern Ocean. There is information that specimens occur infrequently in the diet of sperm whales because of their low abundance. Specimens were caught in the Antarctic Atlantic Ocean south of the Antarctic Convergence from 51° to 65°S, and in the Antarctic Pacific and Antarctic Indian Oceans - up to 67°-69°S. It inhabits the bathypelagic layers, although two specimens were encountered in the epipelagic layer. It is characterised as

a circumpolar Antarctic species, no occurrence was registered north of the Antarctic Convergence. The length of the mantle is up to 24-27 cm. The diet of young specimens contains squids including specimens of the same species, and crustaceans : euphausiids (probably Antarctic Krill), hyperiids, mysids. Squids of family Chroteuthidae, mesopelagic fish, euphausiids (including E. superba<sup>3</sup>) are found in the stomach contents of adult specimens.

Psychroteuthia glacialis (Thiele, 1921) is known in the Southern Ocean from the stomach contents of the Weddell Seal and Antarctic Toothfish extracted from the stomachs of sperm whales. Two specimens were found in the catches of midwater fishing gear at 13 stations and all of them were found south of the Antarctic Convergence, up to 69°S. It inhabits the mesopelagic layer, off the Antarctic islands - in the bathyal layer near the bottom. It is supposed to be able to rise into the lower epipelagic layer. It is characterised as a circumpolar Antarctic species. The length of the mantle is up to 44 cm. There are no data on the feeding habits.

Brachiotenthis riisei (Steenstrup, 1882) is known in the Southern Ocean mainly from the catches of midwater fishing gear (125 specimens were collected at 42 stations). Most specimens were collected in the Scotia Sea between the Antarctic Convergence and 60°S. Three specimens were caught in the Indian Ocean : one north of the Antarctic Convergence and two at 60°S. A total of seven specimens were caught in the Pacific Southern Ocean, mainly at 60°S. There are indications of occurrences of this species in the stomach contents of sei whales and fin whales. It inhabits the meso- and epi- pelagic layers but was also found in the bathypelagic layer. According to present knowledge it is a cosmopolitan species spread widely in the productive temperate waters of the World Ocean except for the boreal Pacific Ocean. In the Southern Ocean it is characterised as a circumglobal

3 The identification was made by some fragments of euphausiids, so the assumption was made that E. Superba is included in the diet of A. antarcticus (Filippova, Yukhov, 1982).

notal-Antarctic species. According to data on its occurrences in the Atlantic Ocean in particular (125 specimens) the assumption is made that squids are concentrated off South Georgia and adjacent waters of the Scotia Sea in the meso- and epi- pelagic layers. The length of the mantle is up to 14 cm. The diet of specimens caught in the Scotia Sea contained euphausiids, including Antarctic krill.

Bathyteuthis abyssicola (Hoyle, 1885) has never been found either in the stomach contents of sperm whales or in midwater fishing gear during the long-term period of Soviet fishery research. At the same time it is believed that the abundance of species is high in the notal area of the Southern Ocean (Roper, 1969). Squids inhabit the bathypelagic layer and young specimens occur occasionally in the lower epipelagic layer. It is characterised as a cosmopolitan species which is widespread in the eutrophic areas of the World Ocean. The distribution is circumglobal in the notal and Antarctic waters. There are indications that abundance is low in the Southern Ocean and therefore the species cannot be a food item for sperm whales as Alluroteuthis antarcticus, (Klumov, 1971). The length of the mantle is up to 6 cm. There are no data on the feeding habits.

Datoteuthis scolops (Young and Roper, 1968) is known in the Southern Ocean from the stomach contents of sperm whales and from the catches of midwater fishing gear. Specimens were caught at 6 stations, 3 of which are in the south west Atlantic in the Antarctic Convergence and north of it. The stomachs of sperm whales caught in the Pacific Southern Ocean contained three specimens, one occurring north of the Bellingshausen Sea. Specimens of the species were not found in the Indian Ocean. It is believed that squid do not migrate and inhabit the bathypelagic layer. It is characterised as a notal-bathypelagic species entering the Antarctic waters. There are no data on the feeding habits.

The abovementioned data indicate that all species of squids occurring in the Southern Ocean in summer can be clearly divided into separate groups according to their types of habitats. The tropical-subtropical and notal types of habitat are characteristic of 5 species : T. pavo, H. atlantica, H. eltaninae, G. antarcticus, M. inges.

The notal type is inherent for 3 species : B. riise, B. abyssicola, B. scolops and 5 species belong to the Antarctic type : K. longimana, A. antarcticus, P. glacialis, M. knipovitchi, G. glacialis the last three species of which may be considered as endemic for the Antarctic because they have never been encountered north of the Antarctic Convergence. Unfortunately, it is not evident to which group we shall refer Mesonychoteuthis hamiltoni (Robson, 1925) since the data on the distribution rely only on the occurrences of beaks in the stomachs of sperm whales.

It is ascertained that information on the occurrences of beaks of squids in the stomachs of sperm whales is not conclusive enough to draw up a true pattern of the spatial and, moreover, the quantitative distribution of these or other species of Cephalopods. Beaks of squids are not destroyed while the food is digested and they are accumulated in stomachs in large numbers (up to 28000 beaks per stomach), but in general a stomach contains 7000-8000 beaks (Akimushkin, 1963; Betesheva, 1961; Korabel'nikov, 1959; Tarasovich, 1968; Berzin, 1971). Nevertheless, an attempt was made by Soviet investigators to delineate the boundaries of the habitat of M. hamiltoni using such indirect data (Klumov, Yukhov, 1975). It was necessary that such an attempt should be made because no specimens of this species have been caught in the Southern Ocean since it was described by Robson in 1925. Efforts of many Soviet and foreign expeditions which included special studies of Antarctic Cephalopoda (as U.S. expeditions on board "Eltanin" started in 1962) were fruitless in this respect and until now no specimens have been caught with the exception of four larvae collected in the Pacific Southern Ocean and in the Drake Passage (McSweeney, 1970). Material from the stomachs of sperm whales analysed by Klumov and Yukhov was collected on board the Soviet whaling motherships "Yuri Dolgoruky" (1961-1965) and "Sovetskaya Rossiya" (1966-1968) and consisted only of beaks. Material collected on board "Sovetskaya Ukraina" (1967-1973) contained not only beaks, but also fragments of bodies and even some intact animals (Klumov, Yukhov, 1975). In their work they provide the results of the analyses of twenty specimens of M. hamiltoni and, for six of them, the description of exterior and interior morphological features with reference to the places where sperm whales were caught.

| <u>Date</u> | <u>Position of Catch</u> | <u>Mantle Length in cm</u> |
|-------------|--------------------------|----------------------------|
| 31.1.1968   | 62°43'S, 170°05'E        | 155                        |
| 4.4.1969    | 68°43'S, 122°W           | 65                         |
| 6.1.1971    | 41°36'S, 48°50'E         | 39 and 45 (2 specimens)    |
| 1.3.1971    | 43°00'S, 46°00'E         | 39                         |
| 17.3.1972   | 42°50'S, 31°20'E         | 47                         |

Unfortunately, no coordinates are given for the remaining specimens, although the lengths of their mantles are provided (from 36 to 200 cm). This indicates that the specimens of M. hamiltoni are larger in size than those of other species occurring in the Southern Ocean. Some morphological and meristic characters of M. hamiltoni are also given in the work. As a result of the study the previously accepted opinion that the species belongs to the family Granchiidae was supported (Clarke, 1966; Roper et al., 1969). The main feature of the family is the presence of a coelom which contains a considerable amount of  $\text{NH}_4\text{Cl}$  in its fluids. Owing to a lower density of the solution (as compared to sea water) neutral buoyancy of the large-sized squid is sustained, therefore investigators believe that this species is a plankton or a semi-plankton form (Nesis, 1982). Judging from the fact that the mantle of the species is gelatinous, without well developed mantle muscles and fibre structure, the squid seems to be slightly movable, it hovers in the water and drifts with water masses (Klumov, Yukhov, 1975).

The analysis of the stomach contents of the collected squids revealed mesopelagic fish of families Myctophidae and Paralepididae, probably Electrona antarctica, Bymnoscopelus braueri and Paralepis atlantica, and some unidentified squids as the main components. So far as maturity is concerned, it is assumed that specimens with mantle smaller than 100 cm are immature.

With the same indirect method it is ascertained that the habitat of M. hamiltoni in the Southern Hemisphere extends from 32°-34°S to 68°-70° S, i.e. from the sub-tropical zone to high Antarctic latitudes. The most frequent occurrences of this specimen in the stomach contents of sperm



whales are registered in the East Atlantic and West Indian sectors of the Southern Ocean between 18W and 90<sup>0</sup>E. Echosounder measurements have shown that sperm whales dive to the 500-600 m layer in some areas of the Southern Ocean in search of this species of squid (Klumov, Yukhov, 1975; Yukhov, 1982).

It seems that all the data obtained by Klumov and Yukhov supports the evidence that M. hamiltoni should be characterised as a notal-Antarctic species which inhabits the meso- and bathy- pelagic layers and with the Antarctic Deep Warm Water Mass it penetrates south of the Antarctic Convergence because it is a plankton or semi-plankton form. The Antarctic Deep Warm Water Mass in the Southern Ocean moves southward with a speed of 5-20 cm/sec in the 200-3000/3500 m layer and according to the results of the investigations conducted under the international program POLEX-SOUTH, the centre of this water mass is in the southwest part of the Indian Ocean (Ledenev, 1969; Sarukhanyan, 1981). However, when data on feeding habits of sperm whales in the Southern Ocean for 13 years were summed up, the scope of material on M. hamiltoni from the stomach contents of sperm whales caught south of the Antarctic Convergence appeared considerably greater than that of sperm whales caught in the notal waters. Therefore the authors came to an unexpected conclusion on the distribution of M. hamiltoni in the Southern Ocean. They characterise the species as a circumpolar Antarctic species, with the centre of its habitat being in the Antarctic including high latitude areas south of 60<sup>0</sup>S. They believe that the squid permanently inhabits the bathypelagic layer and it is restricted within off-bottom cool water mass moving from south to north ; therefore the species, having a planktonic way of life, drifts from the coastal Antarctic waters to the notal and tropical waters.

The conclusion is in contradiction with the warm-water character of the species of the family Cranchiidae and of the subfamily Taoniinae, representatives of which inhabit the tropical, sub-tropical and temperate waters of the Northern and Southern Hemispheres (Voss, 1980; Nesis, 1982), whereas the Antarctic off-bottom water is characterised by a very low temperature up to -0.5<sup>0</sup>C. The conclusion also contradicts the authora' own data when they state that M. hamiltoni occurs in abundance at the depth of

500-600 m feeding on mesopelagic fish and at the same time being a prey for sperm whales (Klumov, Yukhov, 1975). However, the upper boundary of the Antarctic off-bottom cool water mass in the coastal waters of the Antarctic is at the depth of 1500-2000 m ; over the whole Antarctic region - the depth of 3000-3500 m; and in the north of the Southern Ocean, north of the Antarctic Convergence, the boundary lies at the depth of 4500-5000 m (Sarukhanyan, 1981).

We believe, therefore, that M. hamiltoni should be tentatively considered as an Antarctic species for the time being, or rather as a notal-Antarctic species until specimens of the species are captured by midwater fishing gear so that the pattern of its distribution in the Southern Ocean can be better understood.

In general, according to the data available, all the species of pelagic squids of the Southern Hemisphere found in the stomachs of sperm whales and in the catches of the midwater fishing gear, are distributed in the Antarctic Circumpolar Current which is the most powerful circulation system in the World Ocean covering circumpolarly the 0-3000/3500 m layer and having many streams (Neyman, 1961; Deacon, 1937; 1963; Sarukhanyan, 1980). It is ascertained that the north periphery of the ACC extends in the Atlantic Southern Ocean from the Falkland Islands to 43°S and to 37° in the vicinity of the zero meridian; in the Indian Ocean between 43° and 47°S; in the Pacific Southern Ocean between 47° and 55°S and in the Drake Passage between 50° and 56°S. The principal stream of the ACC moves mainly along the Antarctic Convergence between 50° and 55°S shifting south of Australia and New Zealand to 62°-63°S and in the Drake Passage to 56°-59°S. The southern components of the principal stream of the ACC flow along 60°-61°S with some divergences to the north to 57°-58°S in the Scotia Sea and to the south from the Ross sea to the Bellingshausen Sea reaching 66°-68°S. (Trechnikov, Maksimov, Gindysh, 1966; Sarukhanyan, 1980). It is evident that the species of squids with the tropical-subtropical and notal types of habitat are distributed in the north periphery of the ACC (Sub-tropical Convergence which at the same time is a northern boundary of the Southern Ocean). These species do not, as a rule, reach the Antarctic Convergence. Species with notal-Antarctic and Antarctic types of the

habitat are distributed in the principal stream of the ACC, in the Antarctic Convergence and, to the south of it, in the Polar frontal zone, the medium position of which is located between  $50^{\circ}$  and  $60^{\circ}$ S in the Atlantic Southern Ocean, between  $50^{\circ}$  and  $55^{\circ}$  S in the Indian Ocean and between  $57^{\circ}$  and  $61^{\circ}$ S in the Pacific Southern Ocean (Gordon, 1971; Sarukhanyan, 1980). The Antarctic and even notal-Antarctic species can penetrate to fairly high latitudes of the Antarctic (up to  $68^{\circ}$ - $70^{\circ}$ S) in southward moving streams of the ACC. Scientists observe cases where fragments of bodies or intact bodies of squids are found in the stomachs of sperm whales and seals in high latitudes. Several cases of captures of some species with midwater fishing gear are registered (Filippova, Yukhov, 1979; 1982; 1983; Yukhov, 1982; Clarke and MacLeod, 1982). This penetration of squids into high latitudes of the Antarctic is facilitated to a considerable extent by powerful quasi-stationary eddies induced in the ACC system (and for some species the phenomenon seems to be expatriation from the centre of their habitat). The position of eddies of bottom-topographic origin is ascertained in the Drake Passage, Scotia Sea and its adjacent northeast area from the; in the Indian Ocean between Africa and the coastal Lasarev, Riser-Larsen, Kosmonavtov and Sodruzestvo Seas; in the Pacific in waters adjacent from the north to the Ross, Amundsen and Bellingshausen Seas (Sarukhanyan, 1980).

It is fairly safe to say that neither Antarctic nor notal-Antarctic squids of the Southern Ocean can live in cool coastal Antarctic waters because their habitat is the Antarctic Deep Warm Water Mass. At the same time the investigations indicate that this water mass is strongly transformed in the coastal areas due to supercooled shelf waters, loses its characteristics and is not observed any more in the vertical structure of water column (Gordon, 1967; 1975; Deacon, Moorey, 1975; Ledenev, 1969; Foster and Garmack, 1976; Sarukhanyan, 1981).

Rare cases of squid captures with midwater fishing gear during the long-term period of research and indirect data on the distribution and feeding habits of sperm whales in the Southern Ocean provide evidence that this group of species of nekton animals is very scarce in the Antarctic waters south of  $60^{\circ}$ S. In view of the fact that many species of meso- and

bathy-pelagic squids are the main food species of sperm whales in the Antarctic, the relative abundance of squids can be evaluated from the distribution pattern of sperm whales in summer which feed only in places where cephalopods are concentrated (Berzin, 1971; Klumov, 1971).

Long-term investigations of the biology and ecology of the sperm whale and the analysis of all available data, published material and catch statistics of the International Whaling Commission (IWC), summarised in Berzin's monograph (1971), indicate that sperm whales are mainly distributed latitudinally in the zone between  $40^{\circ}$ - $60^{\circ}$ S. It is noted that south of  $60^{\circ}$ S only the large-size solitary male occurs, which constantly moves from area to area and does not gather in groups. Empty whale stomachs are frequently observed which is believed to be the result of unfavourable conditions involving low abundance and species composition of cephalopods (Kirpichnikov, 1949; 1950; Korabellnikov, 1959; Arsenyev, 1969; Berzin, 1971).

Although the area of the mass distribution of sperm whales in the Antarctic is confined to  $60^{\circ}$ S, their habitat extends south of the Antarctic Convergence to  $60^{\circ}$ - $62^{\circ}$ S in the Atlantic and Indian Southern Ocean and to  $62^{\circ}$ - $66^{\circ}$ S in the Pacific (Berzin, 1971). Therefore, not only the area of mass distribution of sperm whales, but their whole habitat in fact is within the boundaries of the principal stream of the ACC. As was shown previously, the principal stream area differs greatly from other areas of the South Antarctic. It is influenced by the circulation systems of the coastal seas, by the climatic conditions, by the oceanographic and biological structure and therefore, it may be described as a "natural zone of open Antarctic waters" in contrast to a "natural zone of drifting ice" (Lubimova, 1982; 1983; 1984).

It is ascertained that the area of the principal stream of the ACC, which corresponds to the natural zone of open Antarctic waters, and particularly the Polar Frontal Zone is the centre of the habitat of mass plankton-eating mesopelagic species of fish, family Myctophidae. The fish feed on abundant copepod plankton in the 500-600 m layer, the secondary production of which amounts to up to 1.2 milliard tons a year. This type

of fish also prevails in the area in terms of biomass (Lubimova, Makarov, Shust, Lisovenko, Zemsky, Studenetskaya, 1983; Lubimova, Shust, Troyanovsky, Semenov, 1983).

Analysis of the stomach contents of squids of families Onychoteuthidae, Cranchiidae and others which are regular food components in the diet of sperm whales and which are found in the stomachs of sperm whales and toothfish, indicates that squids feed mostly on mesopelagic Myctophidae (Yukhov, 1982). Consequently, the area with predominant biomass of notal-Antarctic and Antarctic meso- and bathy- pelagic squids coincides with the area where mesopelagic Myctophidae are in great abundance and where most sperm whales are distributed, since they usually feed in the areas where squids are concentrated. In other words, meso- and bathy- pelagic squids of the Southern Ocean represent one of the components of the biological structure of a large, fairly isolated mesopelagic ecosystem of the natural zone of open Antarctic waters, the trophic dynamics of which rests upon high secondary production of copepod plankton and the final link of the food web is represented by sperm whales, (Lubimova, 1985b). Besides sperm whales, the final link of the web is very likely to include the Southern Elephant Seal (Mirounga leonina) which is characterised as a notal-Antarctic species (Laws, 1977). In accordance with recent observations the diet of the Elephant Seal contains squids of Gonatidae and Onychoteuthidae (Clark and MacLeod, 1982).

At present it is impossible to determine the quantitative characteristics of trophic relations in the mesopelagic community of the natural zone of open Antarctic waters. In regard to such components of the trophic structure as mass mesopelagic Myctophidae, the first approximate assessment has been made of their quantitative distribution and biomass formed in the Polar Frontal Zone where they form schools (Lubimova, Makarov, Shust et al., 1983). There is information on the abundance of sperm whales in the Southern Hemisphere (statistics of IWC). An estimation of the annual secondary production of Antarctic copepods has also been obtained (Voronova, Menshutkin, Tseytlin, 1980). However, there are no direct quantitative data on meso- and bathy- pelagic squids in the Southern Ocean. Furthermore, it has been ascertained that there are no beaks of

squids in the bottom sediments south of the Antarctic Convergence. At the same time, the number of beaks found in the bottom sediments in the notal area ( $50^{\circ}$ - $30^{\circ}$ S) north of the Antarctic Convergence exceeds  $100/m^2$  and their number is up to  $10000/m^2$  in the Equatorial Zone (Belyaev, 1962). As it is known, this index is the most reliable for the assessment of the abundance of pelagic squids in some of the other areas of the World Ocean (Akimushkin, 1968; Zuev, Nesis, 1971). In view of the absence of beaks in the bottom sediments of the Antarctic it is possible to suggest two hypotheses : either all squids eaten by sperm whales migrate here from the sub-tropical and notal areas in the summer seasons, or the abundance of true Antarctic meso- and bathy- pelagic squids is very low.

Relying on the study of the spatial and quantitative distribution of pelagic cephalopods in the World Ocean, the well known Soviet malacologist Nesis (1983) distinguishes three latitudinal zones characterised by higher productivity and biomass of oceanic squids : boreal, equatorial and notal. They alternate with four latitudinal zones characterised by a lower biomass : Arctic, central north, central south and Antarctic. In the Southern Hemisphere the maximum biomass is observed in the Sub-tropical Convergence waters (Nesis, 1983), i.e. near the northern boundary of the Southern Ocean. Nesis made an attempt to assess the biomass and relative distribution of cephalopods in the World Ocean using food rations of specific predators (sperm whales and other marine mammals and birds). The cephalopod biomass in the World Ocean is estimated to be 2.2 milliard tons (Akimushkin, 1970), and the biomass of neritic-ocenic and oceanic squids is assessed at the level from 5-6 million tons (Moiseev, 1969) to dozens or hundreds of million tons (Gulland, 1970). According to the estimates made by Nesis the total consumption of pelagic cephalopods by predators in the World Ocean is 175-200 million tons from the present stock and 325-350 million tons from the initial stock. Using the annual P/B coefficient of 3.5-2.0, which related to pelagic cephalopods with a one- and two- year life span and a 50%-grazing factor, Nesis obtained a rough estimate of the total biomass of pelagic squids in the World Ocean which is equal to 115-150 million tons at the present rate of consumption and to 220-280 million tons at the maximum rate of consumption (Nesis, 1983).

It is difficult to say what portion of the total biomass of the mesopelagic community of the natural zone of open Antarctic waters is referred to squids, and as Nesis points out (1983), the the whole Antarctic area is characterised by a lower biomass of pelagic cephalopods. It is even more difficult to assess the abundance of squids occurring in high latitudes of the Antarctic south of 60°S, where the scale of long-term research of baleen whales and Antarctic krill is much broader but the information available on squids is so small.

The study of the biology of squids (feeding habits, reproduction, life history), regularities of spatial and quantitative distribution and assessment of their biomass in the Antarctic, are very important for the investigation of the structure and functioning of the Antarctic ecosystems and setting up monitoring. These problems may be resolved on the basis of the analysis of the factual data which can be collected in the course of wide-scale specific research expeditions. At first such investigations should be conducted in the North Antarctic, i.e. in the area influenced by the principal stream of the ACC which corresponds with the natural zone of open waters, and particularly in the Antarctic Convergence. The area may turn out to be the closest (in terms of productivity) to the region near the Sub-tropic Convergence which is known for a higher biomass of meso- and bathy- pelagic squids. The reasons may be the well known similarity in such important environmental factors as horizontal and vertical circulation of waters, the heat content in the midwater and the character of bioproductive processes at the initial level of the productive cycle (Lubimova, 1982; 1983; 1985a). It does not seem to be accidental that most species of meso- and bathy- pelagic squids occurring in the Antarctic are known for their subtropical-notal and notal-Antarctic habitats. Special attention should be paid to the notal-Antarctic small-sized squid Brachioteuthis risei which penetrates into the northern part of the Scotia Sea and into the waters off South Georgia where the abundance of squid seems to be fairly high. Besides, this squid inhabits the meso- and epipelagic layer and can feed, to some or other extent, on mass Antarctic euphausiids, such as the relatively deep-sea Euphausia triacantha and E. superba brought here by the Weddell Sea current. In their turn, the squid can be a food component in the diet of numerous birds, southern fur seal (*Aretocephalus gazella*), southern elephant seal (*Miorounga leonina*) and baleen whales on their migration routes to the high Antarctic.

It is worth noting that efforts should be concentrated on the study of the highly productive area where the southern components of the ACC interact with waters of the High-Latitude Modification of the coastal seas. This area is situated in the high Antarctic, south of  $60^{\circ}\text{S}$ , in the region of cyclonic quasi-stationary circulation systems associated with coastal seas. The area corresponds with the natural zone of drifting ice. The area can be comparatively easily found by the high horizontal deep-sea maximum temperature gradient, by the maximum horizontal gradient in the distribution of Si and Si/P (Maslennikov, 1980; Arzhanova, Mikhaylovskij, 1980; Bogdanov, Solyankin, Rodionov, 1980). In accordance with the analysis of data on the distribution of squids of the Southern Ocean, only a few species penetrate into the high latitudes of the Antarctic, up to  $67^{\circ}$ - $69^{\circ}\text{S}$ . Judging from direct captures of some specimens and findings in the stomach contents of seals of ice forms it is possible to note that such meso-bathy-pelagic squids as Kondakovia longimana, Alluroteuthis antarcticus, Psychroteuthis glacialis can play a certain, unknown at present, role in the trophic dynamics of the ecosystem of this natural zone. As mentioned above, these species can rise into the lower epipelagic layer and can therefore feed on Antarctic krill in places of its heavy abundance. When they are in the lower epipelagic and upper mesopelagic layers, at the depths of 300-400 m (Kooyman, 1966; Yukhov, 1982) they can be a food component in the diet of Southern Toothfish, Weddell and Ross seals. At the same time, it is important to ascertain whether these species of squids are permanent inhabitants of the natural zone of drifting ice, whether they migrate from relatively low latitudes of the Antarctic, or penetrate into the high latitudes with the southern components of the ACC in the layer of the Antarctic Deep-sea Warm Water Mass. It is worth recalling that the coastal seas and the adjacent areas up to  $58^{\circ}\text{S}$  in the Atlantic Southern Sea, up to  $60^{\circ}$ - $61^{\circ}\text{S}$  in the Indian Ocean and up to  $64^{\circ}$ - $67^{\circ}\text{S}$  in the Pacific Southern Ocean in the autumn-winter period are covered with ice, and as a result the midwater is supercooled and extreme conditions are formed for these warm-water animals.



Table 1

The species composition of squids occurring in  
the Southern Ocean (from Filippova, Yukhov, 1979)

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| Families                | Species  |
|-------------------------|--|
| <u>Onychoteuthidae</u>  | Moroteuthis ingens (Smith, 1881)<br>Moroteuthis knipovitchi (Filippova, 1972)<br>Kondakovia longimana (Filippova, 1972)  |
| <u>Cranchiidae</u>      | Mesonychoteuthis hamiltoni (Robson, 1925)<br>Galiteuthis glacialis (Chun, 1906)<br>[Synon. Crystalloteuthis glacialis (Chun, 1906) and<br>Galiteuthis asper (Filippova, 1972) - Nesis's<br>recent data (1982)]<br>Taonius pavo (LeSueur, 1821) |
| <u>Histioteuthidae</u>  | Histioteuthis atlantica (Hoyle, 1885)<br>Histioteuthis eltaninae (N. Voss, 1962)<br>Parateuthis tunicata (Thiele, 1921 <sup>x</sup> )  |
| <u>Gonatidae</u>        | Gonatus antarcticus (Lønberg, 1898)  |
| <u>Neoteuthidae</u>     | Alluroteuthis antarcticus (Odhner, 1923)   |
| <u>Psychroteuthidae</u> | Psychroteuthis glacialis (Thiele, 1921)  |
| <u>Brachioteuthidae</u> | Brachioteuthis riisei (Steenstrup, 1882)   |
| <u>Bathyteuthidae</u>   | Bathyteuthis abyssicola (Hoyle, 1885)  |
| <u>Batoteuthidae</u>    | Batoteuthis scolops (Young and Hoper, 1968)  |

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<sup>x</sup> Parateuthis tunicata (Thiele, 1921) is included in the present list arbitrarily because the species was described only by two larvae with mantles 5-8 mm long caught at a depth of over 2000 m in Antarctic waters and since that time no specimens have been encountered. According to the data available, the larvae do not belong to any known family of Oegopsida (the family Insertae sedis according to Nesis, 1982).

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Lista de Cuadros

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