DETERMINATION OF GROWTH AND RELATED PHENOMENA IN *ILLEX ILLECEBROSUS ILLECEBROSUS* (LESUEUR) (DECAPODA: CEPHALOPODA) FROM NEWFOUNDLAND

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by

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ABSTRACT

Sampling of the short-finned squid, Illex illecebrosus illecebrosus was undertaken during October and November, 1965; and July through October, 1966, at Holyrood, Conception Bay, Newfoundland. A total number of 1,262 squid was involved in the study of growth, sexual maturity, food, and various morphometrical indices associated with growth. From these squid, 400 mandibles were chosen to study with respect to the morphometry, pigmentation, and possible growth marks.

Monthly samples show an increase in mantle length from July through October. A decrease in the mantle length occurs in the November samples, suggesting the appearance of a younger generation or second population. It is proposed that the spawning season for this species is from December through May of the following year. The spawning ground is postulated to be in the deeper water (i.e., 200 fathoms) of the various bays, or the deep water on the adjacent continental shelf.

Analyses of the gastric and caecal contents indicate that fish is the main item in the diet. Cannibalism is found to be predominant in larger squid late in the inshore season. The wide variety of food items found in the alimentary canal, suggests that this squid demonstrates little selectivity in choice of prey.

Morphometric indices HLI, HWI, MWI are found to decrease as the animal grows, indicating the growth of this animal is faster in length than in width. Index MEI also decreases as the animal grows, indicating

the rapid development of the gonad and liver in this animal during its inshore migration. The decrease in MEI differs in rate with sex beyond a mantle length of 195 mm. in that the males mature earlier. The fin configuration is maintained unchanged throughout the size range studied, and therefore is identical in growth pattern to that described elsewhere for Lolliguncula brevis.

The mandibles present an interesting field of future study. The growth of the mandible is isometric and detailed analysis indicates that a more valid relationship can be demonstrated between the size of the mandible and mantle length, than can be between mandible size and total body weight. The pigmentation of the wing of the lower mandible was studied by microprojection and microplanimeter and it is evident that a major change in the degree of pigmentation is correlated with an increase in mantle length, gonad weight and the advent of sexual maturity in both sexes.

Microrings have been found on both the lateral wall of the lower mandible and as concentric lines in the otolith. Although the number of these mandibular microrings increases with size of the mandible, and therefore with age and maturity of the squid, no pattern or cyclic nature to their groupings could be distinguished at this time.

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INTRODUCTION

1. Historical Summary

The short-finned squid was first described by LeSueur (1821) as _Loligo illecebrosa_. LaPylaie (1825) studied the common squid in the Newfoundland area, not knowing the previous designation, and suggested the name _Loligo piscatorum_ for the species. The present generic name, _Illex_, was erected in 1880 by Steenstrup to include the common European form (_coindetii_) which was considered as a subspecific form of _illecebrosus_ (Bigelow, 1926; Grimpe, 1933). Numerous fragmental descriptions and various synonyms have appeared in many publications, which makes the survey of the literature time-consuming and difficult. Undoubtedly, some references have escaped the writer's notice. The following list of the synonyms used by various authors for this species is based in large part upon Pfeffer (1908), Grimpe (1933), Adam (1952) and Voss (1956):

	Designation	Author
1821	_Loligo illecebrosa_	LeSueur
1823	_Loligo brogniartii_	de Blainville
1825	_Loligo piscatorum_	LaPylaie
1825	_Loligo sagittata_	de Blainville
1835	_Loligo brogniartii_	Férussac and Orbigny
1837	_Loligo coindetii_	Vérany
1839	_Ommastrephes sagittatus_	Férussac and Orbigny
1844	_Loligo coindeti_	Philippi
1844	_Loligo sagittata_	Philippi

	Designation	Author
1845	Ommastrephes sagittatus	Orbigny
1848	Ommastrephes sagittatus	Férussac and Orbigny
1849	Ommastrephes sagittatus	Gray
1851	Loligo coindetii	Vérany
1851	Loligo sagittata	Vérany
1851	Loligo pillae	Vérany
1852	Ommastrephes sagittatus	Forbes and Hanley
1869	Ommatostrephes sagittatus	Jeffreys
1867	Ommastrephes sagittatus	Fischer
1869	Ommastrephes sagittatus	Targioni-Tozzetti
1882	Ommastrephes illecebrosus	Verrill
1875	Ommastrephes sagittatus	Fischer
1879	Ommastrephes coindetii	Tryon
1880	Ommastrephes sagittatus	Stossich
1880	Ommastrephes coindetii	Steenstrup
1880	Ommastrephes sagittatus	Steenstrup
1880	Illex coindetii	Steenstrup
1881	Illex illecebrosus	Verrill
1882	Illex illecebrosus	Verrill
1890	Ommastrephes coindetii	Norman
1890	Ommastrephes coindetii	Girard
1890	Illex illecebrosa	Girard
1890	Illex illecebrosa	Norman
1890	Illex illecebrosa	Carus

	Designation	Author
1890	*Illex coindetii*	Posselt
1890	*Illex coindeti*	Carus
1891	*Illex illecebrosa*	Lönnberg
1891	*Illex coindeti*	Lönnberg
1890	*Illex illecebrosa*	Posselt
1894	*Illex illecebrosus*	Joubin
1896	*Illex illecebrosa*	Jatta
1896	*Illex coindeti*	Jatta
1896	*Todaropsis veranyi*	Jatta
1900	*Illex illecebrosa*	Pfeffer
1902	*Illex coindeti*	Hoyle
1905	*Illex coindetii*	Lozano and Rey
1908	*Illex coindeti*	Tesch
1909	*Illex coindetii*	Lo Bianco
1912	*Illex illecebrosus coindetii*	Pfeffer
1913	*Illex illecebrosus*	Chun
1916	*Illex coindeti*	Naef
1920	*Illex illecebrosus*	Joubin
1921	*Illex coindeti*	Naef
1921	*Illex illecebrosus coindeti*	Grimpe
1922	*Illex coindetii*	Grimpe
1923	*Illex coindeti*	Naef
1924	*Illex illecebrosus coindeti*	Grimpe
1925	*Illex illecebrosus coindeti*	Grimpe

	Designation	Author
1925	Illex illecebrosus coindeti	Degner
1926	Illex coindeti	Robson
1931	Illex coindeti	Robson
1932	Ommatostrephes coindetii	Nobre
1932	Illex illecebrosa	Frost and Thompson
1933	Illex illecebrosus	Grimpe
1933	Illex illecebrosa	Frost and Thompson
1934	Illex illecebrosus	Frost and Thompson
1936	Ommastrephes coindetii	Nobre
1936	Illex coindeti	Bouxin and Legendre
1938	Illex coindeti	Desbrosses
1942	Illex coindetii	Adam
1944	Illex illecebrosus coindeti	Stephen
1950	Illex coindeti	Dieuzeide
1951	Illex coindeti	Adam
1952	Illex illecebrosus illecebrosus	Adam
1955	Illex illecebrosus	Voss
1956	Illex illecebrosus	Voss
1957	Illex illecebrosus	Squires
1959	Illex illecebrosus	Squires
1960	Ommastrephes argentinus	de Castellanos
1963	Illex illecebrosus illecebrosus	Mangold-Wirz
1964	Illex illecebrosus illecebrosus	Aldrich
1964	Illex illecebrosus argentinus	de Castellanos
1965	Illex illecebrosus illecebrosus	Mercer
1966	Illex illecebrosus	Zuev

	Designation	Author
1966	Illex illecebrosus illecebrosus	Brown, et al.
1967	Illex illecebrosus illecebrosus	Squires
1968	Illex illecebrosus illecebrosus	Aldrich and Bradbury
1968	Illex illecebrosus illecebrosus	Aldrich, et al.
1968	Illex illecebrosus illecebrosus	Aldrich and Lu
1968	Illex illecebrosus illecebrosus	Aldrich

According to Voss (1956), the taxonomic position of the species is:

Phylum	Mollusca
Class	Cephalopoda
Order	Decapoda
Family	Ommastrephidae
Genus	Illex
Species	I. illecebrosus

There are three subspecies now recognized. Illex illecebrosus illecebrosus (LeSueur) of the Northwest Atlantic, and Illex illecebrosus coindeti (Verany) of European waters were erected by Pfeffer (1912). Voss (personal communication to de Castellanos, 1964) suggests that Ommastrephes argentinus de Castellanos of the Southwest Atlantic should be considered as the third subspecies and to be designated Illex illecebrosus argentinus (de Castellanos). Abbott (1954) proposed that "Further study may show that the genus Illex is the same as Ommastrephes Orbigny 1835". However, many competent cephalopod systematists, notably Dr. G. L. Voss (personal communication to Dr. F. A. Aldrich) discount this, saying that

Illex and Ommastrephes are both perfectly valid genera.

Very little is known of this species, although much has been reported on other species of decapods of commercial importance. Frost and Thompson (1932, 1933, 1934) published the first discussions of the annual and geographic variations in their inshore-migrations, as well as the effects of hydrographic conditions on this squid in Newfoundland waters. Recently, Squires (1957, 1959) has reported on the distribution, relative annual abundance, growth, sexual maturity, food, parasites, and the annual migratory movements of Illex illecebrosus in this area. Dr. F. A. Aldrich (1964) reported the results of observations on the Newfoundland bait squid and the netting of the animal. Mercer (1965) repeated Squires' work and agreed with his previous results. Williamson (1965) published underwater observations which offered fragmentary knowledge on the behaviour of the species.

Since Cephalopods are soft-bodied animals subject to great change in shape due to different methods and degree of preservation, identification and evaluation of Cephalopods have been greatly facilitated through the use of precise measurements and proportional indices. Morphometric analysis would give information on the size range, possible age groups, differences between sexes, and trends in body proportions during growth of the animals. Verrill (1881), being the first one to use such ratios, compared the length of various parts of Loligo pealei to the mantle length. Pfeffer (1912) further established this system and expressed the relative size of various body parts as a percentage of either the mantle length or other parts. Since then, Robson (1929), Pickford (1945), Adam (1934, 1941, 1952), Voss (1954, 1956, 1963, etc), Haefner (1964) and Squires (1957) in various papers have used similar indices or have presented additional ones as the need arose.

Very little information is available on the growth of Cephalopods, since there are difficulties in keeping them alive in aquaria for extended periods. Furthermore, analysis of population samples is complicated by migrations. Growth of several continental shelf species has been studied by various authors, i.e., Todarodes sagittatus (Fridriksson, 1943), Loligo vulgaris (Tinbergen and Verwey, 1945), Loligo opalescens (Fields, 1950, 1963 and 1965), Illex illecebrosus (Squires, 1957), Ommastrephes sloani pacificus[1] (Otsuki and Araya, 1958; and Katoh, 1959, 1960 and 1964), and Eledone cirrosa (Wirz, 1963)[2]. Most recently, Squires (1967) has published a reworking of growth data on Newfoundland Illex illecebrosus illecebrosus.

Some workers have tried to determine methods of aging in Cephalopods, similar to otolith- or scale-reading in fish. Tinbergen and Verwey (1945) examined the beaks of Loligo vulgaris and Wirz (1963), the beaks and radulas of several Cephalopods for purposes of achieving criteria for aging. Yagi (1960b)and Choe (1963) studied certain species of the Sepiidae, concluding that the shell-stripe pattern of these cuttlefish increased with the age. Clarke (1965) described the cycles of growth indicated by "growth lines" or "microrings" on the lower beak of Moroteuthis ingens (Smith) and stated that the darkening of the beaks is related to sexual maturity of the animals (Clarke, 1962a, b, 1965 and 1966).

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[1] (=Todarodes pacificus)

[2] Mangold-Wirz (1963)

Various fragmentary studies on Cephalopod mandibles may be found in the literature. Early literature includes Verrill (1879-1882) where he described the mandibles of ten species. Later, Naef (1923) published careful drawings of the mandibles of representative species of several families. It was Clarke (1962b), however, who first published a specific study of mandibles, giving details of variation and changes he describes as being correlated with growth. Clarke went on to erect criteria by which the mandibles can supposedly be used as a basis for identification of several families of Cephalopods.

Since the information concerning mandibles is sparse and scattered at best, it was considered important to assemble some of the pertinent references here. A list of various authors who have published illustrations of the mandibles for different species of Cephalopods is given below.

Date	Author	Species
1879-82	Verrill	*Architeuthis* (5 species) *Histioteuthis collinsii*, *Loligo pealei* *Heteroteuthis tenera*, *Octopus bairdii*, *Stauroteuthis syrtensis*.
1881	Owen	*Enoploteuthis cookii*
1885	Hoyle	*Cirroteuthis magna*, *Octopus panctatus*, *Octopus marmoratus*.

Date	Author	Species
1896	Jatta	*Eledone moschata*, *Ocythoe tuberculata*.
1898	Steenstrup	*Architeuthis* sp., *Gonatus fabricii*, *Ommastrephes pteropus*, *Loligo forbesi*,
1910	Chun	*Spirula australis*.
1909	Williams	*Loligo pealii*.
1912	Berry	*Polypus bimaculatus*.
1914	Ishikawa	*Enoploteuthis chunii*.
1918	Berry	*Calliteuthis miranda*, *Loligo etheridgei*, *Sepia chirotrema*, *Opistoteuthis persephone*.
1923	Naef	*Chiroteuthis veranyi*, *Alloteuthis media*, *Loligo vulgaris*, *Sepietta oweniana*, *Octopus salutii*, *Octopus unicirrus*, *Eledone moschata*, *Ocythoe tuberculata*, *Argonauta argo*.
1924	Joubin	*Vitreledonella richardi*.
1932	Robson	*Grimpoteuthis meangensis*, *Haploclaena lunulata*, *Graneledone setobos*.
1941	Adam	*Loliguncula mercatoris*.

Date	Author	Species
1949	Thore	*Dorsopsis taningi*, *Eledonella pygmaea*, *Amphitretus pelagicus*, *Vitreledonella richardi*, *Alloposus mollis*.
1949	Pickford	*Vampyroteuthis infernalis*, *Octopus bimaculatus*.
1951	Dell	*Histioteuthis cookiana*.
1951	Voss	*Octopus burryi*.
1952	Dell	*Nototodarus sloanii*, *Sepioteuthis bilineata*, *Sepioloidea pacifica*, *Octopus maorum*, *Robsonella australis*, *Argonauta nodosa*.
1953	Voss	*Pickfordiateuthis pulchella*.
1954	Adam	*Grimpoteuthis* sp., *Meleagroteuthis hoylei*, *Stigmatoteuthis* sp.
1956	Voss	*Architeuthis physeteris*.
1962b	Clarke	*Sthenoteuthis caroli*, *Sthenoteuthis pteropus*, *Todarodes sagittatus*, *Todarodes eblanae*, *Illex coindeti*, *Illex illecebrosus*, *Ommastrephes sloanei*, *Hyaloteuthis pelagica*, *Symplectoteuthis oualaniensis*, *Onychoteuthis banksi*, *Ancistroteuthis lichtensteinei*, *Moroteuthis ingens*, *Histioteuthis bonelliana*,

Date	Author	Species
		Calliteuthis reversa, Calliteuthis döfleini, Architeuthis clarkei, Abraliopsis morisi, Enoploteuthis leptura, Pyroteuthis margaritifera, Octopodoteuthis sp., Cucioteuthis unguiculata, Thysanoteuthis rhombus, Gonatus antarcticus, Gonatopsis borealis, Chiroteuthis imperator, Mastigoteuthis magna, Lepidoteuthis grimaldi, Euzygaena sp., Helicocranchia sp., Phasmatopsis cymoctypus, Taonius megalops, Mesonychoteuthis hamiltoni, Loligo forbesi, Loligo vulgaris, Sepioteuthis sp., Sepioteuthis lessoniana, Rossia macrosoma, Sepia officinalis hierreda, Sepia officinalis, Sepia latimanus, Octopus vulgaris, Octopus indicus, Octopus macropus, Octopus arcticus, Eledone cirrhosa, Pareledone charcoti, Argonauti hians, Argonauta argo.
1962a	Voss[1]	See Footnote.
1962	Voss & Voss	Calliteuthis reversa, C. elongata, C. corona.
1965	Clarke	Moroteuthis ingens.
1966	Mangold and Fioroni	Illex coindetii, Todarodes eblanae, Todarodes sagittatus, Loligo vulgaris, Alloteuthis media, Sepia officinalis, Sepia orbignyana, Sepia elegans, Rossia macrosoma, Rossia caroli, Sepietta oweniana, Octopus vulgaris, Octopus salutii, Pteroctopus

[1] Lycoteuthis diadema, Oregoniateuthis springeri, Selenoteuthis scintillans.

Date	Author	Species
		tetracirrhus, *Bathypolypur sponsalis*, *Eledone cirrosa*, *Eledone moschata*.
1966	Zuev	*Illex illecebrosus*
1967	Voss	*Abraliopsis gilchristi*, *Chiroteuthis capensis*, *Pyrgopsis pacifica*, *Megalocranchia megalops australis*.
1968	Aldrich and Bradbury	*Illex illecebrosus illecebrosus*, *Gonatus fabricii*.

The present work deals with the biology of the mandibles of *Illex illecebrosus illecebrosus*, extending the knowledge of the relationship between mandible size and body size; mandible size and body weight. An attempt is made to correlate "growth lines" on the lower mandible with body size. Quantitative analyses of the darkened area on the wings have been carried out to test for correlation with sexual maturity. As a corollary of all this, data are presented on phenomena, sexual maturity and food, as well as morphometric changes in different size groups of *Illex illecebrosus illecebrosus*. Observations made on the fishery for the species and its general natural history are also presented.

2. General Description of the Species

The Animal

The main diagnostic characteristics of the short-finned squid, *Illex illecebrosus illecebrosus* are those of the genus, namely, that the funnel groove has no folds or pockets, the indistinct nature of the fixing apparatus on the tentacular arms, the strongly developed locking apparatus, the suckers on the club, and less certainly, the configuration of the hectocotylus.

The mantle is oblong and slender, tapering gradually toward the posterior. The fins are short, united posteriorly forming a right angle at the junction. The head is short and compact, being about the same in width as is the mantle.

The arms are stout, tapering to sharp points. In almost all cases, the arm formula is 2.3.4.1. The dorsal arms are keeled, while the third arms are equipped with a narrow swimming membrane. The tentacles are long and stout, with four rows of suckers on the hand, or palm, portion and eight rows on the distal portion. In Figure 1 are shown the external features of the squid.

The Mandibles

All living Cephalopods have two horny mandibles described as either "upper" or "lower" with respect to the functional dorsal or ventral side of the head. Both mandibles are partially embedded in a mass of muscle and are connected with the cephalic cartilages.

The terminology used to designate the parts and features of both mandibles has been described by Clarke (1962b). Figure 2 shows the configuration of both mandibles, the mandibles *in situ*, and the descriptive terms. Those terms used in this work will be described later.

Clarke (1962b) has derived a cataloging of mandibles belonging to squid of several families. For the Family Ommastrephidae (including I. illecebrosus) a description has been devised as follows:

(a) The upper mandible:

Hood not noticeably short, shoulder covered by cartilage, jaw

Figure 1. External features of the short-finned squid, Illex illecebrosus illecebrosus (LeSueur). a) dorsal view (functional), b) ventral view (functional).

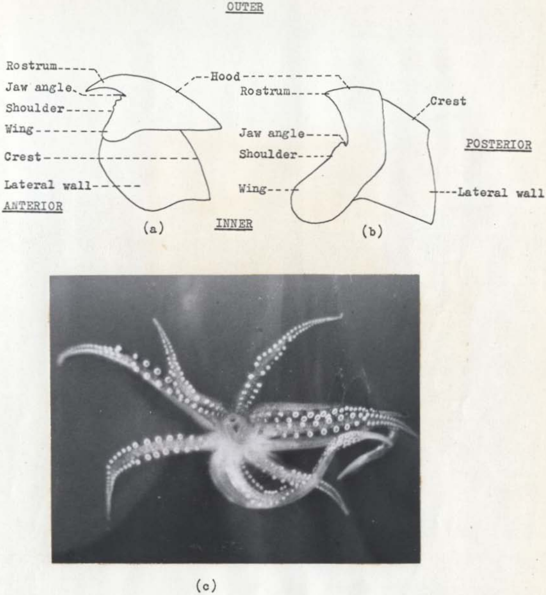

Figure 2. External features of the mandibles.

a) The upper mandible
b) The lower mandible
c) Mandibles in situ.
(a and b after Clarke, 1962b)

angle not clearly curved, no false angle, and the inner end of the wing is transparent and the outer edge of the transparent region is straight.

(b) The lower mandible:

A distinct jaw angle present, tip of rostrum is pointed. There is a clear strip between the medial surface of the wing and the anterior of the lateral wall; no ridge across the lateral wall but there may be a poorly-defined fold of the wall.

3. Distribution and Migration

Illex illecebrosus was reported by Verrill (1881) from Cumberland Sound, Nova Scotia, to Cape Hatteras, North Carolina. Bigelow (1926) reported that Loligo was the common genus south of Cape Cod, Illex north of Cape Ann, with the ranges of the two overlapping in Massachusetts Bay, Illex occurring as far south and west as the Woods Hole region. He described that Illex was very abundant from Massachusetts Bay northward to the shores of Newfoundland and Labrador, and believed that its numbers increased from southwest to northeast around the coasts of the Gulf of Maine. Later, Grimpe (1933) extended the range from Greenland to 35°34½'N, 47°48'W, a point south of Cape Hatteras. Voss (1955) reported this species in the Gulf of Mexico at a depth of 105 fathoms, and from Cuban waters.

It is known that pelagic squid are found in a wide range of depths, from the surface waters to a depth of 3500 metres (Marshall, 1954). Illex i. illecebrosus is usually caught at a depth of 10 to 15 feet beneath the surface, however, Aldrich (1964) netted them in schools at depths of 13 fathoms. It is presumed that Illex seldom extend to deep water, but when they remain offshore their vertical distribution is not known. It should be reiterated, however, that Voss (1955) found this species at 105 fathoms.

It is said that certain squid, in their oceanic environment, show diurnal migration since their euphausid food exhibit this behaviour (Fowler, 1905; MacDonald, 1927). Suzuki (1963) correlated the vertical migration of Todarodes pacificus (Steenstrup), a squid common in Japanese waters, with the diurnal migrations in the deep scattering layer (DSL) which consists mainly of crustacean zooplankton of the genera Euphausia and Parathemisto. He found that this squid fed more in the daytime than at night, presuming that they live in daytime in the DSL in which their food organisms are abundant. Hamabe (1964) reported that the vertical as well as horizontal migrations of this squid are active on moonlight nights, especially on the nights of the first and last quarters of the moon.

Since Illex is a fast-swimming species, horizontal migrations do obviously occur (Lane, 1960). In Newfoundland waters, they usually come inshore in late July and stay until October or November. However, they have appeared in inshore waters as early as June and remained as late as November. The migration course,according to Squires (1957, 1959), seems to originate from south of the Grand Banks in early May. As the season advances, they move northward to Holyrood, in Conception Bay; Fogo, Notre Dame Bay; and westward to Francois, on the southwest coast (Squires, 1957, 1959; Aldrich, 1964).

4. Fisheries and Abundance

"Oh! this is the place where the fishermen gather,
With oil-skins and boots and Cape-Anns battened down.
All sizes of figures with squid lines and jiggers,
They congregate here on the squid jiggin' ground."
-- "Squid-jiggin' Ground" by Arthur Scammel

As has been mentioned earlier, this squid ranges the entire length of the east coast of North America, especially in Newfoundland waters where it is most abundant. People in Newfoundland, with few exceptions, do not regard squid as food. However, squid plays an important role in the long-line fishery in this area. It is said that if the squid fails to arrive in large numbers, the cod-fishery would fail, and up to one-third of the year's catch is lost, because the squid is the main bait of this fishery in Newfoundland.

In Newfoundland, the traditional method of catching squid is by jigging. Squires has described it as follows:

> "(The jigger) is a lead weight shaped somewhat like a small squid but painted red, and with one end fitted with a circle of barbless hooks which are not painted. When the squid are plentiful, the 'jigger' is merely dangled over the side of the boat just below the surface of the water. When the squid rush at this moving object, the fisherman captures several with a deft sweep of a hand net. In this way he is kept busy dipping squid that rush

> at the jigger and does not bother to hook any. When the squid are scarcer, the jigger may have to be lowered a few fathoms, and jigging with occasional quick jerks may hook* any squid that comes near, whereupon it is hauled into the boat." (Quoted from Lane, 1960).

By means of the so-called Neyle's patent jigger (Figure 4), an individual fisherman may take 1,200 squid an hour when they are abundant. Recently, this hand-line jigger has been largely replaced by Japanese machines which consist of drum haulers, special lure hooks, and a light attraction system. It has been repeatedly demonstrated that this jigger is considerably more efficient (Figure 5).

The squid season begins soon after the first squid appear in inshore waters. Numerous boats congregate at the place (Figure 3). Fishing mostly takes place at hours of dawn and dusk, and at night. However, it is not unusual to encounter jigging during daylight hours.

Although _Illex_ is regarded to be plentiful in Newfoundland, annual fluctuations do occur. In some years they are extremely abundant in most coastal regions while in other years they are very scarce. Even in years of great abundance, they may only appear locally in certain areas. Local weather conditions as well as hydrographic conditions such as wind, rainfall, availability of food, water temperature, salinity and so on, are considered

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*Contrary to what Squires here says, squid are not necessarily "hooked" by the jigger but most often are caught due to the squid's arms and tentacles becoming fouled about the jigger. Furthermore, it is always observed that the squid follow the jigger, even to the extent of leaving the water.

Figure 3. Squid boats gather at the "squid jigging ground", Holyrood Bay, Conception Bay, Newfoundland. The newly adopted Japanese jigging machines can be seen on these boats.

Figure 4. A "Neyles Patent" squid jigger, weighing 110 grams and measuring 9 centimeters in length. These are traditionally painted red.

Figure 5. An operating Japanese jigger, showing a squid jigged, as used on the M.V. MARILYN MARIE in Conception Bay, Newfoundland.

as factors influencing squid abundance (Miyamoto, 1935; Kojima, 1956; Nagata, 1957; Squires, 1957, 1959; Hodder, 1964; Aldrich, 1964).

During the course of this study, according to our records, the squid season of 1965 lasted until mid-November. In 1966, the first squid was not caught until July 15th, and the season ended effectively in early November. Fishermen in Holyrood Bay (one of the "traditional" squid jigging grounds) reported no squid jigged after November 7th. This late-coming and early-leaving migration in 1966 seems to agree with the postulation of Frost and Thompson that the "leanest" years, based on data accumulated from 1914 to 1932, occurred at intervals of from four to eight years (Frost and Thompson, 1932).

5. Predators

As stated by Lane (1960): "More marine animals prey on squids than on all other Cephalopods combined". The predators range from Antarctic penguins to the huge sperm whale, Physeter catodon L. Akimushkin (1955) reported 28,000 undigested mandibles from one sperm whale.

The main predator of Illex is reported to be the pilot, or pothead, whale, Globicephala melaena (Traill). Sergeant (1962) described:

> "In observations from 1951 through 1956 no food organisms were observed except short-finned squid Illex illecebrosus LeSueur. This period corresponded with a cycle of abundance of squid inshore, when large catches of squid and pilot whales were made by man.
>
> In late August of 1957 the squid rather rapidly disappeared

> from inshore waters, presumably as the result of some unfavourable hydrographic or planktonic conditions which remain unknown. The majority of the pilot whales followed the squids; those few that remained were reported to contain cod, Gadus morhua L. in their stomachs. In 1958 squid were scarce and few pilot whales were taken; they were again reported to be feeding on cod. In 1959 pilot whale stomachs examined early in the season contained squid with a proportion of cod, but no other fish."

He concluded that squid are the preferred food of pilot whales, with fish as an alternative. However, Aldrich and Bradbury (1968), although not denying the importance of I. illecebrosus in the diet of the pilot whale, demonstrated that other squid, namely, the Arctic squid Gonatus fabricii, are preyed upon by these cetaceans in Newfoundland waters.

Vladykov (1946) reported that in the Beluga or white whales, Delphinapterus leucas (Pallas), the female shows a preference for Illex as food. Squires (1957) contemplated that herding of the squid by large aquatic mammals may account for localized migrations of Illex.

Many sea birds feed on Illex as well. The Greater Shearwater, Procellaria gravis O'Reilly, was reported consuming large numbers of Illex. In an observation made by E. I. S. Rees (1961), nine of thirty-eight (24 percent) contained squid in their stomachs.

Additionally, sharks, tuna, cod, and some other large fish in this area generally take squid as food. A blue shark, Prionace glauca (L.)

4.2 feet in length, has been found with more than 30 squid mandibles in the stomach (Templeman, 1963). The author has found 120 mandibles in a bluefin tuna, *Thunnus thynnus* (L.) from Conception Bay in July, 1966.

MATERIALS AND METHODS

Sampling Method

A random sample of 448 squid was obtained from October 11 to November 12, 1965 from Conception Bay. From July 15 to October 13, 1966, sampling was carried out at about weekly intervals at Holyrood, Conception Bay. A total of 814 squid were obtained. All samples were taken by means of a Japanese jigging machine by the author and his colleagues in the Department of Biology, Memorial University of Newfoundland. Figure 6 shows the location where samples were taken.

During the course of this study, therefore, a total of 1,262 squid were sampled and examined. Squid taken in 1965 were preserved in 40 percent isopropyl alcohol for later examination. Those taken in 1966 were examined in either fresh or frozen condition.

From these squid, a random sample of 400 mandibles was chosen for examination and measurement.

Measurements

(a) Body Measurements

All measurements were carried out by using a uniform method. Lengths were measured on a board marked in millimeters. For the lengths of tentacles and arms, an ordinary centimeter ruler was used. Mantle length was used as the standard length for comparison and calculation. The morphological dorsal extremity of the mantle was placed against the head of the measuring board, and the length was estimated dorsally

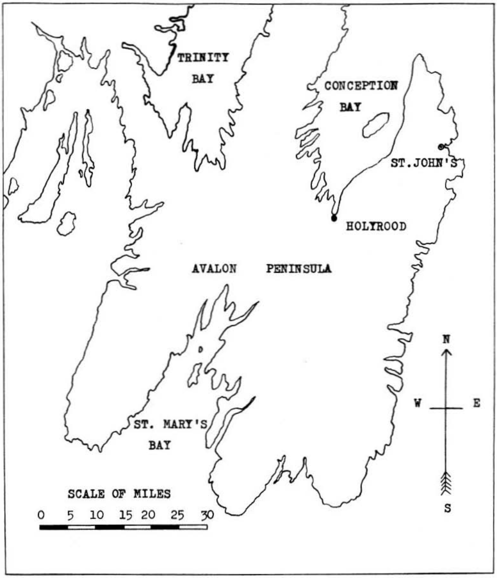


Figure 6. Location where squid samples were obtained.

(functionally). A protractor was used for measuring the fin angle to the nearest degree.

Weights were taken on a laboratory balance with an accuracy of ± 1 gram. Before weighing, the specimen was placed on a board and excess fluid inside the mantle withdrawn. Paper towels were used to wipe the body surface. All weights were measured in grams.

Since squid show a less than 3 percent loss of body weight in formalin (Squires, 1957) all weights (i.e., those of preserved, fresh and frozen specimens) were considered comparable.

Twenty-two morphometric characters were observed and recorded. In Table I and Figure 7 are presented those measurements and indices which have been used by various authors (Voss, 1956; Soeda and Araya, 1958; and Haefner, 1964), and are the basis of this study.

(b) Mandible Measurements

All mandibles used for this study were dissected from squid which were used in other phases of the study, and the pertinent data carried with them throughout the study. Terms and measurements for the mandibles used followed Clarke (1962b, 1965). In Figure 8 are indicated the measurements taken.

A microprojector (Bausch & Lomb Optical Co., Type 42-63-59) was employed for the quantitative analysis of the darkening in the "wings" of the lower mandibles. The image of a wing was projected on a plain surface and then traced. From this tracing the darkened area was calculated

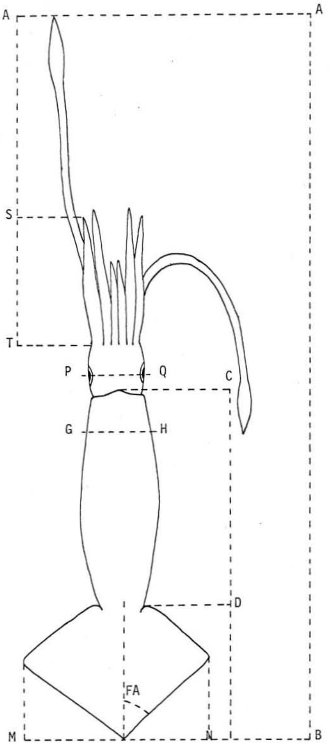
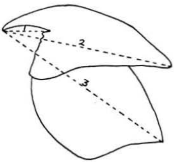
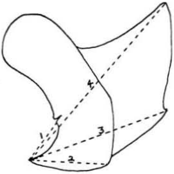


Figure 7. Diagram illustrating measurements used in this study.



a. Upper Mandible



b. Lower Mandible

Figure 8. The mandibles of *Illex illecebrosus illecebrosus*, indicating the measurements used in this study. 1: rostral length. 2: hood length. 3: crest length. 4: wall length.

Table I. Morphometric characters and indices used.

Measurements

ML - Mantle length, from distal protuberance of the mantle to the posterior extremity, C to B in Figure 7. Mantle length is sued as standard length throughout this work.

MW - Mantle width, G to H, at greatest width.

HW - Head width, measured across the eyes, P to Q.

HL - Head length, from the anterior protuberance of the mantle to the base of dorsal interbrachial area, T to C.

FL - Fin length, from anterior border to posterior border, or the point of union of the fins, D to B.

FW - Fin width, greatest distance across the fin, M to N.

ARMS I, II, III, IV - Length of arms, dorsal, dorsolateral, ventrolateral, and ventral respectively; measured from first basal sucker to distal extremity of the arm, S to T.

TL - Total length, from tip of tentacles to posterior end of mantle, A to B.

WE - Wet weight of the entire animal.

WM - Wet weight of the mantle alone.

PL - Pen (gladius) length.

Table I (continued)

Measurements

PW - Greatest width of the pen.

SW - Width of the siphon.

SL - Length of the siphon

GL - Length of gill, measured from point of union with the branchial heart to distal extremity of the gill.

T - Length of tentacle, measured from base of tentacle to its distal extremity, A to T.

FA - Fin angle, angle that trailing edge of fin makes with an imaginary line along mid-line of mantle.

VG - Gonad volume.

Liv. W - Wet weight of liver.

Indices

HWI - Head width expressed as a percentage of mantle length.
HLI - Head length expressed as a percentage of mantle length.
MWI - Mantle width expressed as a percentage of mantle length.
FLI - Fin length expressed as a percentage of mantle length.
FWI - Width of both fins expressed as a percentage of mantle length.
MEI - Mantle weight expressed as a percentage of entire weight.
FL/FW - Ratio of fin length to fin width.
PL/PW - Ratio of pen length to pen width.

as a percentage of the total area of the wing, using a Polar Planimeter.

The lateral wall of the lower mandibles were used to study the growth lines observed. The sample here was 317 mandibles.

Sex and Maturity

All squid were examined upon dissection for sex and sexual maturity. Gonad volumes were measured by displacement of water in a 10 ml. graduated cylinder. Conversion factors obtained by previous authors (Squires, 1957; Mercer, 1965) were used to convert volume to weight, i.e., 1.1 gm./c.c. for testes and 1.0 gm./c.c. for ovaries.

Presence of spermatophores in Needham's sac in males and ripe eggs in the oviduct in females were used as the criteria of maturity.

Food Analysis

The contents of stomach and caeca of all specimens were examined. However, no systematic analysis was made owing to the partially digested nature of the food materials.

What statistical analyses that were done were by methods following those presented in Simpson, *et al.* (1960).

RESULTS

Size and Sexual Maturity

(a) Size

The longest continuous series of data was obtained for the period July to October, 1966. The monthly average mantle lengths for each sex are shown in Figures 9 and 10. The average mantle length increased from approximately 190 mm. in July to 240 mm. in October for males, and from approximately 190 mm. to 265 mm. for females over the same period.

Likewise, the average body weight for males increased over this same period from approximately 120 grams in July to approximately 265 grams in October, while for the same period females increased from approximately 120 grams to 350 grams (Figure 11).

However, the data obtained in 1965 are quite different. Data on the November samples indicate a decrease in both mantle length and body weight. The average mantle length for males was 235 mm. as compared to 242 mm. for October. The average mantle length for females was 255 mm., while it was 265 mm. in October. The average body weights for males and females (1965, November) were approximately 255 grams and 308 grams, respectively. This represents a decrease from the October values of 265 grams and 350 grams for males and females respectively (Figures 9, 10 and 11).

Males and females differ in total body weight and mantle length. In the size range studied, males larger than 195 mm. are heavier than

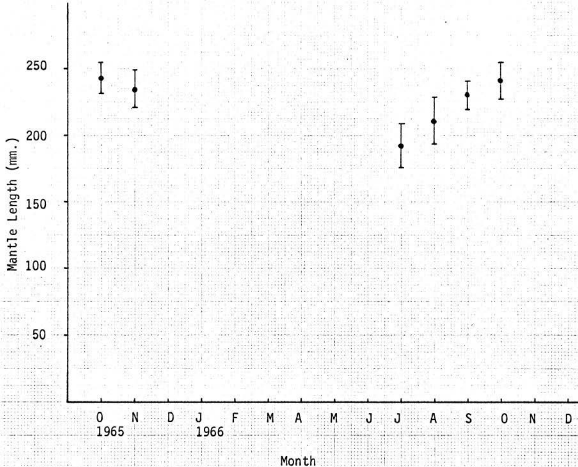


Figure 9. Average mantle length, with standard deviation, of male Illex illecebrosus illecebrosus, over the sampling periods of 1965 and 1966.

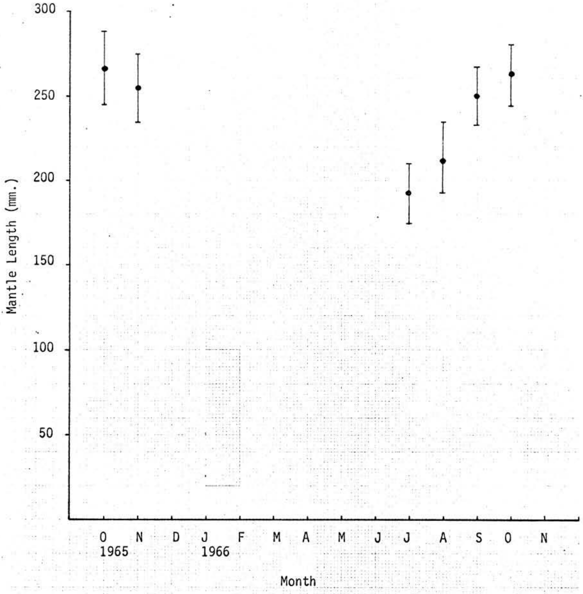


Figure 10. Average mantle length, with standard deviation, of female Illex illecebrosus illecebrosus, over the sampling periods of 1965 and 1966.

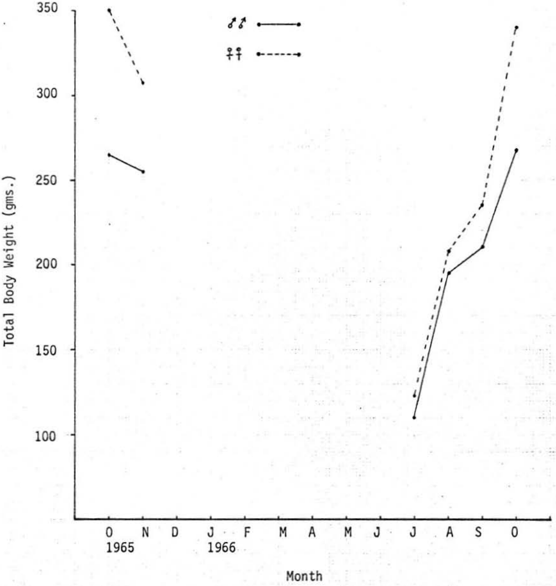


Figure 11. Average body weight of Illex illecebrosus illecebrosus taken at Holyrood, Conception Bay.

females of the same length. However, the females are longer than the males (Figure 12).

(b) Sexual Maturity

In both sexes it was observed that the gonads were not well developed. The ovary weights, as computed from volume determinations, ranged throughout the sampling periods of 1965 and 1966 from 0.1 to 4.0 grams. No mature or near-mature females were found*.

In the September (1966) and October (1965 and 1966) samples, fewer than ten mature males were found. One of these, measuring 240 mm. in mantle length, had a spermary weighing 11.5 grams.

With respect to the incidence of the two sexes in the monthly samples, this information is summarized and presented in Table II. From this datum,the ratio of males to females could be calculated. Of the 1,262 squid examined, 39.38 percent were males.

Food

The gastric and caecal contents were roughly classified into those containing (a) crustaceans, (b) fish, (c) cephalopod molluscs, and (d) unidentified colloidal substances. In Table III is presented the incidence (in percentage) of various foods present in different size groups of the squid examined.

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*The first incidence of sexually mature female _I. i. illecebrosus_ was noted by Dr. F. A. Aldrich's group in the late autumn of 1967, after this study was terminated.

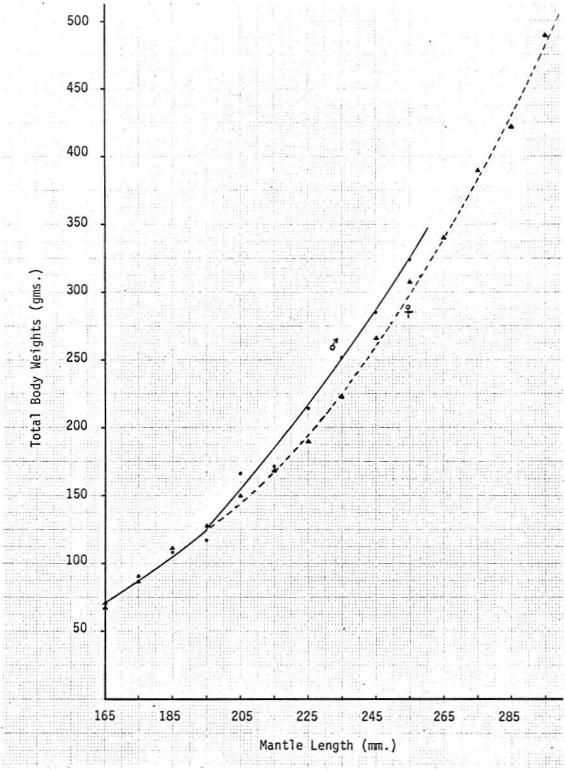

Figure 12. Average weights of male and female <u>Illex illecebrosus illecebrosus</u> of various mantle lengths.

Table II. Percentage of respective sex in monthly samples.

Month	Year	No. examined	Male No.	Male %	Female No.	Female %
October	1965	215	77	35.81	138	64.19
November	1965	233	96	41.20	137	58.80
July	1966	204	95	46.57	109	53.43
August	1966	275	116	42.18	159	57.82
September	1966	188	68	36.17	120	63.83
October	1966	147	45	30.61	102	69.39
TOTAL		1,262	497	39.38	765	60.62

Table III. Gastric and caecal contents of <u>Illex illecebrosus illecebrosus</u> in samples studied.

	Mantle Length (mm.)					
	145-165	175-195	205-225	235-255	265-285	295-315
No. of squid examined	16	27	113	281	128	19
No. of squid with food	13	23	74	206	102	19
Frequency of occurrence as food (%):						
Crustacea	23	9	20	30	27	21
Fish	39	35	45	39	32	32
Cephalopod	15	26	27	41	54	47
Unidentified	31	35	20	8	8	16
Squid with more than one kind of food (as % of number of squid with food):	15	13	7	18	19	16

In most cases, contents were digested beyond recognition. However, fish were recognized by remains of hard tissues such as vertebrae and vertebral spines, otoliths, and scales. Crustaceans were distinguished by chitinous exoskeletal fragments and parts of appendages. Cephalopods were identified by fragments of mandibles, chitinous rings of suckers, remains of arms and mantles, and pigmented integument.

Fish were the main diet for the range of sizes studied. Apparently, cannibalism was markedly evident, especially in squid larger than 260 mm., late captures in the season. Crustaceans were also abundant.

Morphometry of Growth

Six important morphometric indices, following Haefner (1964), of separate sexes and both sexes combined are shown in Figures 13 through 29. These were computed using the data achieved from measurements and are indicated in Figure 7.

No sexual dimorphism is indicated, except in the case of the index MEI which demonstrates a difference between the two sexes. Of the six indices, four (HWI, HLI, MWI, and MEI) decrease with an increase in the size of the individual, while two (FWI and FLI) increase with an increase in size. In Tables IV and V are presented some measurements and computed indices of the largest and smallest specimens studied.

The decrease of HWI, HLI, and MWI with age indicate that both the head and the mantle increase in length at a faster rate than they do in width.

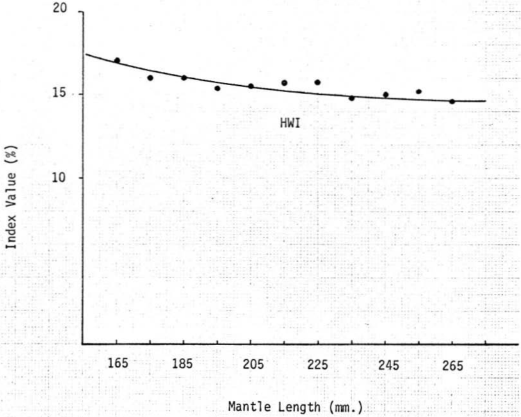

Figure 13. Change in value of morphometric index HWI during growth of Illex illecebrosus illecebrosus. Males.

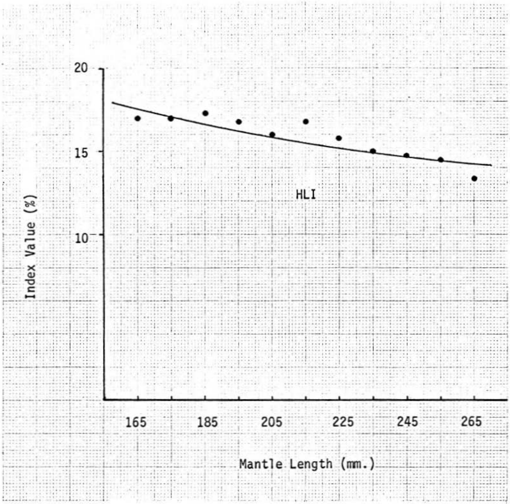

Figure 14. Change in value of morphometric index HLI during growth of *Illex illecebrosus illecebrosus*. Males.

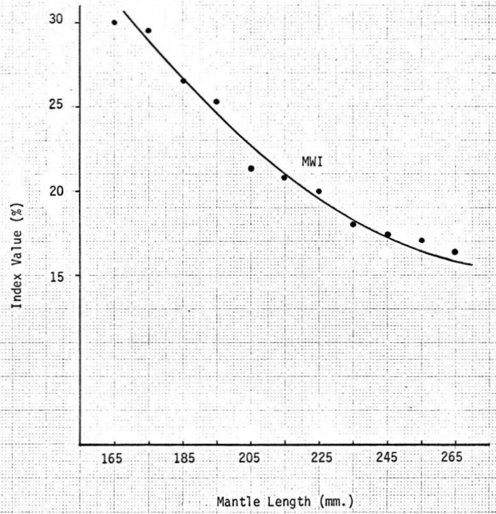

Figure 15. Change in value of morphometric index MWI during growth of Illex illecebrosus illecebrosus. Males.

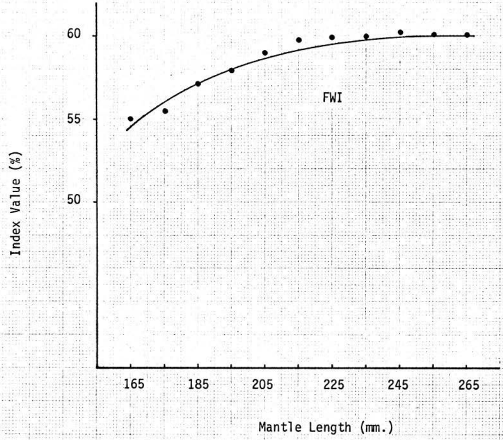

Figure 16. Change in value of morphometric index FWI during growth of *Illex illecebrosus illecebrosus*. Males.

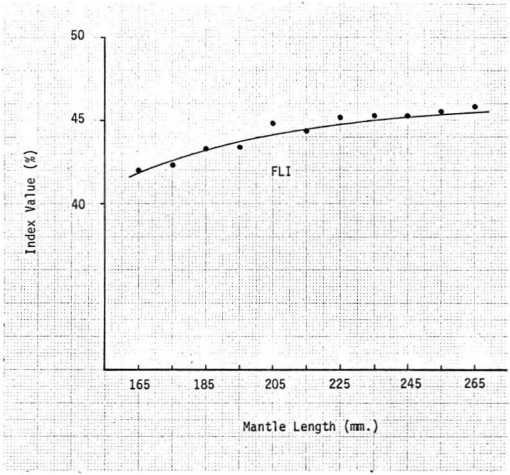

Figure 17. Change in value of morphometric index FLI during growth of Illex illecebrosus illecebrosus. Males.

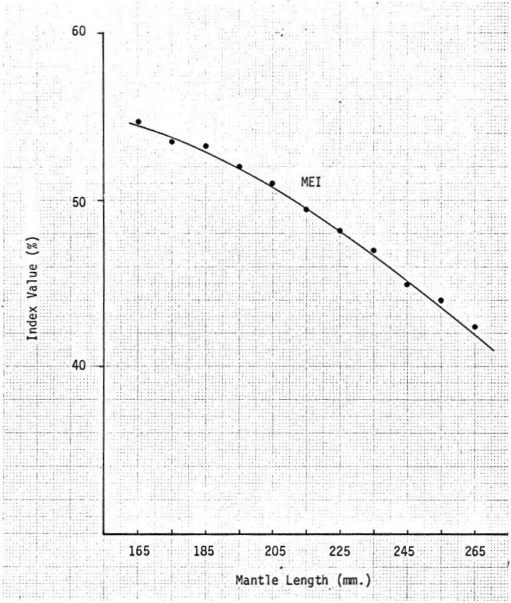

Figure 18. Change in value of morphometric index MEI during growth of _Illex illecebrosus illecebrosus_. Males.

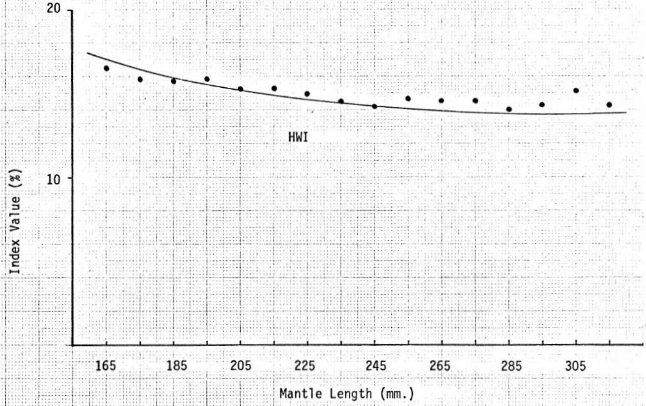

Figure 19. Change in value of morphometric index HWI during growth of <u>Illex illecebrosus illecebrosus</u>. Females.

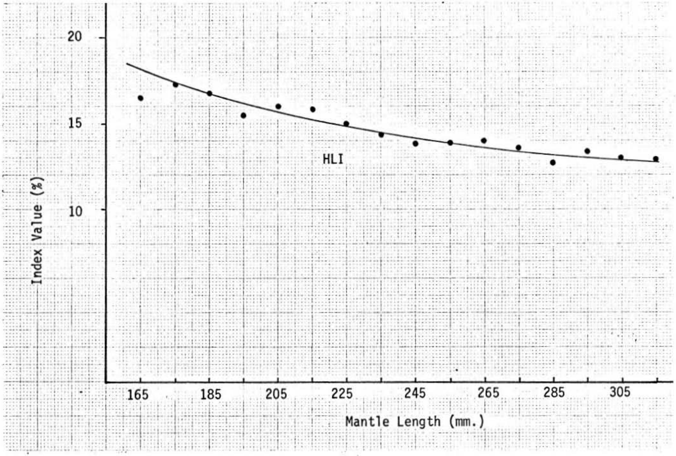

Figure 20. Change in value of morphometric index HLI during growth of *Illex illecebrosus illecebrosus*. Females.

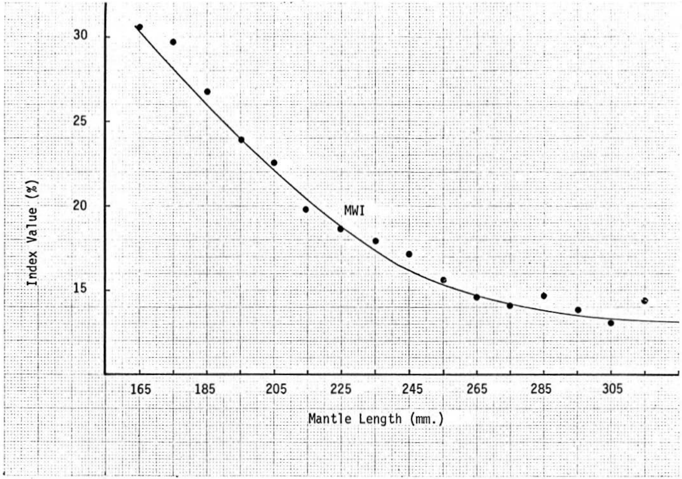

Figure 21. Change in value of morphometric index MWI during growth of *Illex illecebrosus illecebrosus*. Females.

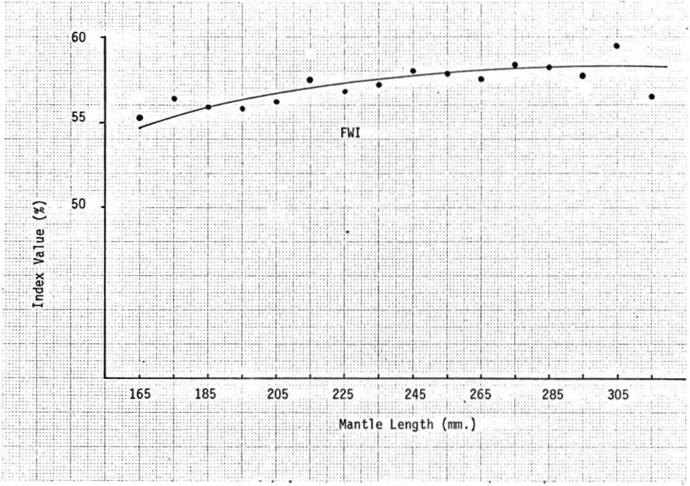

Figure 22. Change in value of morphometric index FWI during growth of *Illex illecebrosus illecebrosus*. Females.

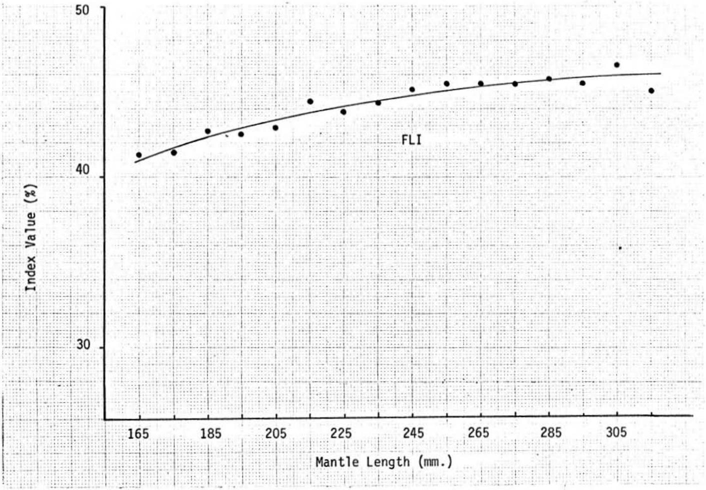

Figure 23. Change in value of morphometric index FLI during growth of *Illex illecebrosus illecebrosus*. Females.

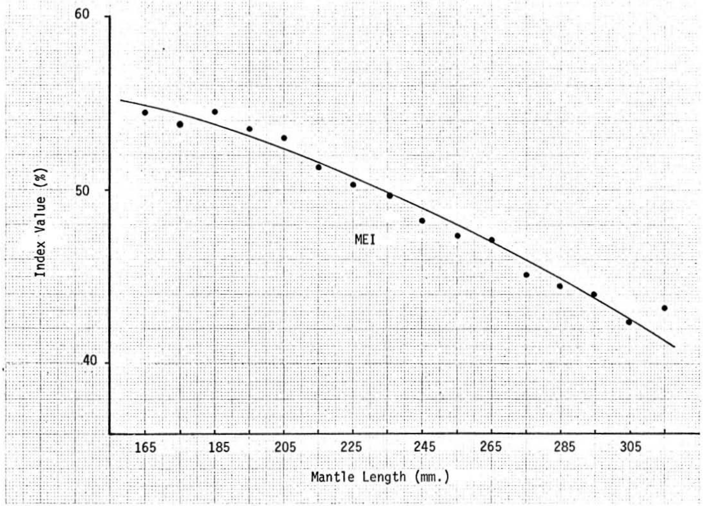

Figure 24. Change in value of morphometric index MEI during growth of _Illex illecebrosus illecebrosus_. Females.

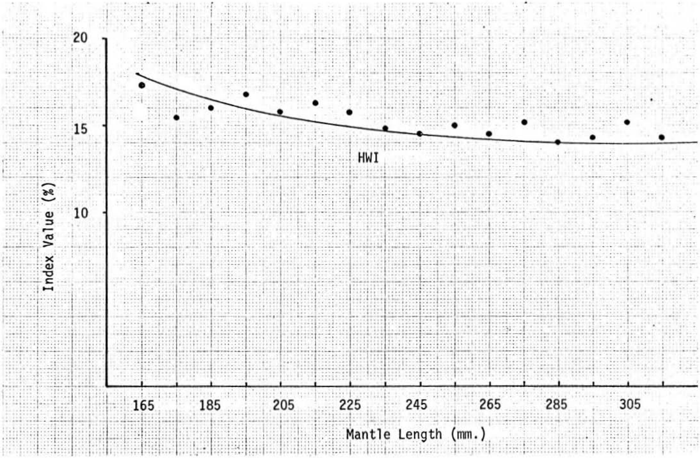

Figure 25. Change in value of morphometric index HWI during growth of <u>Illex illecebrosus illecebrosus</u>. Sexes combined.

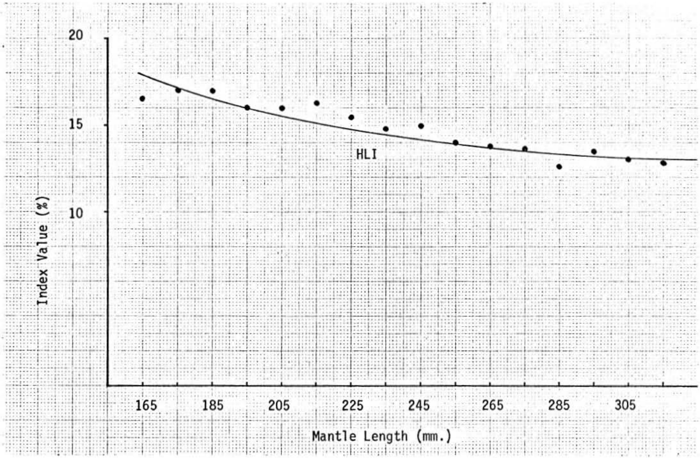

Figure 26. Change in value of morphometric index HLI during growth of *Illex illecebrosus illecebrosus*. Sexes combined.

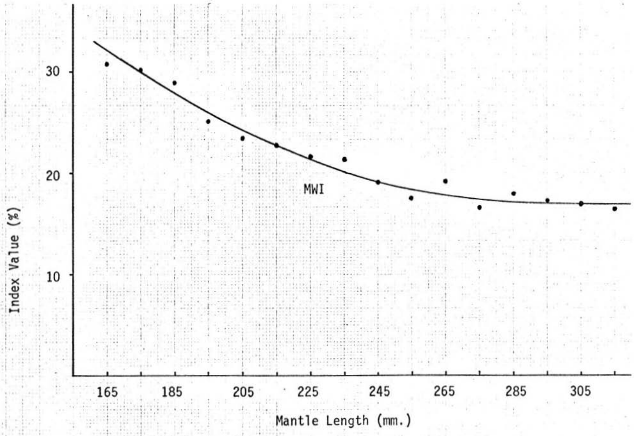

Figure 27. Change in value of morphometric index MWI during growth of Illex illecebrosus illecebrosus. Sexes combined.

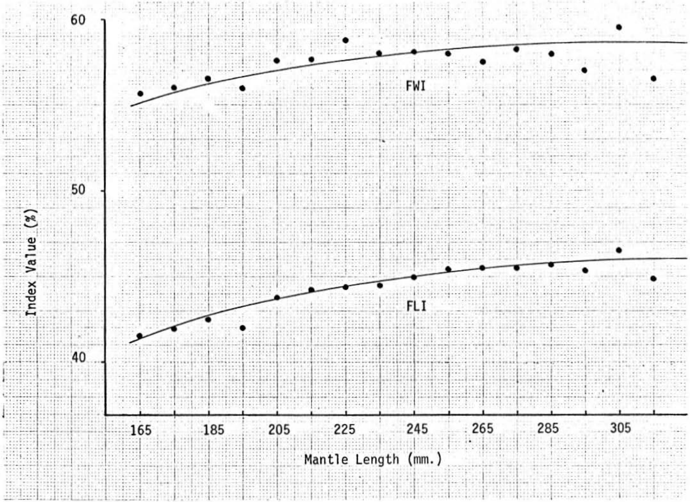

Figure 28. Change in value of morphometric indices FLI and FWI during growth of <u>Illex illecebrosus illecebrosus</u>. Sexes combined.

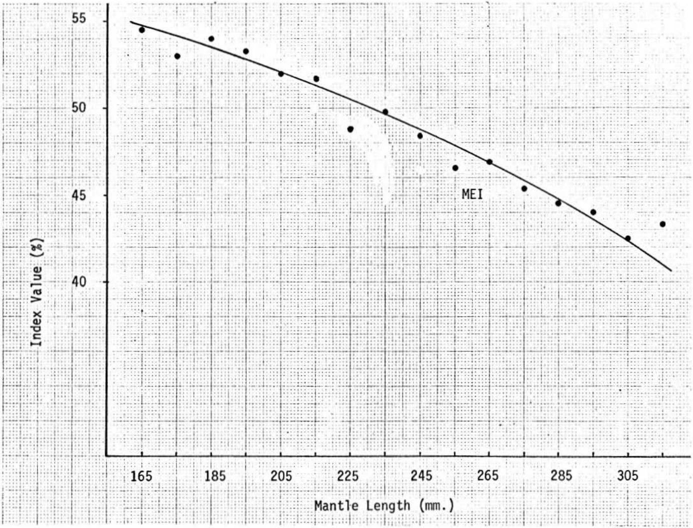

Figure 29. Change in value of morphometric index MEI during growth of *Illex illecebrosus illecebrosus*. Sexes combined.

Table IV. Morphometric data on the smallest and the largest specimens of *I. i. illecebrosus* collected, 1965-1966.

	Male			Female			
Character	S	L	L	S	S	L	L
ML	164	266	266	165	165	311	311
TL	347	492	495	359	331	550	563
MW	51	48	47	51	51	54	55
HW	28	39	36	29	22	49	39
HL	29	41	34	27	26	43	37
FL	69	132	120	72	66	142	137
FW	89	155	157	97	88	177	174
A_{I}	72	107	113	73	67	112	119
A_{II}	85	140	147	91	79	134	137
A_{III}	83	134	134	88	86	131	137
A_{IV}	72	112	123	78	67	122	129
T	160	210	223	169	153	232	221
PL	160	246	247	162	156	299	286
PW	5	9	9	6	6	11	10
SL	20	32	33	25	22	36	38
SW	20	24	24	18	20	35	25
GL	60	87	84	68	60	94	97
WE	68	441	366	83	64	618	441

Table IV (continued)

	Male			Female			
Character	S	L	L	S	S	L	L
WM	38	160	162	44	36	273	224
FA	47	46	48	45	47	--*	45

(All values given in mm. except: FA, in degrees, and WE and WM in grams.
S = smallest specimen, L = largest specimen).

*Measurements not available.

Table V. Morphometric indices for smallest and largest specimens of <u>I. i. illecebrosus</u> collected, 1965-1966.

	Male			Female			
Index	S	L	L	S	S	L	L
HWI	17	15	14	17	13	16	13
HLI	17	16	13	16	16	14	12
MWI	30	18	18	30	30	17	18
FLI	42	50	45	43	40	46	44
FWI	53	58	59	58	53	57	56
MEI	55	36	44	52	56	44	42
FL/FW	1:1.27	1:1.17	1:1.31	1:1.34	1:1.32	1.1.25	1:1.27
PL/PW	30:1	29:1	28:1	27:1	26:1	28:1	30:1

Values presented as percent of mantle length, except: FL/FW and PL/PW, which as ratios.

Both sexes show the same tendency toward a decrease of the MEI value during growth.

Both FLI and FWI increase with age, while the value of FL/FW remains unchanged during growth. The fin angle also maintains a value of about 45 to 50 degrees during growth.

The significance of the changes of all these indices during growth will be discussed later.

Morphometry of the Mandibles

Relative Growth of the Mandibles

The several dimensions measured for both the upper and lower mandibles of *I. i. illecebrosus* increase in size as the squid increase in size. The relationship between various dimensions of the mandibles are shown in Figures 30 through 54.

All these relationships fit the general straight-line equation $y = m x + c$. Constants m and c are given in the respective figures.

Correlations Between Various Dimensions of the Mandibles Mantle Length, and Total Body Weight.

Rostral length, hood length, and crest length of both mandibles, as well as the lateral wall length of the lower mandibles, were chosen for use in a study to determine the relationships between these dimensions, the mantle length, and the total body weight. The results of this study are shown in Figures 55 through 68.

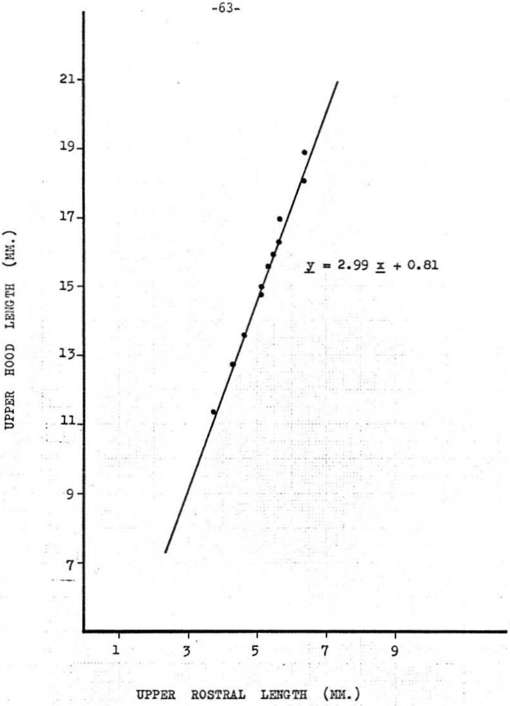

Figure 30. Relationship between rostral length and hood length of the upper mandible of Illex illecebrosus illecebrosus.

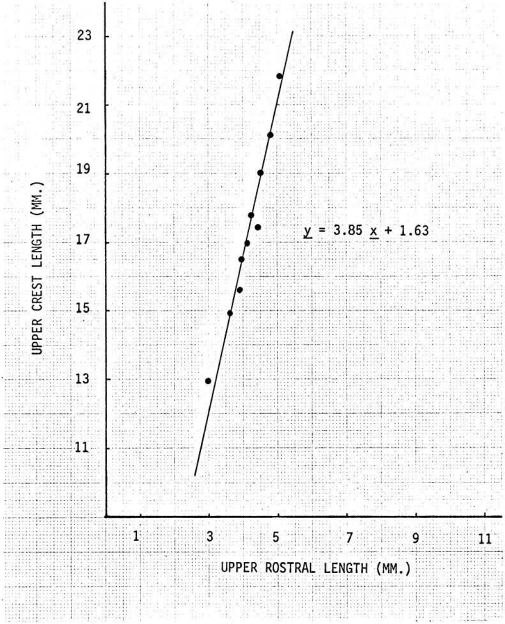

Figure 31. Relationship between rostral length and crest length of the upper mandible of <u>Illex illecebrosus illecebrosus</u>.

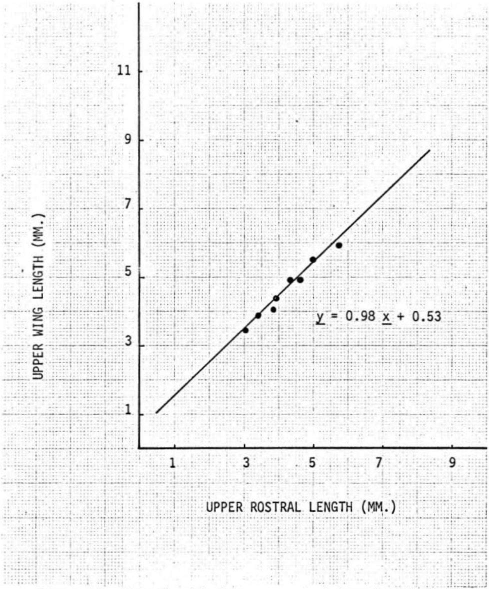

Figure 32. Relationship between rostral length and wing length of the upper mandible of *Illex illecebrosus illecebrosus*.

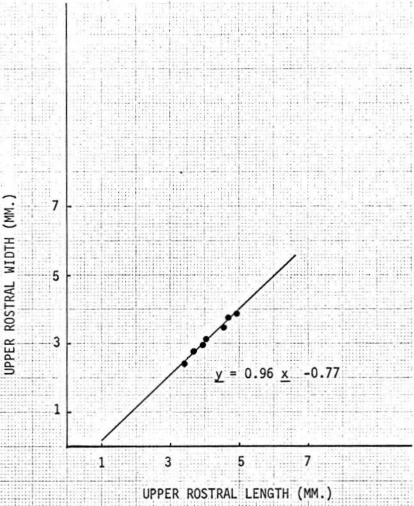

Figure 33. Relationship between rostral length and rostral width of the upper mandible of *Illex illecebrosus illecebrosus*.

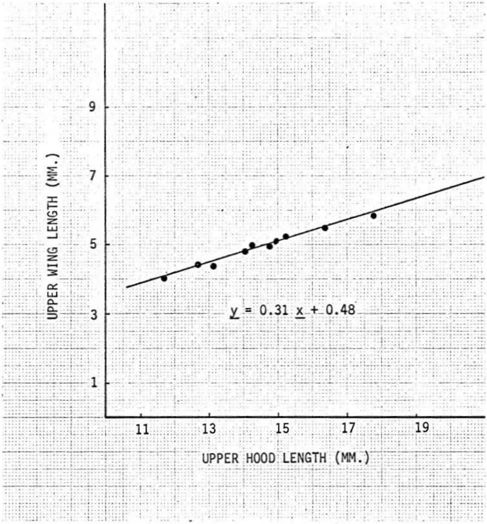

Figure 34. Relationship between hood length and wing length of the upper mandible of *Illex illecebrosus illecebrosus*.

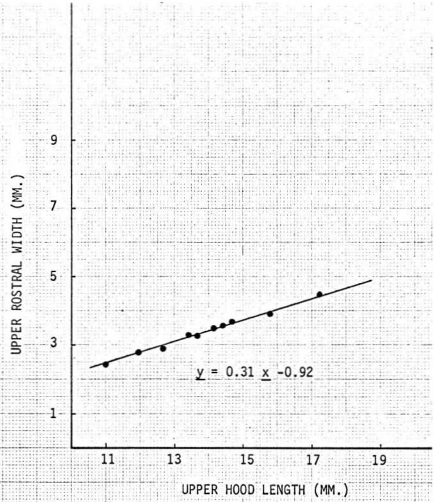

Figure 35. Relationship between hood length and rostral width of the upper mandible of *Illex illecebrosus illecebrosus*.

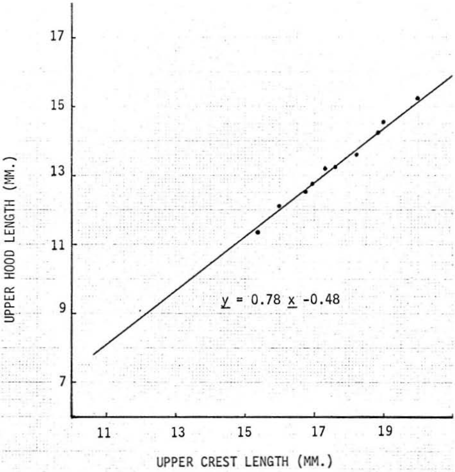

Figure 36. Relationship between crest length and hood length of the upper mandible of Illex illecebrosus illecebrosus.

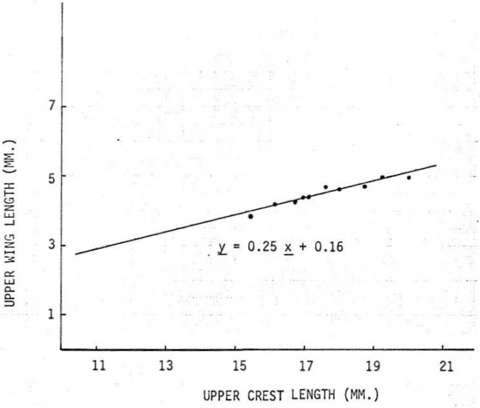

Figure 37. Relationship between wing length and crest length of upper mandible of *Illex illecebrosus illecebrosus*.

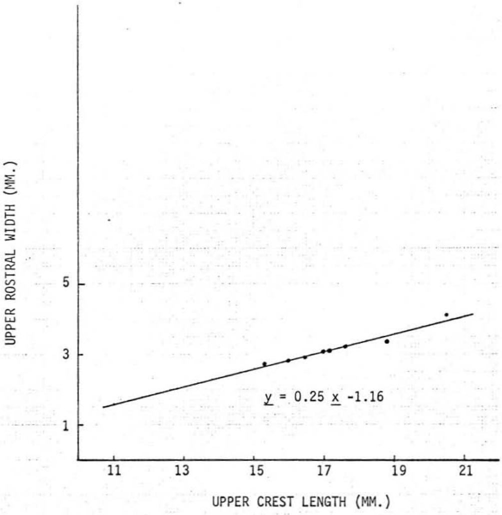

Figure 38. Relationship between crest length and rostral width of upper mandible of Illex illecebrosus illecebrosus.

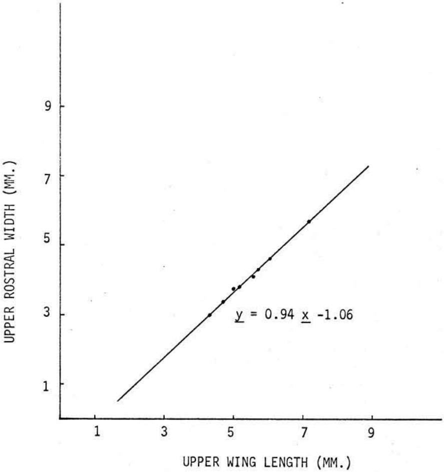

Figure 39. Relationship between wing length and rostral width of upper mandible of *Illex illecebrosus illecebrosus*.

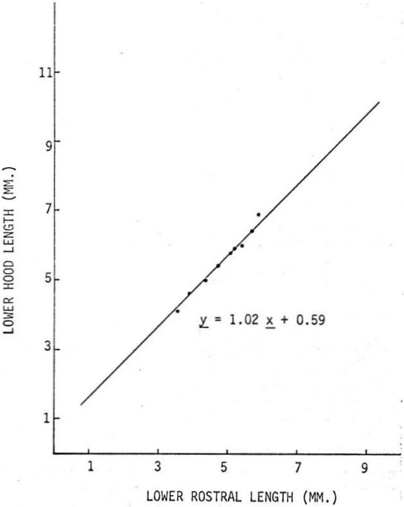

Figure 40. Relationship between rostral length and hood length of lower mandible of Illex illecebrosus illecebrosus.

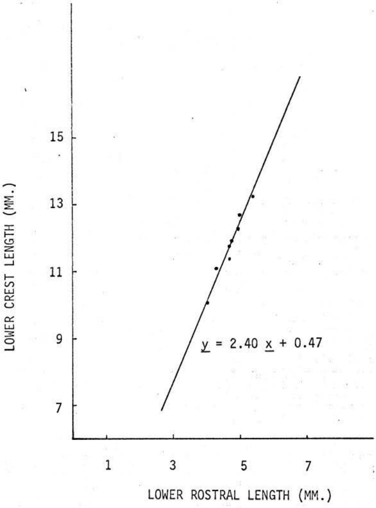

Figure 41. Relationship between rostral length and crest length of lower mandible of *Illex illecebrosus illecebrosus*.

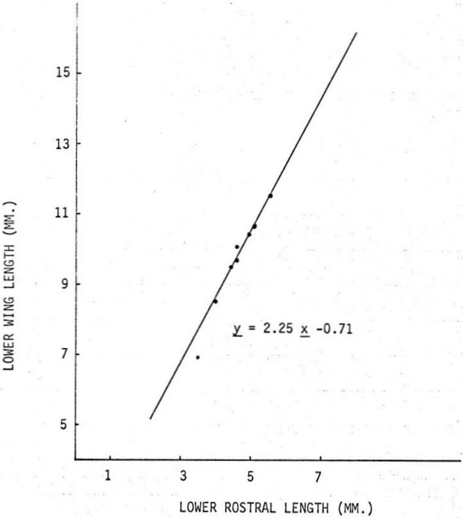

Figure 42. Relationship between rostral length and wing length of lower mandible of <u>Illex illecebrosus illecebrosus</u>.

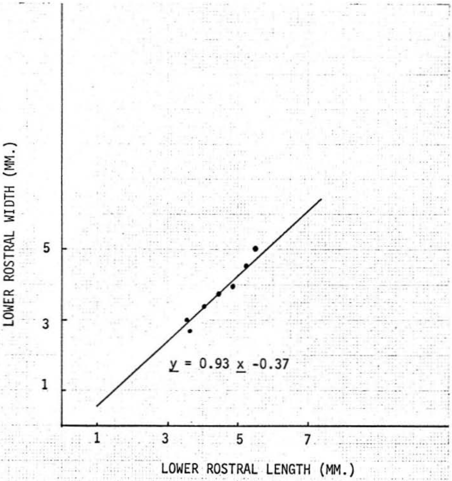

Figure 43. Relationship between rostral length and rostral width of lower mandible of _Illex illecebrosus illecebrosus_.

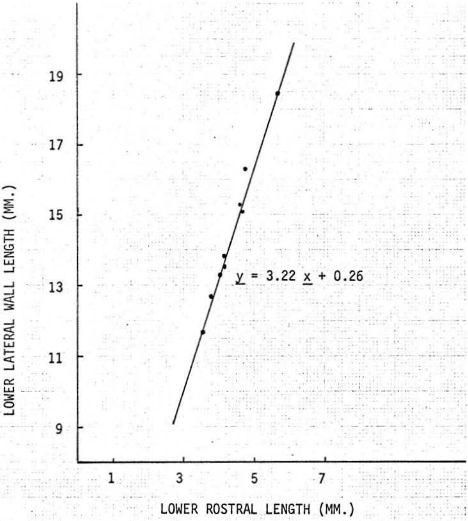

Figure 44. Relationship between rostral length and lateral wall of lower mandible of Illex illecebrosus illecebrosus.

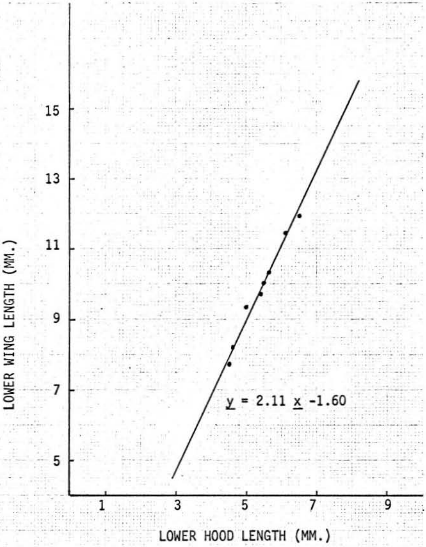

Figure 45. Relationship between hood length and wing length of lower mandible of Illex illecebrosus illecebrosus.

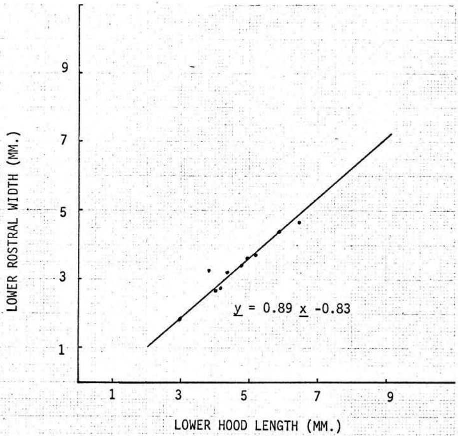

Figure 46. Relationship between rostral width and hood length of lower mandible of Illex illecebrosus illecebrosus.

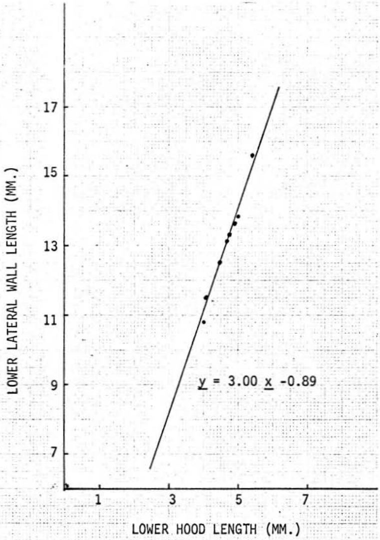

Figure 47. Relationship between hood length and lateral wall length of lower mandible of *Illex illecebrosus illecebrosus*.

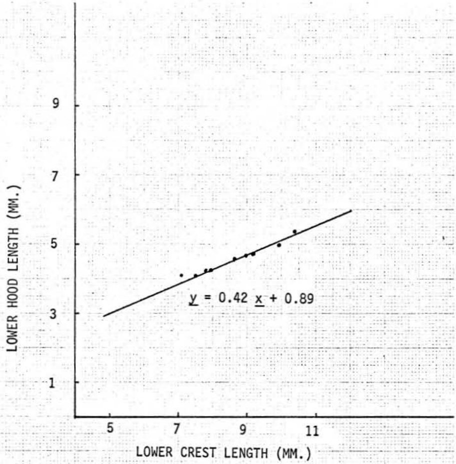

Figure 48. Relationship between crest length and hood length of lower mandible of *Illex illecebrosus illecebrosus*.

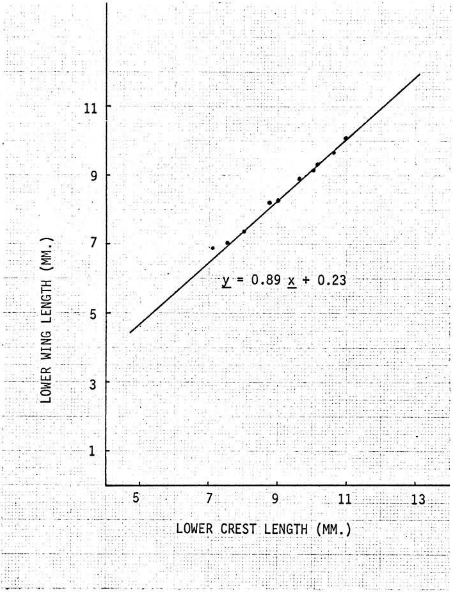

Figure 49. Relationship between crest length and wing length of lower mandible of *Illex illecebrosus illecebrosus*.

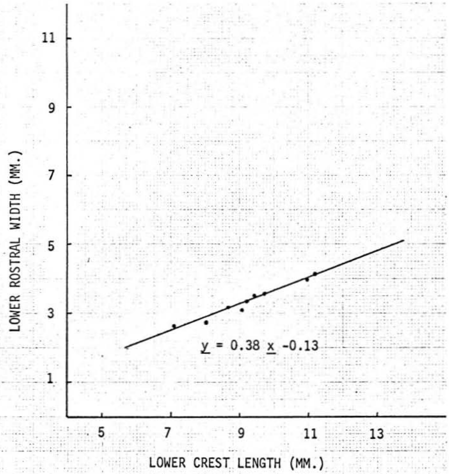

Figure 50. Relationship between crest length and rostral width of lower mandible of Illex illecebrosus illecebrosus.

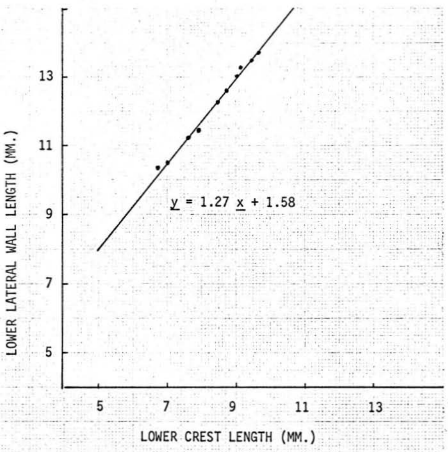

Figure 51. Relationship between crest length and lateral wall length of lower mandible of Illex illecebrosus illecebrosus.

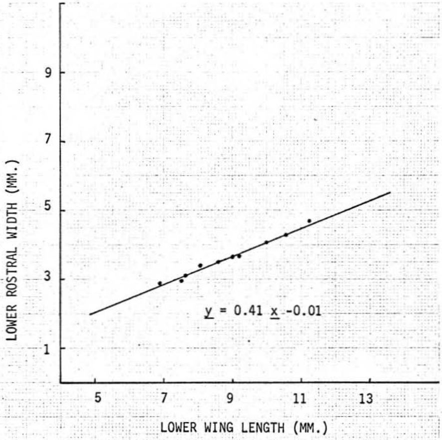

Figure 52. Relationship between wing length and rostral width of lower mandible of Illex illecebrosus illecebrosus.

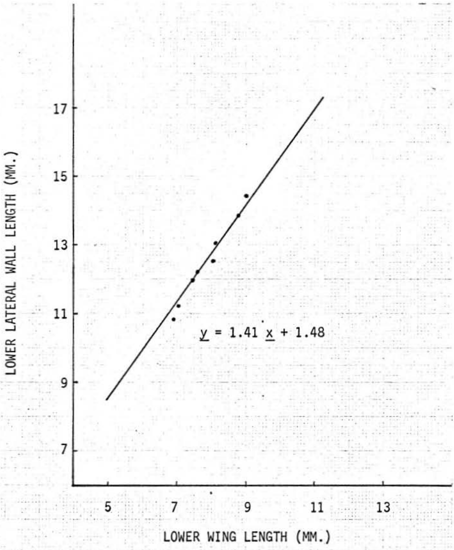

Figure 53. Relationship between wing length and lateral wall length of lower mandible of <u>Illex</u> <u>illecebrosus</u> <u>illecebrosus</u>.

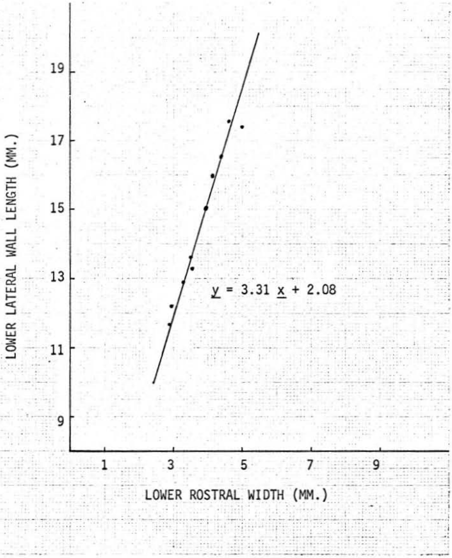

Figure 54. Relationship between rostral width and lateral wall length of lower mandible of _Illex_ _illecebrosus illecebrosus_.

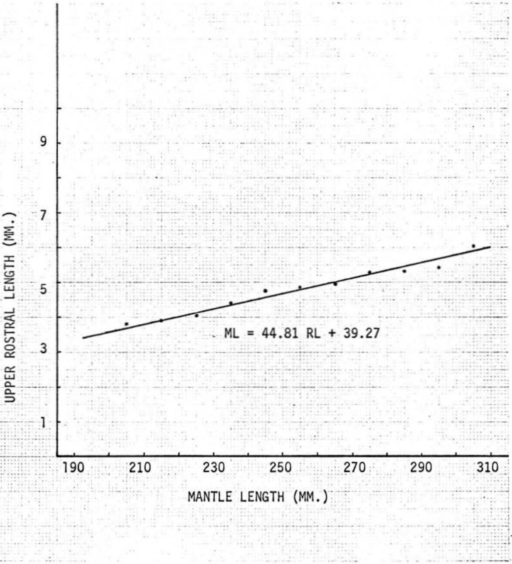

Figure 55. Relationship between dorsal mantle length and rostral length of upper mandible of *Illex illecebrosus illecebrosus*.

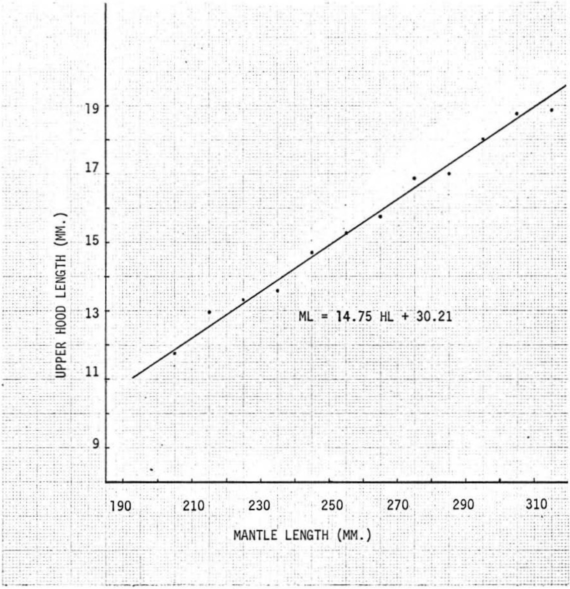

Figure 56. Relationship between dorsal mantle length and hood length of upper mandible of _Illex illecebrosus illecebrosus_.

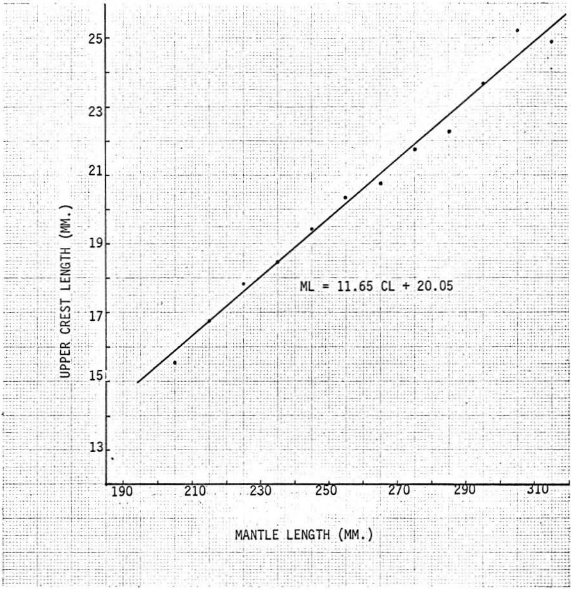

Figure 57. Relationship between dorsal mantle length and crest length of upper mandible of *Illex illecebrosus illecebrosus*.

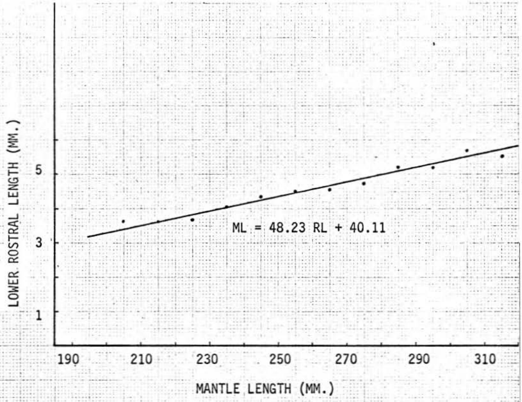

Figure 58. Relationship between dorsal mantle length and rostral length of lower mandible of <u>Illex illecebrosus illecebrosus</u>.

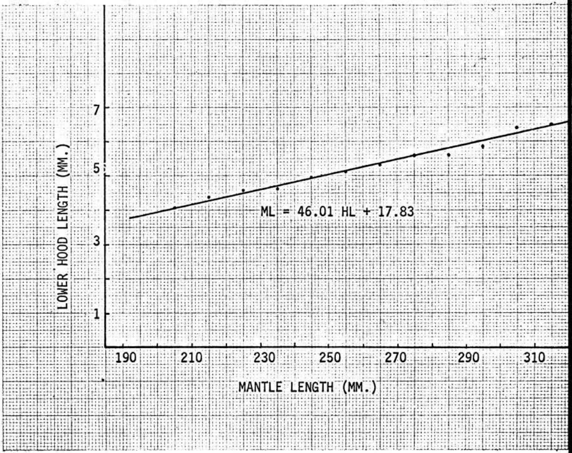

Figure 59. Relationship between dorsal mantle length and hood length of lower mandible of <u>Illex illecebrosus illecebrosus</u>.

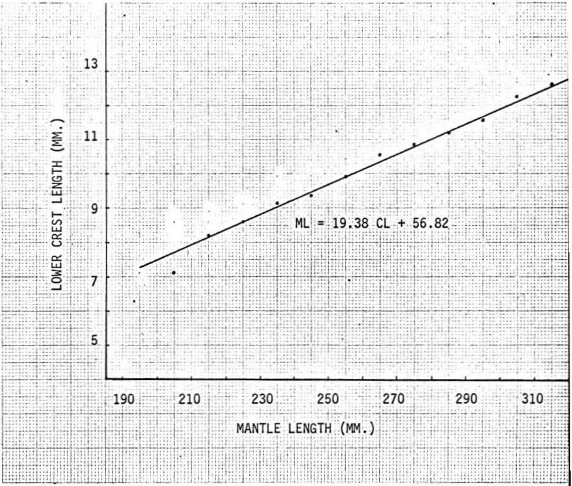

Figure 60. Relationship between dorsal mantle length and crest length of lower mandible of _Illex illecebrosus illecebrosus_.

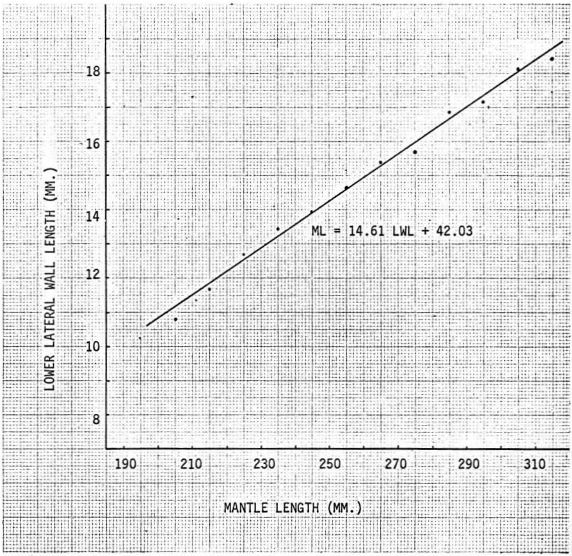

Figure 61. Relationship between dorsal mantle length and lateral wall length of lower mandible of *Illex illecebrosus illecebrosus*.

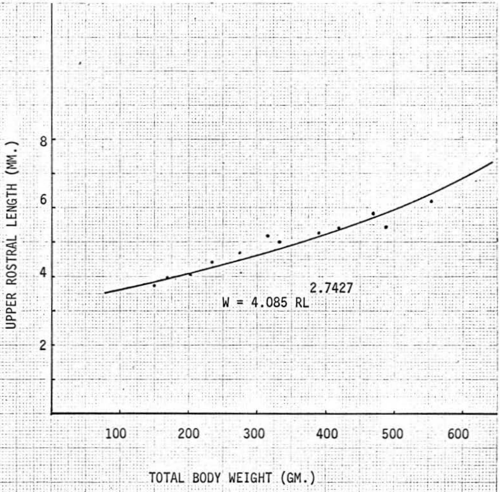

Figure 62. Relationship between total body weight and rostral length of upper mandible of *Illex illecebrosus illecebrosus*.

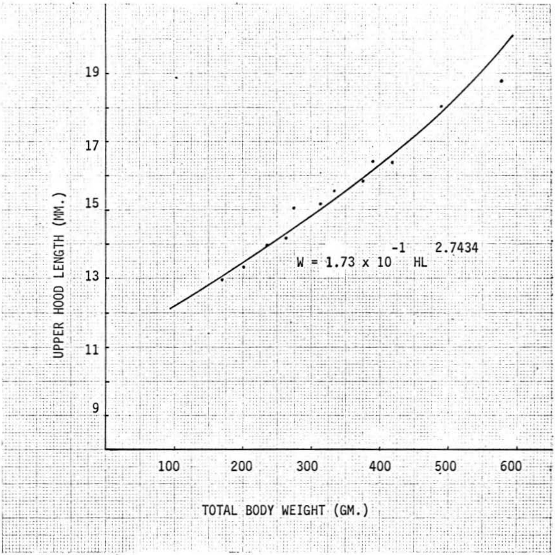

Figure 63. Relationship between total body weight and hood length of upper mandible of <u>Illex illecebrosus illecebrosus</u>.

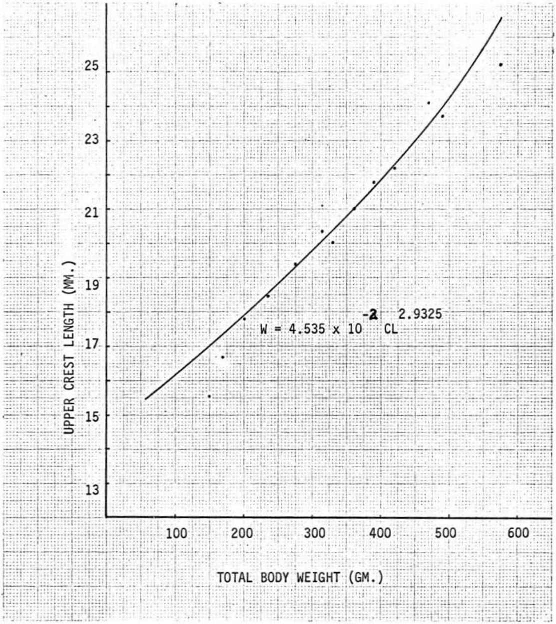

Figure 64. Relationship between total body weight and crest length of upper mandible of <u>Illex illecebrosus illecebrosus</u>.

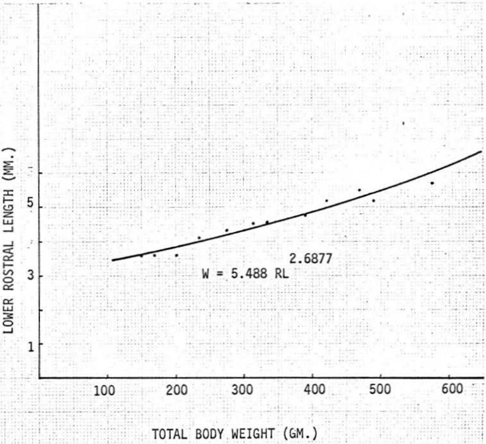

Figure 65. Relationship between total body weight and rostral length of lower mandible of Illex illecebrosus illecebrosus.

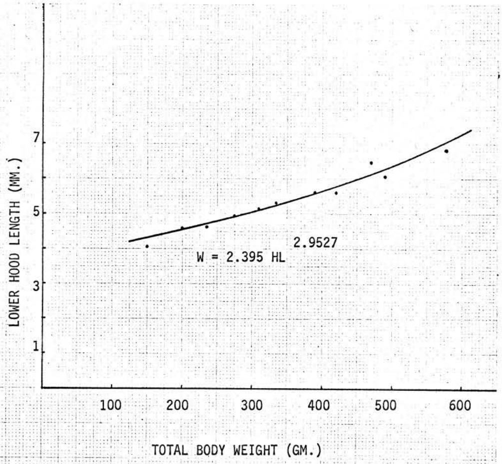

Figure 66. Relationship between total body weight and hood length of lower mandible of <u>Illex illecebrosus illecebrosus</u>.

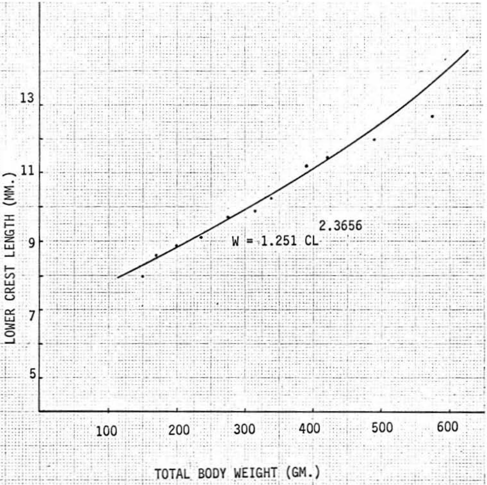

Figure 67. Relationship between total body weight and crest length of lower mandible of *Illex illecebrosus illecebrosus*.

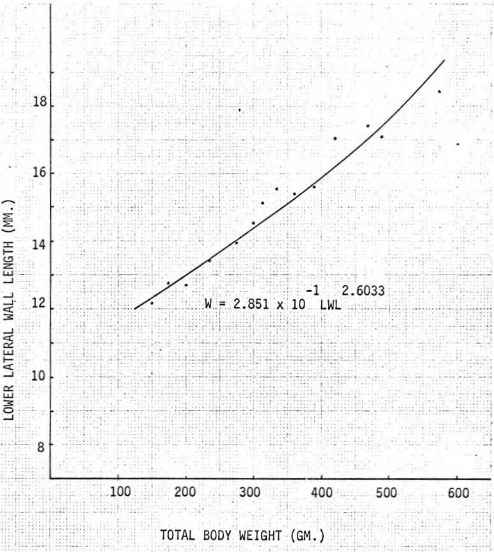

Figure 68. Relationship between total body weight and lateral wall length of lower mandible of Illex illecebrosus illecebrosus.

The relationship between the mantle length and various dimensions of the mandibles fit the straight-line equation $\underline{y} = \underline{m}\,\underline{x} + \underline{c}$. Constants $\underline{m}$ and $\underline{c}$ are given in the respective figures (Figures 55 through 61) and Table VI.

The general equation for the length-weight relationship, namely, $\underline{W} = \underline{a}\,\underline{L}^{n}$*, was used to calculate the correlations between total body weight and various dimensions of the mandibles. Constants $\underline{a}$ and $\underline{n}$ were calculated and are given in respective figures (Figures 62 through 68) and Table VII.

A sample set of calculations is presented in Appendix I.

Pigmentation of the Lower Mandibles

The wings of the lower mandibles of I. i. illecebrosus are found to be transparent in younger individuals. By the time the animal reaches 170 mm. in mantle length, a darkened area appears at the center of the wing. As the animal continues growing this darkened area expands. In the largest individuals examined (over 270 mm. in mantle length) the darkening has spread to such an extent that the entire surface of the wing appears to be dark brown in color, with the exception of the growing edge at the point of insertion into the buccal mass, which remains transparent.

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*The use of this generally acceptable formula in fisheries biology has been applied to decapod morphometry in the classic study of the Japanese squid O. sloani pacificus (=Todarodes pacificus) by many oriental workers, chiefly Ido (1952).

Table VI. The relationship between the dorsal mantle and various dimensions of the mandibles of *I. i. illecebrosus*.

I UPPER MANDIBLES:

y	x	m	c
	1	44.81	39.27
	2	14.75	30.21
	3	11.65	20.05

II LOWER MANDIBLES:

y	1	48.23	40.11
	2	46.01	17.83
	3	19.38	56.82
	4	14.61	42.03

All relationships fit the equation $y = m x + c$. In the Table, y: mantle length; x: dimensions of the mandibles; 1: rostral length; 2: hood length; 3: crest length; 4: lateral wall length. All measurements are in mm.

Table VII. The relationship between total body weight and various dimensions of the mandibles of *I. i. illecebrosus*.

I UPPER MANDIBLES:				
	W(gm.)	*L*	*a*	*n*
		1	4.085	2.7427
		2	1.73×10^{-1}	2.7434
		3	4.535×10^{-2}	2.9325
II LOWER MANDIBLES:				
	W(gm.)	1	5.488	2.6877
		2	2.395	2.9527
		3	1.251	2.3656
		4	2.851×10^{-1}	2.6033

All relationships fit the equation $W = a L^{n}$. In the Table, W: total body weight (in grams); L: dimensions of the mandibles (in mm.); 1: rostral length; 2: hood length; 3: crest length; 4: lateral wall length.

The color here referred to can best be described as "soot brown", or 5F5, in the Reinhold Color Atlas (Kornerup and Wanscher, 1962). It must be pointed out, however, that the color is not uniform in the pigmented area. At its darkest it is "soot brown", but toward the edges of the wing it is lighter (5E8, or yellowish brown), paling perceptibly to a shade that can best be described as being Pompeian yellow (5C6) in color.

Gradually, this darkening process can be classified into three stages, i.e., (a) the earliest or transparent stage, (b) the intermediate or darkening stage, and (c) the final or darkened stage (Figure 69).

It was considered important to express this darkening process in quantitative terms. As was indicated earlier under Materials and Methods, a procedure was derived to enable this quantitization by use of a B & L Microprojector, and a microplanimeter. The method used follows in more detail.

An image of the wing of a given lower mandible was projected on a flat surface and paper using the microprojector. The wing, and its darkened area, if any, were traced in outline. A line was then drawn through the jaw angle to the inner posterior edge of the wing. This line follows a naturally occurring discontinuity of the pigmentation. Above, rather outside of and anterior to this line of discontinuity, the mandible is always pigmented (Mangold and Fioroni, 1966), or at least in the sizes here studied.

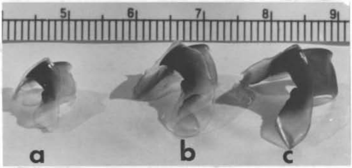

Figure 69. Lower mandibles of <u>Illex illecebrosus illecebrosus</u>, showing three stages of pigmentation on the wings.

a) Transparent Stage

b) Darkening Stage

c) Darkened Stage

By using the microplanimeter, the area of pigmentation on the now delimited posterior portion of the wing, plus the area of whole wing, could be measured. The percentage of the whole wing area that bore the pigmentation could then be calculated. The calculated percentage of pigmentation (i.e., pigmented area) was then plotted against both mantle length and gonad weight in separate sexes.

Data on 400 lower mandibles were treated in this manner.

It was learned that the degree of pigmentation of the wing of the lower mandible is positively correlated with increasing mantle length. Likewise, in both sexes, the degree of pigmentation of the lower mandible wing increases with an increase in the weight of the gonad, be it spermary or ovary. This information is presented graphically in Figures 70, 71, 72 and 73. Differences between the two sexes do, however, exist with respect to this phenomenon, as can be seen when the slopes in the curves presented in Figures 70 and 71 are compared with those from Figures 72 and 73. These differences will be discussed later.

Microrings on the Lower Mandibles

When the lower mandible of I. i. illecebrosus is cut along its crest and the medial surface of the lateral wall is exposed and viewed by oblique reflected light, series of growth lines or "microrings" can be seen when observed under a dissecting microscope.

These microrings are the record of the extension of the lateral wall during the growth of the lower mandibles. As the mandible

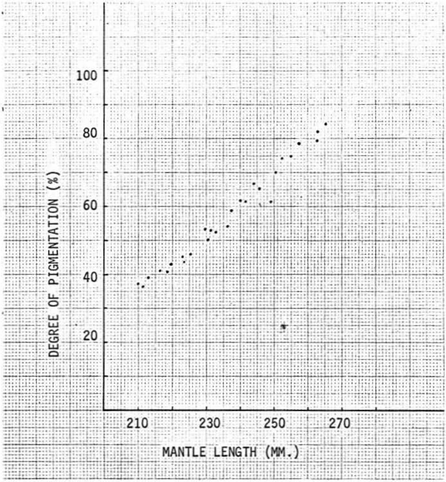

Figure 70. Relationship between mantle length and degree of pigmentation of wing of lower mandible of male *Illex illecebrosus illecebrosus*.

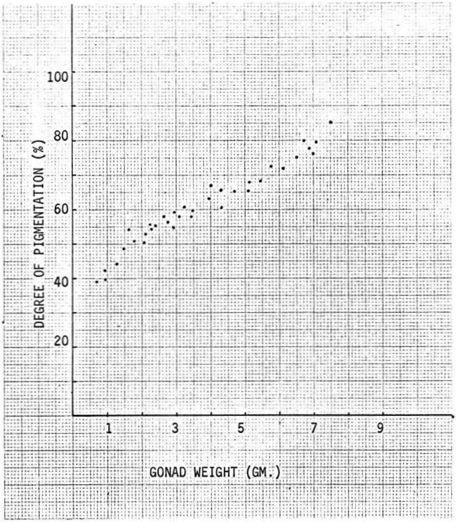

Figure 71. Relationship between gonad weight and degree of pigmentation of wing of lower mandible of male Illex illecebrosus illecebrosus.

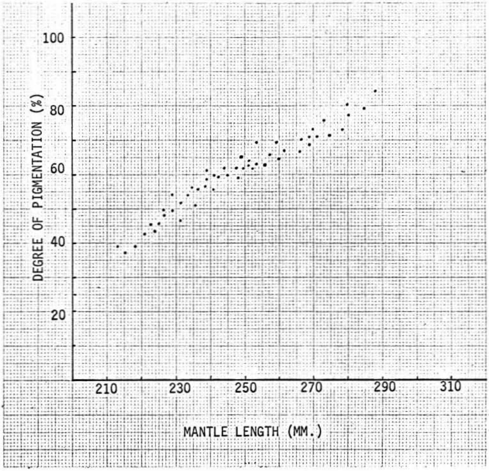

Figure 72. Relationship between mantle length and degree of pigmentation of wing of lower mandible of female Illex illecebrosus illecebrosus.

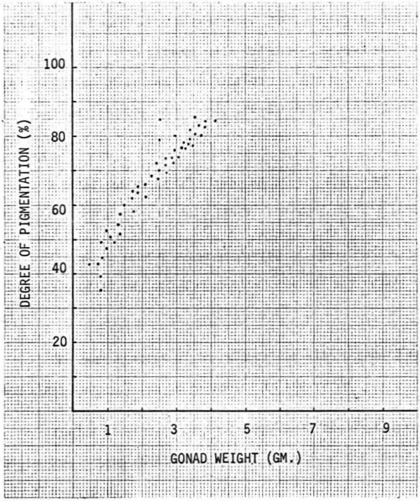

Figure 73. Relationship between gonad weight and degree of pigmentation of wing of lower mandible of female Illex illecebrosus illecebrosus.

grows, additional chitinous material is secreted and added to the growing edge of the mandibles, forming the successive microrings. Figure 74 shows the exposed lateral wall with microrings. This photograph was taken by a special preparation. The lateral wall was dissected and softened in a 16 percent solution of sodium hypochloride for six hours, and then stained with aniline blue (alcohol solution), and de-stained in 70 percent alcohol. Final mounting was in glycerol-gel.

A total number of 317 lower mandibles dissected from the squid used in other phases of this study were used in this phase of study.

The squid were grouped according to **their** mantle lengths in class intervals of 10 mm. and then plotted against the number of microrings counted.

The mean numbers of the microrings with standard deviation for each class interval are so presented in Figure 75.

Cycles of microrings, although described by Clarke (1965) for Moroteuthis ingens (Smith), were not evident on the lower mandibles of I. i. illecebrosus.

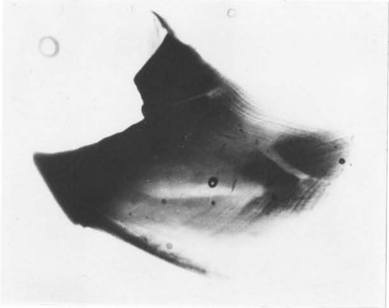

Figure 74. Lateral wall of lower mandible of _Illex_ _illecebrosus_ _illecebrosus_ showing microrings.

This is a photograph of an aniline blue-stained mandible.

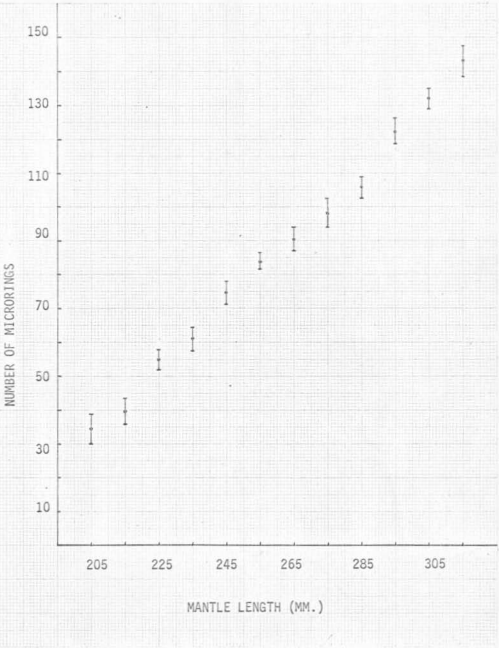

Figure 75. Number of microrings on the lateral wall of the lower mandible of Illex illecebrosus illecebrosus with standard deviations.

DISCUSSION

Growth and Sexual Maturity

Growth rate of Cephalopods varies with the species. Tinbergen and Verwey (1945) found that Loligo vulgaris Lam. reaches an average mantle length of 140 mm. in the first year and that the species spawns from April to August of that year. Males of two years of age had an average mantle length of 210 mm., while females grew more slowly with an average mantle length of 170 mm. after two years. Ommatostrephes todarus (=Todarodes sagittatus (Lam.)) increases in average length from 180 mm. to 310 mm. between July and October (Fridriksson, 1943). He postulated from the size data that Todarodes sagittatus spawns at the age of two years. In Loligo opalescens Berry, it was reported by Fields (1965) that squid of one, two and three years of age had mantle lengths of 65, 120 and 165 mm., respectively.

The growth rate of Illex is poorly documented. Squires (1967), from analysis of Illex illecebrosus illecebrosus taken by otter-trawl in Newfoundland offshore waters, concluded that this species had a faster growth rate than those quoted for either L. opalescens or L. vulgaris. He postulated from Bertalanffy's (1938) equation $L_t = L_\infty (1 - e^{-kt})$ that the time of hatching of I. i. illecebrosus could be three or four months prior to the arrival of the squid on the Grand Banks in May, with spawning occurring at the age of one year. Mangold-Wirz (1963) also suggested that the European form, Illex illecebrosus coindeti, spawned at an age of from one year to 15 months. In the related ommastrephid, Ommastrephes sloani pacificus (Steenstrup) (=Todarodes pacificus), it was reported that mantle lengths of 120, 190, 250 and 260 mm. are reached 3, 6, 9 and 12 months after hatching, respectively (Isahaya and Kawashida, 1934). This squid reaches sexual maturity at one year of age, according to Katoh (1959).

Different species of squid have different sex ratios. Sex ratio also varies with respect to size, and with respect to the time of sampling. For example, in T. pacificus, it was found that females appeared to be more numerous than males in autumn, with the reverse true in spring months (Endo, 1928). Fields (1950, 1965) reported that L. opalescens had a sex ratio of basically 1:1. Watasenia scintillans was reported to have a ratio which ranged from 2:1 to 281:1 in different samples (female:male) (Sasaki, 1913) dependent on many factors, not the least important of which was season and differing population. Illex i. illecebrosus has been reported to have a ratio of 1:1 (Squires, 1957; Mercer, 1965). However, in the present study, the ratio of female to male was roughly 3:2, with the percentage of females in the sample increasing and the percentage of males in the sample decreasing as the season progressed (Table II). It may suggest an introduction of larger, more mature females or the exodus of the larger males. Either one of these possibilities may suggest that I. i. illecebrosus come to Newfoundland waters for spawning.

Hamabe and Shimizu (1966) found that the gonad of male T. pacificus matured earlier than did that of the female and that the male initiated mating activity. In copulation, the "sperm-bulb" (spermatophore) containing inactive spermatozoa is delivered from the male to the buccal membrane of the female. Three months later, the sperm in the capsules on the female become active, moving into the seminal receptacle where they are kept until fertilization. The female later deposits ova when the ovary weight reaches one-tenth or more of the body weight. The males, having matured earlier than the females and having exhausted their reproductive and nutritive organs earlier, begin to die in the latter half of the reproductive period and thus decrease their numbers in the population in comparison to females. From the fact that the male I. i. illecebrosus become mature earlier than the female in Newfoundland waters (Squires, 1957; and the present study) and that the sex-ratio differs as the season progressed, it is postulated that this species may follow a similar reproductive pattern as described above for T. pacificus, although the mating activity in the short-finned squid has never been observed. It is interesting to note, however, that early ontogenic phenomena described for I. i. illecebrosus are remarkably similar to that in T. pacificus, and tends to strengthen my contention that the reproductive phenomena of the two related ommastrephids are similar (Aldrich, et al., 1968).

Eggs of Cephalopods are generally classified as either pelagic eggs or adhesive eggs, the latter further classified into four types on the basis of means of adhesion. These four types are: (i) adhesion by a viscous substance outside the egg-membrane, (ii) adhesion by gelatinous case enveloping many eggs separated from each other, (iii) adhesion by gelatinous peapod-like case containing many eggs, and (iv) adhesion by a long thread-like stalk. Eggs of W. scintillans are pelagic. Squid belonging to the suborder Myopsida lay eggs of types (i), (ii) and (iii).

Eggs of octopods belong to type (iv) (Nishikawa, 1906; Yamamoto, 1942, 1943; Shimomura and Fukataki, 1957). Recently, Hamabe (1966) found that the egg masses of T. pacificus consisted of three components, namely ova, oviducal secretions and nidamental secretions. About 300 to 4,000 ova were embedded in the oviductal secretion in each egg mass. The oviductal secretion was viscous and buoyant, like human saliva. This secretion was again enveloped in a thick capsule of the nidamental secretion which was also viscous, albuminous, and heavier than sea water. Since T. pacificus and I. i. illecebrosus are related forms, it is strongly believed that their patterns of reproductive behaviour and their egg structures are similar. Spawning would likely take place near the bottom in offshore waters, where the physical and chemical conditions, i.e., current and salinity, are comparatively constant. Hatching would occur at the bottom where the eggs adhere to the substratum.

Two explanations are currently used to explain the decrease of length and weight which occur in the November sample. However, the possibility being due to large squid migrating out of this area in November was negated by the fact that measurements of squid in November, January, February and March indicated that none were larger than the large squid taken in October (Squires, 1957, 1967; and the present study). The squid must then (October) approach maximum size and spawning may soon follow. Simultaneously, in addition to those reaching maximum size, a group of small squid, similar in size to those early arrivals in July, was found in October and November samples (Figure 76). Presence of these small squid would then cause a decrease of the average size in those samples, affecting length frequency distribution in the samples.

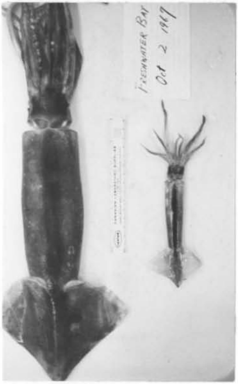

Figure 76. Photograph of two specimens of Illex illecebrosus illecebrosus collected from Freshwater Bay, Newfoundland, on October 2, 1967, showing extremes in size and indicating two possible generations or populations.

De Castellanos (1964) reported that spawning in Illex illecebrosus argentinus did not take place en masse but occurs over a prolonged period, with greatest spawning activity in the summer months of December to March in Argentine waters. Migrations of two groups of Illex illecebrosus coindeti take place each year in the northwest Mediterranean (Mangold-Wirz, 1963). She reports, that in January a group of sexually advanced squid was found by her near the bottom between 60-150 meters and an immature group near the bottom between 150-400 meters. The more advanced group moves into shallower water from March through July, returning to deeper water in August. The immature group follows the advanced group inshore, entering the littoral zone in August and September, then migrating back into deep water.

Katoh (1959, 1960 and 1964) studied populations of Todarodes pacificus in the waters of Oki Island, Shimane Prefecture, Japan, and found four groups occurring annually in that area. Two appeared in the summer (April to September) and two in the winter (November to March). The two summer groups consist of one sexually immature group and one mature group, while the two winter groups are mature in males and either mature or immature in females. He proposed that the immature group in summer represented the same population of the mature one in winter. He also found that the squid in winter decrease gradually in body size, nidamental length and testis weight with the progress of time and considered this as the result of the fact that the largest squid arrived first in these waters in the southern Japan Sea and successively smaller ones continued to appear until March of the following year.

Aldrich (1964) in his observations on I. i. illecebrosus in Newfoundland waters reported, "Definitely a much lower incidence of the tapeworm Phyllobothrium plerocercoids was present in the alimentary tracts of Placentia Bay specimens compared with the incidence from Trinity Bay and Conception Bay". He contended from this that Squires might be wrong in his contention that the squid in all Newfoundland embayments were part of one population.

From the present results and previous work on this species, subspecies and related species, it is proposed that the short-finned squid in Newfoundland waters comprises, at least, two different populations. The major group arrives on the Grand Banks* in May, moves northward inshore, and appears in coastal waters, such as Holyrood Bay, by July, staying inshore until October or November, when it then moves back to deeper waters.

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*It is worthy of note that I have been informed by fishermen of Bonavista Bay and Trinity Bay areas, that in early September, small squid two inches in length, have been found in the stomachs of Turbot (Reinhardtius hippoglossoides (Walbaum)) which were captured by use of gill-nets from those areas. Unfortunately, they were not available for study. Due to the abundance of I. i. illecebrosus in their waters and the fact that the fishermen are convinced that the squid are definitely "Newfoundland squid" (local name for I. i. illecebrosus) rather than Labrador squid (Gonatus fabricii (Lichtenstein)), it may then be proposed that this squid spawns in the deep waters of the various bays or near offshore waters at depths of about 200 fathoms. The larvae may spend a certain period of time on the bottom. The subsequent inshore migration may be caused by a combination of factors, such as food availability and distribution, and temperature. (The different times of occurrence of this squid in various bays, may be due to temperature differences. Notre Dame Bay and Bonavista Bay are more open to the cold waters of the Labrador Current, causing water temperatures colder than those in Conception Bay at the same time. Squid appear in these two bays (Notre Dame and Bonavista) later each year than they do in Conception Bay). However, this problem has yet to be solved and can only be solved when different populations can be distinguished and the migration of each population traced.

The second, or minor group follows the major one,arriving inshore in October and November, then moving back to deep waters. Growth curves of these two groups are shown in Figure 77. Curves A and B indicate the major and minor group, respectively. The broken line indicates the possible extension of the respective curve. From these curves, the spawning season of this squid seems to be a prolonged period, suggesting from November to May of the following year, a situation not unlike that described for I. i. argentinus by de Castellanos (1964).

As mentioned previously, the details of the life cycle of this species are unknown, since neither the larvae nor the eggs have been found. Further studies on this problem are extremely necessary.

Food

Frost and Thompson (1933) recorded that squid usually fed on crustaceans, even near the coast, in 1932, but generally found no food in stomachs of squid in their 1931 inshore samples. Squires (1957) reported that euphausids were the main food items for small squid (100-180 mm.) from the Grand Banks; larger squid (190 mm. and above) taken inshore fed mainly on fish. Of the crustaceans eaten, euphausids of the genera Thysanoessa and Meganyctiphanes were identified as most important. Fish in the diet were identified as capelin (Mallotus villosus (Müller)), redfish (Sebastes marinus (L.)), cod (Gadus morhua L.), haddock (Melanogrammus aeglefinus (L.)) and mailed sculpin (Triglops pingeli Reinhardt). In addition to these, fragments of mysids, amphipods, copepods, shrimp,

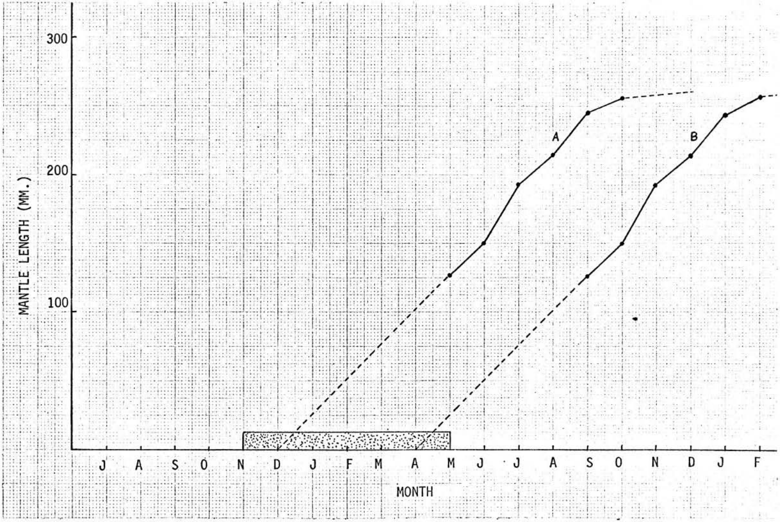


Figure 77. Growth curve of Illex illecebrosus illecebrosus in Newfoundland waters. Data of May and June obtained from Squires (1957). Broken lines indicate possible extensions of the curve. Hatched area indicates the suggested spawning period. Both sexes combined.

pteropods, whelks, polychaetes and chaetognaths were also found. He also reported (1959) that squid taken by the C.G.S. A. T. CAMERON were feeding on lantern[1] fish. Mercer (1965) stated that crustaceans made up the bulk of the diet of squid from the Grand Banks and Placentia Bay. In samples from Holyrood, fish was the most important food item. Cannibalism was found in all the areas studied but was particularly prevalent at Holyrood (Mercer, 1965).

In the spring, *I. i. illecebrosus* remains in offshore waters where planktonic organisms, such as euphausids, are abundant. In July, the major group of squid come into the inshore waters following and feeding upon the capelin. However, copepods are as numerous as are capelin at that time and the squid feed on these also. Late in the year, the disappearance of the capelin and the scarcity of other food organisms may account for the high incidence of cannibalism.

Bidder (1966) reviewed the records of food of Cephalopods and found that *Ommastrephes sloani pacificus* is the only species where cannibalism exists, quoting Sasaki (1929). Apparently, Bidder overlooked the reference to cannibalism in *Loligo pealei* by Williams (1909), where the latter author wrote, "Squid of every age are greedy and persistent cannibals". Larger squid (20-30 mm. in length) reported Williams, accompany schools of smaller specimens and "feed constantly upon them".

[1] *Lampanyctus lacerta* (Goode & Bean)

The remains of as many as seven squid were reported from the stomachs of individual L. pealei. Missed as well, was the reference in Lane (1960) of the report from the Michael Lerner Expedition of cannibalism in the Humboldt Current squid, Dosidicus gigas. But, to return to I. i. illecebrosus Verrill (1882) reported that food in the diet of this ommastrephid consisted solely of crustaceans and fish. However, the present study and previous investigations (Squires, 1957, 1966; Aldrich, 1964; Mercer, 1965) show evidence of cannibalism in I. i. illecebrosus.

Illex i. illecebrosus migrates inshore in large schools (Aldrich, 1964, and others), and supposedly these schools follow populations of food organisms, such as the capelin, M. villosus. The feeding activity of these concentrated populations of squid could cause local depletions of the desired or acceptable food organisms, resulting in what may be, at best, temporal deprivation. Such a condition could, therefore, lead the larger and more active or hungry squid to resort to cannibalism, in that they turn on members of their own species for food.

Squires (1957) and Mercer (1965) both refer to the fact that squid fragments are not uncommon in "stomach samples" of the short-finned squid. Mercer (1965) also reported observations of autophagy. He (Mercer) is quoted as saying that squid fragments found in the stomachs of the sampled squid "may be derived from bites taken after capture and when thrown together, and that cannibalism inshore may be rated higher than it actually is" (Squires, 1966). However, the author has observed that squid can live no longer than 15-20 minutes after being taken on board ship and all the fragments of squid found in the alimentary tract of examined specimens are, at least, partially digested. Since in most decapods the enzymes necessary for both gastric and caecal digestion are delivered from the midgut gland, or hepatopancreas (Bidder, 1950, 1966), and since Takahashi (1963) reported that in O. s. pacificus total autodigestion of the "liver" (or hepatic portion of the midgut gland) occurs in three hours, it therefore seems unlikely that the rate of digestion could be so rapid. In fact, Bidder (1966) quotes four to six hours as a minimal period for digestion of ingested food. It is not unreasonable to propose that the incidence of cannibalism as observed is indicative of cannibalism being a naturally occurring phenomenon, and that the incidence here reported (Table III) is indicative of the rate of its occurrence in nature. The differences caused by biting one another upon capture would not be great enough to alter the situation to any significant degree, despite what Mercer may contend.

The proportion of the various food items in the diet of a given species of squid, and even in the same squid, varies with the investigation. This may suggest that this squid does not select a particular food; any animal that may be caught can be eaten. Studies on Todarodes pacificus (Sasaki, 1929; Soeda, 1956; Araya and Nakamichi, 1962; Okutani, 1962; and Okiyama, 1965a)and on Loligo opalescens (Fields, 1965) have shown this to be the case. Food organisms which are abundant where the squid live are generally predominant in the diet. This may account for Squires' reports (1957, 1959) of the wide varieties of the diet, for his materials were taken from the Grand Banks.

However, Aldrich (1964) pointed out that small squid appeared to prefer a diet of invertebrate organisms, while the larger squid appeared to prefer fin fish. If this is the case, alternation in the choice of food organisms with age of the squid may, presumably, be due to sequential changes in enzyme activity. Further investigations in this area are necessary.

Morphometry of Growth

One must agree with Voss (1963) when he observes that Teuthologists have been criticized for being slaves to measurement and detailed description, but it must be remembered that Cephalopods are soft-bodied animals subject to great change in shape due to different methods and degree of preservation and, except in a few forms, no hard skeletal parts are present to preserve original shape. Haefner (1964) pointed out that the changes in the morphometric indices during growth of Cephalopods are important in taxonomy.

The morphometry of I. i.illecebrosus has never been studied in detail, although several authors have included some measurements and proportions in various publications (Verrill, 1882; Adam, 1952; Voss, 1955 and 1956; and Squires, 1957). This is the first time that this species has been studied in detail morphometrically.

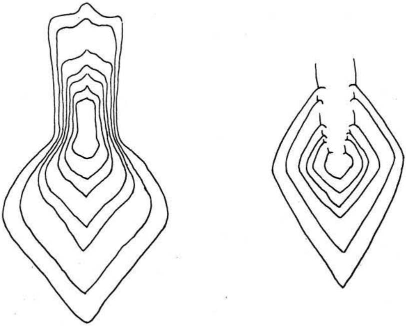
In Figures 18 and 24, the value of MEI of both sexes shows a tendency toward a decrease during growth, which I postulate is due to the rapid development of the gonad, the liver, and organs of alimentation.

Since the male reaches sexual maturity earlier than does the female, the increase in weight of those organs is greater in males than in females of the same size. The respective value of the index is thus smaller in the male than in the female. The point of inflection is found to be at a size corresponding to 195 mm. in mantle length.

As both FLI and FWI increase with age, while the value FL/FW remains unchanged during growth and the fin angle also maintains constancy, growth of the fin, within the size range studied, is then isometric and the triangular shape is maintained throughout the life of the animal (Figure 78).

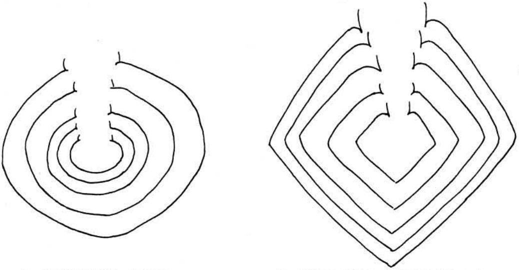
Due to the compressable mantle cavity, it is found that, among these six indices, MWI is the most unreliable one. However, it may be corrected, the author believes, by cutting through the mid-ventral line and taking a measurement across the widest part, although the contraction during fixing and preservation may still exist. Such a procedure would, however, cause for a new definition of MWI and necessitate re-evaluation of all existing information based on the old definition.

Haefner (1964) reports that fin growth in L. pealei is allometric, that is, the fin shape changes from a rounded, heart-shaped configuration, to a long and slender rhomboidal shape during growth, while the fin growth in Lolliguncula brevis (Blainville), like that in I. i. illecebrosus, is isometric. In L. brevis the ellipsoidal fin shape is maintained throughout the life of the individual (Haefner, 1964). The change of fin angle and shape of these three species of squid, plus the situation reported by



A. *Loligo indica*

B. *Loligo pealei*



C. *Loliguncula brevis*

D. *Illex illecebrosus illecebrosus*

Figure 78. Nested outlines of fins of four species of squid showing change in fin angle and shape.
A: After Hoyle, 1885
B and C: After Haefner, 1964.

Hoyle (1885) for Loligo indica are shown in Figure 78.

Adam (1952) published comparative studies on some morphological characteristics including some morphometric data of the two subspecies, I. i. illecebrosus and I. i. coindeti. Since he combined all sizes in one group (cf. Adam, 1952; Table: Valeurs statistiques des dimensions relatives), it is not possible to trace changes in those characters during growth. He also included illustrations of sexual dimorphism involving suckers on various arms. However, upon closely examining my specimens, I must conclude that the differences to which he referred are too minor to be significant or constant.

With respect to the short-finned squid, Verrill (1882) (in his study of 123 specimens from various regions stated),"The Mediterranean form, usually identified with the var. b of Loligo sagittata Lamarck, 1799, is closely related to our species, but if the published figures and descriptions can be relied upon, it can hardly be identical, as d'Orbigny and other writers have considered it. The American form has a more elongated body, with a differently shaped caudal fin, which is relatively shorter than the best authors attribute to O. sagittatus."

De Castellanos (1960) described a new species named Ommastrephes argentinus from Argentinian waters, which was then considered as a third subspecies of Illex illecebrosus and now known as I. i. argentinus (de Castellanos, 1964). By studying the data of her male and female holotypes, it seems that this subspecies has a larger FWI than our specimens of the same size.

Recently, Zuev (1966) published data on 15 specimens of the short-finned squid from three regions (five from Africa, six from the Adriatic Sea, and four from North America) and concluded that the squid genus Illex consists of a single species I. illecebrosus, divided however, into several geographic "races", the total number of which is at least three. However, after studying his data on the four specimens from the Northwest Atlantic, it is found that his squid have a very short fin. Furthermore, his figure of the beaks of squid show a surprising difference: the beaks from our specimens based on Zuev's, are of the Adriatic Sea type. (Further discussion on this point concerning the mandibles will be presented in the next section). Apparently, Zuev is unaware of de Castellanos' subspecies, I. i. argentinus. At any rate, Zuev's paper makes little, if any, contribution to the study of the systematics of this genus, if for no other reason than his making such broad conclusions on the basis of so few and ill-defined specimens from such widely separated geographical areas (Aldrich and Lu, 1968).

Through the kindness of Dr. G. L. Voss, the author has recently received two specimens, one male and one female, of I. illecebrosus (his identification) taken from Cuban and Floridian waters. When one compares these two specimens with the short-finned squid from Newfoundland waters, one notices the differences in external features. The most noticeable difference exists in the configuration of the head, i.e., these two specimens have heavier and wider heads. Furthermore, the female specimen which measures 212 mm. in mantle length, is completely mature with a pair of long nidamental glands (96 mm. in length) and an enormous ovary filled with ripe ova. In Newfoundland waters, as mentioned earlier, mature females have never been obtained. Females with a mantle length of 300 mm. generally have a poorly-developed ovary weighing less than four grams. Obviously, the short-finned squid from these two areas are different. The differences which exist may be due to environmental or ecological factors.

Studies on the growth of arms and tentacles are omitted in the present effort because of the great deviation due to preservation and handling.

Due to the relatively narrow size range present in this study, it was impossible to study the changes of the several indices used throughout the project in earlier stages of this species. It is intended to complete this study when the larvae and earlier forms of _I. I. illecebrosus_ are available.

In spite of the various publications on the short-finned squid and the now recognized three subspecies, the taxonomy of squid of the genus _Illex_ still remains unclear. Whether the three subspecies are three distinct species, three subspecies, or three geographical races[1] still needs to be systematically studied. However, it is evident that the tail fin configuration remains constant throughout the range of sizes here studied, and can be used as a valid criterion of morphological significance. This is evident when one observes the constancy of the tail fin indices as presented earlier.

[1] G. L. Voss considers that geographical races and subspecies of squid are identical. (Personal communication).

Morphometry of the Mandibles

In spite of numerous descriptions, mandibles of cephalopods have never been studied in detail. Recently, cephalopod mandibles are suddenly discussed. Clarke (1962b) published the first specific study on this subject. More recently, Mangold and Fioroni (1966) reported on the morphology and biometry of the mandibles of 18 species of cephalopods from the Mediterranean region.

In 1959 and 1962, Belyaev published discoveries made by cruises on the Russian oceanographic vessel, the VITIAZ. About a hundred thousand mandibles had been collected in bottom samples from the Pacific Ocean, Indian Ocean, and more particularly in the Arabian Sea and the Gulf of Aden. The concentration of mandibles (up to 15,000 per square metre) has not only revealed the existence of currents but also has given some indications of their direction and speed of transport, etc.

The importance of cephalopod mandibles is now being recognized. Studies of this organ may provide a new tool for the taxonomist, not only in studies at the family or generic rank, but also possible at the specific level. It is true that certain species of cephalopods are known only from their mandibles, especially members of the genus Architeuthis. Of these, A. princeps Verrill and A. monachus Steenstrup are two examples.[1]

Studies of the mandibles may also provide knowledge of predators, of their feeding habits such as selection of the prey squid, both species and size, and their distribution,as well as migration.

[1] Further study of the systematics of the Architeuthidae may prove these are identical species.

The relative growth of various dimensions of the mandibles of I. i. illecebrosus have been shown in Figures 30 through 54. When one compares these values with those presented by Clarke (1962b) in his Table II, several questions are raised. The constants m and c of the various dimensions in the present study are far beyond the values expressed by Clarke for the Family Ommastrephidae in that table (cf. Table VIII).

This is really not too surprising, since Clarke summarily combined mandibles at the family level. The errors one might expect at the generic and specific levels, due to variations in mandibles at these levels, are therefore magnified when one lumps them at the family level, causing a prejudicial slanting and therefore increasing the error. The resultant interpretation for the family would therefore be an erroneous one, and perhaps erroneous to a remarkable degree. Moreover, his sample is too small to represent the family (94 specimens for the entire family Ommastrephidae)*, thus causing a greater bias in his interpretation. Since the method and measurements of this study followed Clarke, I am convinced that for the above-mentioned reasons, the criteria used by Clarke to set morphometric definitions for the Family Ommastrephidae based on mandibles has little value. Certainly, the criteria do not apply to I. i. illecebrosus from Newfoundland.

Mangold and Fioroni (1966) studied 18 species of cephalopods from the Mediterranean region and established a key for their identification.

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*As Clarke (1962b) admits himself (p.432).

Table VIII. Mandible dimensions of *Illex illecebrosus illecebrosus* with comparisons with other ommastrephids (cf. Clarke, 1962b).

I. Upper Mandibles	x	y	m	c
Illex illecebrosus	1	2	2.9986	0.8086
Ommastrephidae			0.97	0.48
Stenoteuthis caroli			0.89	0.50
Todarodes sagittatus			1.00	0.47
Illex illecebrosus	1	3	3.8497	1.6337
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				
Illex illecebrosus	1	4	0.9775	0.5258
Ommastrephidae			1.00	-0.10
Sthenoteuthis caroli			0.98	-0.07
Todarodes sagittatus			1.01	-0.14
Illex illecebrosus	1	5	0.9569	-0.7652
Ommastrephidae			0.92	-0.10
Sthenoteuthis caroli			0.84	-0.07
Todarodes sagittatus			0.94	-0.13

Table VIII (continued)

I. Upper Mandibles	x	y	m	c
Illex illecebrosus	2	4	0.3128	0.4677
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				
Illex illecebrosus	2	5	0.3125	-0.9202
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				
Illex illecebrosus	3	2	0.7797	-0.4801
Ommastrephidae			1.04	-0.11
Sthenoteuthis caroli			0.98	-0.07
Todarodes sagittatus			1.02	-0.11
Illex illecebrosus	3	4	0.2516	0.1587
Ommastrephidae				
Stenoteuthis caroli				
Todarodes sagittatus				
Illex illecebrosus	3	5	0.2478	-1.1555
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				

Table VIII (continued)

I. Upper Mandibles	x	y	m	c
Illex illecebrosus	4	5	0.9380	-1.0614
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				
II. Lower Mandibles				
Illex illecebrosus	1	2	1.0247	0.5916
Ommastrephidae			0.94	-0.02
Sthenoteuthis caroli			0.91	0
Todarodes sagittatus			0.95	-0.03
Illex illecebrosus	1	3	2.4033	0.4729
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				
Illex illecebrosus	1	4	2.2465	-0.7088
Ommastrephidae			0.96	0.23
Sthenoteuthis caroli			1.03	0.24
Todarodes sagittatus			0.97	0.21

Table VIII (continued)

II. Lower Mandibles	x	y	m	c
Illex illecebrosus	1	5	0.9328	-0.3736
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				
Illex illecebrosus	1	6	3.2156	0.2587
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				
Illex illecebrosus	2	4	2.1148	-1.5976
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				
Illex illecebrosus	2	5	0.8942	-0.8273
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				
Illex illecebrosus	2	6	3.0028	-0.8856
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				

Table VIII (continued)

II. Lower Mandibles	x	y	m	c
Illex illecebrosus	3	2	0.4167	0.8946
Ommastrephidae			0.95	-0.25
Sthenoteuthis caroli			0.93	-0.25
Todarodes sagittatus			0.94	-0.24
Illex illecebrosus	3	4	0.8874	0.2297
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				
Illex illecebrosus	3	5	0.3827	-0.1331
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				
Illex illecebrosus	3	6	1.2724	1.5791
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				
Illex illecebrosus	4	5	0.4083	-0.0133
Ommastrephidae				
Sthenoteuthis caroli				
Todarodes sagittatus				

Table VIII (continued)

II. Lower Mandibles	x	y	m	c
Illex illecebrosus Ommastrephidae Sthenoteuthis caroli Todarodes sagittatus	4	6	1.4101	1.4762
Illex illecebrosus Ommastrephidae Sthenoteuthis caroli Todarodes sagittatus	5	6	3.3105	2.0772

Dimensions compared are 1: rostral length
2: hood length
3: crest length
4: wing length
5: rostral width
6: lateral wall length

The relationship between two dimensions has the general form $y = mx + c$.

Number of Illex used in this study was 400.

It is apparent that characteristics described by them for I. coindeti (=I. i. coindeti) applied generally to I. i. illecebrosus. Through the kindness of Dr. Katharina Mangold, the author has received a sample of mandibles from specimens of I. i. coindeti. The cutting edge of the upper mandibles in this sample is rather smooth, a situation unlike that in I. i. illecebrosus where it is serrated (Figures 79 and 80).

It is interesting that Zuev (1966) in his contribution on the systematics of the decapod genus Illex presented illustrations of the mandibles of I. illecebrosus from three regions. Upon examination of his illustrations and Figure 79, one could interpret the upper mandibles from Newfoundland as a combination of Zuev's three types. That is, it is characterized by the long and concurved rostrum of his African type (Form A); the serrated or toothed cutting edge of his Adriatic Sea type (Form B); and the large notch between rostrum and wing of his North Atlantic type (Form C). I do not doubt his observation but merely question the existence of individual and geographical variations. Since his sample consisted of only 15 specimens (six of Form A, five of Form B and four of Form C) from such a widely defined area, obviously the material is inadequate to serve as the basis of a sweeping re-evaluation of the genus. At least, mandibles of Illex illecebrosus illecebrosus from Newfoundland does not fit the criteria he established.

As the relative growth among those dimensions studied is a straight-line relationship, it is obvious that the growth of the mandibles is isometric. Since differences in growth rate exist in different species,

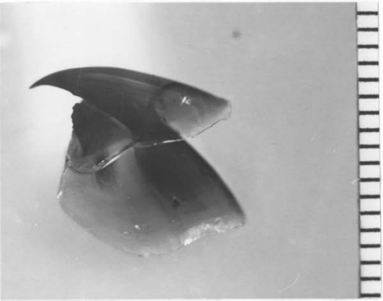

Figure 79. Upper Mandible of Illex illecebrosus illecebrosus from Newfoundland.

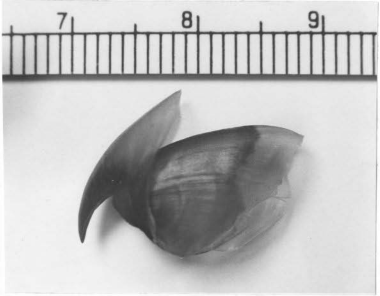

Figure 80. Upper mandible of Illex illecebrosus coindeti from Las Rosas, Spain.

there is no reason why mandibles of cephalopods can not be used as a taxonomical tool. If the geographical variations do exist so obviously as Zuev (1966) has described, mandibles may be considered as a powerful tool to solve the, as yet unsolved, problems of the taxonomy of the genus Illex, since mandibles and the gladius, or pen, are the only two parts of this animal which experience little, if any, change upon fixing and preservation. However, the individual variations and the fact of wearing away of the rostral tip, especially in larger or older individuals,should be taken into consideration.

As mentioned previously, studies of the cephalopod mandibles may provide knowledge of squid predators. Since cephalopods, especially squid, are a very important food item for larger marine animals such as tuna, whales and sea birds, and if one can identify cephalopod mandibles to specific levels and knows the relationship between mandibles and animal size, knowledge of the predator's feeding habit can be determined by an analysis of the mandibles in the gut of the predator. Information so learned can include the selection of food, the distribution and migration may then be elucidated. Cephalopod mandibles are the only part of the animal, with the exception of the lens of the eye, which is readily found undigested in the stomach contents (Aldrich and Bradbury, 1968).

Clarke (1962c) analyzed the stomach contents of the sperm whales and calculated the body weight of the cephalopods taken by the cetacean. Sergeant (1962) and more recently Aldrich and Bradbury (1968) also studied stomach contents of the pilot or pothead whale, Globicephala melaena (Traill) in Newfoundland waters and found I. i. illecebrosus and Gonatus fabricii, especially the former, to be the main food item.

Data in Tables VI and VII provide information on the correlation between mandible size and animal size and weight of I. i. illecebrosus in the Newfoundland area. These correlations are evidently valid and may be used to convert mandible size to animal size and weight.

In a recent effort to do much the same thing, Clarke (1962b) studied the relationship between mandible size and total body weight. He plotted both measurements on log-log paper, using the equation $\log y = m \log x + \log c$. However, as was pointed out by Van Norman (1963) it is almost a laboratory joke that use of log-log paper makes a straight line out of any set of data. Since the length-weight relationship represents a curve rather than a straight line, I am convinced that the calculation using $W = aL^n$ would be more accurate and more close to the natural state.

Since individual variations exist throughout the animal kingdom, the accuracy of these two Tables (VI and VII) is only within certain limits, as can be demonstrated by cross checking observed with calculated values for either weight or mantle length (see Appendix 1). However, despite what Clarke (1962b) thought, I agree with Mangold and Fioroni's (1966) opinion that the relationship between mandible size and dorsal mantle length is more accurate and of greater value than that between mandible size and body weight. Weight is an extremely variable factor, since the nutritional condition and sexual maturity of the animal, whether it be in a pre- or post-spawning period affect it to a great extent.

Pigmentation of the Lower Mandibles

Clarke (1962, a, b) did not ignore pigmentation in his study of the mandibles of cephalopods. Indeed, he described the distribution and spreading of pigmented areas in the mandibles of such species as Sthenoteuthis caroli and Todarodes sagittatus of the Family Ommastrephidae. Mangold and Fioroni (1966) studied the ontogenic stages in both morphology and, to a lesser extent, pigmentation of the mandibles of 18 species, including I. i. coindeti .

It is believed that this present work clearly establishes that a correlation exists between the increasing size of the mandible (and therefore, the increasing size of the squid) and with the extent or degree of pigmentation of the wing of the lower mandible. This has been shown quantitatively, as well as qualitatively. That this is true places Clarke's (1962, a, b; 1965, 1966) assumption that "it would be possible to distinguish between many specimens . . . on the basis of the darkening process (of the beak)" (1962b, p. 436) in doubt, since pigmentation is clearly a function of size.

Furthermore, pigmentation is also a function of sexual maturity. As data here presented show, male I. i. illecebrosus in Newfoundland waters mature at an earlier time than do the females. The darkening process of the male mandible is much more rapid than it is in the case of females, as can be seen from a comparison of the data presented in Figures 71 and 73. This may be associated with as yet uninvestigated hormonal changes concurrent with the advent of sexual maturity in the male, as is the production of the hectocotylus, although the site of production of these postulated hormones need not be the primary sex organs (Callan, 1940). It is here postulated that the pigmentation of the wing of the lower mandible be considered as but another secondary sexual characteristic of *I. i. illecebrosus*.

In all fairness one must acknowledge that Clarke (1962b, p. 436) stated, "the size at which darkening (of the mandible) takes place differs in the two sexes of species adequately represented in the collection, and the onset of maturity nearly coincides with the intermediate stage of the beak. This suggests a relationship between darkening and sexual maturity". Clarke's contribution, however, does not present data of a scale or nature to warrant his conclusion. However, he is undoubtedly correct in his overall assumption.

Microrings on the Lower Mandibles

In spite of being considered as belonging to the same group of animals (Phylum Mollusca), age-determination in pelecypods is greatly different from in cephalopods. In pelecypods, growth rings on the shell have been used and are considered as a reliable means of aging (Comfort, 1957), on the contrary, aging in cephalopods has long been a troublesome problem.

As was mentioned previously, very little has been published about growth of cephalopods, with the exception of some species of proven commercial importance, i.e., *Loligo vulgaris* (Tinbergen and Verwey, 1945),

L. opalescens (Fields,1950, 1963, 1965), Illex illecebrosus illecebrosus (Squires, 1957, 1967), Todarodes pacificus (Katoh, 1959) and T. sagittatus (Fridriksson, 1943). Growth in these species was studied by determining the size groups present in samples of a population and employing Peterson's methods which are generally acceptable in fisheries biology. This method has several disadvantages, however. The sample may be too small to show age groups, or the selection of sampling gear may lead to the capture of some sizes of animals, and not others, thereby distorting the conclusions obtained. For these reasons, biologists have long been seeking a method for aging cephalopods similar to scale reading in fish and growth ring analysis in pelecypods.

Yagi (1960b)and Choe (1963), both studied the sepions or cuttlebones of Sepia esculenta Hoyle, and found that the shell stripe pattern thereon increased with age. Earlier workers, such as Appellöf (1893), Naef (1928) and Yasuda (1951), had shown that the "growth" of the shell stripe pattern followed a "set periodicity". This periodicity, by its very nature, would lead one to suspect that there is a time element involved in its formation. Choe (1963) rightly indicated that the periodicity of the stripe-pattern on the sepion in S. esculenta is under the influence of certain nutritive and environmental factors. However, under good conditions of nourishment the addition of striped lines in the sepion averaged one per day (Choe, 1963). Yagi (1960b)concluded from his study that "the number of stripes is preferable to the shell length for age determination". Thus, a means of aging at least one species of cephalopod was established.

The first report of the presence of microrings on cephalopod mandibles was that of Clarke (1965). He found that the distance between microrings on the lower mandibles of Moroteuthis ingens (Smith) varied in width and that these variations occur in cycles. He predicted the possibility of relating cycle formation to periods of growth of the squid, even though he did not establish what the actual relationship between these two phenomena would be.

As was indicated in Figure 75, a positive relationship exists between the number of microrings and the mantle length of the short-finned squid. However, cyclic arrangements of these microrings could not be demonstrated, although they may exist. If the microrings in I. i. illecebrosus are arranged in cycles as in the case of M. ingens, the variation may be due to some environmental influences such as food availability or water temperature, as was suggested by Clarke (1965) and shown by Choe (1963) to be true in the case of stripe-line formation in Sepia esculenta.

Squires (1957), using Bertalanffy's (1938) formula $L_t = L_\infty (1 - e^{-kt})$, calculated the growth rate of I. i. illecebrosus and concluded that "most of the squid taken by fishermen inshore in Newfoundland would appear to be less than one year old. The majority of these probably spawn and die during the following winter at an age of about one year". However, as was discussed before, the selection of gear for the capture of this animal may lead to some sizes being favoured in the data. Moreover, the life history of this species still remains unclear. There is no reason to postulate that this species does not have a two-year life cycle with a long larval life, although it seems unlikely, as it is difficult to explain the life history as it can be read from available specimens.

The problem of age determination in cephalopods still remains to be solved. Both Clarke (1965) and the author suggest that microrings on the mandibles may be a source of the necessary information, although this method has great disadvantages, namely, the absence of mandibles from early stages or juveniles and the wearing away of the rostral tip. Obviously, if the rostral tip is destroyed, so is the evidence of early microrings.

Recently, the author and his colleagues have developed a technique to detect what appear to be growth rings on the otoliths of _I. i. illecebrosus_ (Figure 81). This figure represents a cleared, stained otolith dissected from a squid. It was cleared in xylene and then stained with aceto-carmine. In the otolith, as in this photograph, can clearly be seen what is referred to here as "growth rings", which appear as concentric lines about the center. Unfortunately, all of these lines are not on the same focal plane, and those nearer the center in this photograph are not visible. There definitely seems to be a periodic cycle to the arrangement of these concentric rings, but study of this is still in progress. The significance of this discovery must await further analysis. It is hoped that the use of the analysis of lines in the otoliths would overcome the disadvantages inherent in the use of mandibles, in that a complete growth record would exist, supposedly buried safely in the cephalic cartilages. However, the problem remains of using gear that would enable us to secure specimens of all sizes of squid present at a given time in Newfoundland waters.

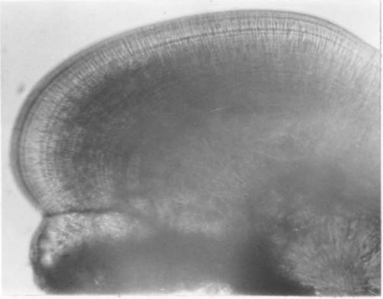

Figure 81. Otolith of Illex illecebrosus illecebrosus showing concentric growth lines.

Aldrich (personal communication) has indicated that some form of regular and periodically arranged lines appear, upon clearing and staining, in the gladius or pen of _I. i. illecebrosus_. Therefore, it may be that the otoliths, mandibles and gladius in this decapod all leave a record of their growth which awaits further study and decoding.

CONCLUSIONS

At least two different populations or generations of the short-finned squid Illex illecebrosus illecebrosus (LeSueur) take part in the inshore migration in Newfoundland waters each year.

The sex ratio in monthly samples from July to October suggests that this squid spawns in Newfoundland waters, the males leaving the inshore populations during the months of September and October.

There is no predominant food selection in the short-finned squid. The high incidence of cannibalism during the inshore migration is due to the scarcity of other food organisms. It is contended that the observed cannibalism is a natural phenomenon and is not an accidental, artificial condition associated with capture.

Both the head and the mantle increase in length at a faster rate than they do in width. The fin shape maintains constancy throughout the size range studied, indicating that its growth is isometric. Males longer than 195 mm. in mantle length are heavier than females of the same size. This is due to the rapid development in liver and gonad.

Growth of the mandibles is isometric, that is, the relationship between their various dimensions can be expressed by the formula $y = m x + c$. The conversion from mandible size to mantle length is more valid and of greater value than the conversion to total body weight in the study of cephalopod mandibles collected from predators, despite what M. R. Clarke (1962b) contends.

The pigmentation on the wings of the lower mandibles of _I. i. illecebrosus_ varies with the size of the squid and is correlated with sexual maturity.

Microrings present on the lateral wall of the lower mandibles increase in number as the length of the squid increases. Further studies on these microrings and the concentric "growth rings" found on the otolith may prove to be valid means for aging cephalopods.

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APPENDIX I

Data and calculations demonstrating relationship between calculated and observed mantle length and total body weight, based on criteria from mandible measurements.

RL	Rostral Length in mm.
HL	Hood Length in mm.
CL	Crest Length in mm.
LWL	Lateral Wall Length in mm.
ML meas.	Mantle Length in mm. (measured)
ML calc.	Mantle Length in mm. (calculated)
WE meas.	Body Weight in gms. (measured)
WE calc.	Body Weight in gms. (calculated)

Selected Sample in each instance is 40.

I. UPPER MANDIBLE

A. Based on Rostral Length

RL	ML meas.	ML calc.	Accuracy %	WE meas.	WE calc.	Accuracy %
3.5	209	196.1	93.83	156.6	126.9	81.03
4.0	210	218.5	95.95	176.8	183.0	96.49
3.9	215	214.0	99.53	187.3	170.8	91.19
3.6	213	200.6	94.18	152.4	137.1	89.96
4.1	213	223.0	93.90	178.2	195.8	90.12
4.5	226	240.9	93.41	208.1	253.3	79.28
4.8	228	254.4	88.42	273.0	301.6	89.52
3.9	229	214.0	93.45	181.8	170.8	93.95
4.2	235	227.5	96.80	236.6	209.2	88.42
4.3	237	232.0	97.89	199.8	223.2	88.29
4.8	237	254.4	92.66	264.7	301.6	82.28
4.3	235	232.0	98.87	245.1	223.2	91.06
5.0	247	263.3	93.40	268.8	337.5	74.45
4.4	240	236.4	98.50	247.2	237.8	96.20
4.6	245	245.4	99.94	234.8	268.6	85.61
4.6	242	245.4	98.60	273.5	268.6	98.21
5.0	247	263.3	93.40	348.1	337.5	96.95
5.3	252	276.8	90.16	312.6	396.0	73.32
5.4	250	281.2	88.52	388.3	414.0	93.38
5.5	252	285.7	86.63	392.5	430.4	88.31
5.7	254	294.7	83.98	347.1	483.0	60.85
4.9	266	258.8	97.29	224.5	319.3	57.78
4.7	263	249.9	95.02	220.4	284.9	70.73
4.8	262	254.4	97.10	316.2	301.6	95.38
5.4	276	281.2	98.12	374.9	414.0	89.57
5.3	278	276.8	99.57	384.2	396.0	96.93
5.8	270	299.2	89.19	363.1	507.0	60.37
5.7	281	294.7	95.12	330.6	483.0	53.90
5.6	280	290.2	96.36	350.7	460.5	68.69
5.8	281	299.2	93.52	423.3	507.0	80.23
6.0	282	308.1	90.75	430.5	556.5	70.73
4.8	287	254.4	88.64	496.6	301.6	60.73
5.9	290	303.7	95.76	415.1	531.5	71.96
5.2	299	272.3	91.07	484.1	375.8	77.63
5.5	294	285.7	97.18	553.1	438.4	79.26
6.6	305	335.0	90.16	548.0	722.4	68.18
6.0	309	308.1	99.71	602.6	556.5	92.35
6.0	301	308.1	97.64	531.9	556.5	95.38
6.3	303	321.6	93.86	628.3	636.0	98.78
5.7	311	294.7	94.76	529.4	483.0	91.24

I. UPPER MANDIBLE

B. Based on Hood Length

HL	ML meas.	ML calc.	Accuracy %	WE meas.	WE calc.	Accuracy %
13.0	210	222.0	94.29	176.8	196.8	88.69
13.8	212	233.8	89.72	190.1	232.0	77.96
12.5	215	214.6	99.81	187.3	176.8	94.39
11.3	213	196.9	92.44	152.4	134.0	87.93
10.9	212	191.0	90.09	170.7	121.3	71.06
13.6	213	230.8	92.29	178.2	222.6	75.08
11.4	209	198.4	94.93	156.6	137.2	87.61
14.0	226	236.7	95.27	208.1	241.1	84.15
14.8	228	248.5	91.01	273.0	280.9	97.11
12.6	229	216.1	94.37	181.8	180.7	99.39
12.3	228	211.6	92.81	212.8	169.0	79.42
12.9	238	220.5	92.65	265.7	192.7	72.53
12.2	230	210.2	91.39	206.0	165.3	80.24
14.3	237	241.1	98.27	199.8	255.6	72.08
16.0	247	266.2	92.23	268.8	347.8	70.61
14.4	240	242.6	98.92	259.0	260.6	99.38
15.5	242	258.8	93.06	273.5	318.9	83.40
15.0	247	251.5	98.18	348.1	291.4	83.71
16.7	251	276.5	89.84	312.1	391.2	74.66
15.4	252	257.4	97.86	312.6	313.2	99.81
16.4	250	272.1	91.16	388.3	380.7	98.04
17.2	252	283.9	87.34	392.5	424.1	91.95
16.3	262	270.6	96.72	405.8	366.0	90.19
15.2	262	254.4	97.10	316.2	302.1	95.54
17.0	276	281.0	98.19	374.9	410.7	90.45
17.5	278	288.3	98.10	384.2	444.6	84.28
16.4	274	272.1	99.31	434.1	372.2	85.74
16.9	276	279.5	98.73	441.7	404.2	91.51
16.8	278	278.0	100.00	402.2	397.6	98.86
16.5	270	273.6	98.67	363.1	378.5	95.76
16.7	281	276.5	98.40	330.6	391.2	81.67
18.8	281	307.5	90.50	423.3	541.5	72.08
17.6	288	289.8	99.37	450.1	451.7	99.64
18.4	294	301.6	97.41	553.1	510.3	92.26
19.4	294	316.4	92.38	521.4	590.1	86.82
17.9	291	294.2	98.90	421.3	473.3	87.66
19.5	305	317.8	95.80	548.0	598.4	90.80
19.9	309	323.7	95.24	602.6	633.0	94.96
18.6	304	304.6	99.80	577.8	525.6	90.97
18.2	311	298.7	96.05	529.4	495.4	93.58

I.UPPER MANDIBLE

C. Based on Crest Length

CL	ML meas.	ML calc.	Accuracy %	WE meas.	WE calc.	Accuracy %
15.9	209	205.3	98.23	156.6	151.3	96.62
17.0	210	218.1	96.14	176.8	184.0	95.93
16.3	215	210.0	97.67	187.3	162.7	86.87
16.8	213	215.8	98.69	152.4	177.7	83.40
14.4	212	187.8	88.58	170.7	113.1	66.26
16.7	213	214.6	99.25	178.2	174.7	98.04
18.4	226	234.4	96.28	208.1	232.0	88.52
19.2	228	243.7	93.11	273.0	262.9	96.30
17.3	228	221.6	97.19	212.8	193.6	90.98
18.2	236	232.1	98.35	254.4	224.8	88.36
18.6	238	236.7	99.45	265.7	239.6	90.18
19.0	237	241.4	98.14	264.7	255.1	96.37
17.8	235	227.4	96.77	245.1	210.6	85.92
19.4	247	246.1	99.63	268.8	271.0	99.18
18.9	240	240.2	99.92	247.2	251.1	98.42
19.2	240	243.7	98.46	259.0	262.9	98.49
20.1	242	254.2	94.96	273.5	300.8	90.02
19.7	247	249.6	98.95	348.1	283.6	81.47
21.0	251	264.7	94.54	312.1	342.0	90.42
20.2	252	255.4	98.65	312.6	305.3	97.66
22.6	250	283.3	86.68	388.3	424.1	90.78
22.7	254	284.5	87.99	347.1	429.6	76.23
21.5	266	270.5	98.31	224.5	366.3	36.84
20.3	263	256.5	97.53	220.4	309.6	59.53
20.9	262	263.5	99.43	405.8	337.1	83.07
20.4	262	257.7	98.36	316.2	314.1	99.34
23.1	274	289.2	94.45	434.1	452.3	95.81
22.0	278	276.4	99.42	402.2	391.9	97.44
20.0	280	253.1	90.39	350.7	296.3	84.49
23.0	281	288.0	97.51	423.3	446.5	94.52
24.1	282	300.8	93.34	430.5	513.5	80.72
23.5	285	293.8	96.91	435.7	475.8	91.80
22.8	290	285.7	98.52	415.1	435.1	95.18
23.9	299	298.5	99.83	484.1	499.8	96.76
25.0	294	311.3	94.12	553.1	570.0	96.94
25.4	305	316.0	96.39	548.0	597.3	91.00
26.6	309	330.0	93.20	602.6	684.0	86.49
24.8	304	309.0	98.36	577.8	557.1	96.42
24.0	301	299.7	99.57	531.9	505.8	95.09
24.6	311	306.6	98.59	412.0	543.7	92.31

II. LOWER MANDIBLE

A. Based on Rostral Length

RL	ML meas.	ML calc.	Accuracy %	WE meas.	WE calc.	Accuracy %
3.4	208	204.1	98.13	150.4	147.2	97.87
4.0	209	233.0	88.52	156.6	227.9	54.47
3.6	210	213.7	98.24	176.8	171.6	97.06
3.3	212	199.3	94.01	190.1	135.8	71.44
3.0	215	184.8	85.95	187.3	105.1	56.11
3.2	218	194.4	89.17	199.8	125.0	62.56
3.7	213	218.6	97.37	152.4	184.8	78.74
3.6	212	213.7	99.10	170.7	171.6	99.47
3.9	213	228.2	92.86	178.2	212.9	80.53
4.3	226	247.5	90.49	208.1	276.7	67.04
4.0	227	233.0	97.36	185.4	227.9	77.08
3.5	229	208.9	91.22	181.8	159.1	87.51
3.8	221	223.4	98.91	226.1	198.5	87.79
4.7	235	266.8	86.47	236.6	351.4	51.48
4.0	230	233.0	98.70	206.0	227.9	89.37
3.9	235	228.2	97.11	245.1	212.9	86.86
4.7	240	266.8	88.84	259.6	351.4	64.64
3.8	240	223.4	93.08	247.2	198.5	80.30
4.1	245	237.9	97.10	234.8	243.4	96.34
4.4	240	252.3	94.87	259.0	294.4	86.33
5.0	247	281.3	86.11	348.1	415.1	80.75
4.3	252	247.5	98.21	312.6	276.7	88.52
4.5	250	257.1	97.16	388.3	312.6	80.50
4.7	266	266.8	99.70	224.5	351.4	43.47
4.3	266	247.5	93.05	365.7	276.7	75.66
4.6	278	262.0	94.24	384.2	331.8	86.36
5.0	276	281.3	98.08	441.7	415.1	93.98
5.0	278	281.3	98.82	402.2	415.1	96.79
5.3	281	295.7	94.77	330.6	485.4	53.18
5.2	281	290.9	96.48	423.3	461.1	91.07
5.8	282	319.8	86.60	430.5	618.3	56.38
5.2	288	290.9	98.99	450.1	461.1	97.56
5.5	299	305.4	97.86	427.5	536.2	74.57
5.0	291	281.3	96.67	476.9	415.1	87.04
6.0	305	329.5	91.97	548.0	677.5	76.37
5.6	309	310.2	99.61	602.6	562.8	93.40
5.3	304	295.7	97.27	577.8	485.4	84.01
6.0	303	329.5	91.25	628.3	677.5	92.17
5.7	311	315.0	98.71	412.0	590.1	56.77
5.3	311	295.7	95.08	529.4	485.4	91.69

II. LOWER MANDIBLE

B. Based on Hood Length

HL	ML meas.	ML calc.	Accuracy %	WE meas.	WE calc.	Accuracy %
4.3	208	216.7	95.82	150.4	177.7	81.85
3.5	209	178.9	85.60	156.6	96.8	61.81
4.5	210	224.9	92.90	176.8	203.3	85.02
4.6	215	229.5	93.26	187.3	216.9	84.20
4.4	218	220.3	98.94	199.8	190.3	95.25
4.5	213	224.9	94.41	152.4	203.3	66.60
4.1	212	206.5	97.41	170.7	154.4	90.45
4.5	213	224.9	94.41	178.2	203.3	85.91
4.8	226	238.7	94.38	208.1	245.8	81.84
5.0	228	247.9	91.27	173.0	277.5	39.60
4.3	229	216.7	94.63	181.8	177.7	97.74
4.8	228	238.7	95.31	212.8	245.8	84.49
4.6	238	229.5	96.43	265.7	216.9	81.64
4.7	237	234.1	98.78	199.8	231.1	84.34
4.4	247	220.3	89.19	268.8	190.3	70.80
5.3	240	261.7	90.96	259.0	329.5	72.78
5.4	247	266.3	92.19	348.1	348.2	99.93
6.2	251	303.1	79.24	312.1	523.6	32.24
5.0	252	247.9	98.37	312.6	277.5	88.77
5.3	252	261.7	96.15	392.5	329.5	83.95
5.8	266	284.7	92.97	324.5	430.0	67.49
5.0	262	247.9	94.62	405.8	277.5	68.38
5.0	262	247.9	94.62	316.2	277.5	87.76
5.5	274	270.9	98.87	434.1	429.9	99.03
6.5	276	316.9	87.09	441.7	601.9	63.73
6.0	270	293.9	91.15	363.1	475.4	69.07
5.2	280	257.1	91.82	350.7	311.4	88.79
6.0	282	293.9	95.78	430.5	475.4	89.57
5.4	285	266.3	93.44	435.7	348.2	79.92
5.3	287	261.7	91.18	496.6	329.5	66.35
5.7	299	280.1	93.68	427.5	408.5	95.56
6.3	291	314.0	92.10	476.9	548.6	84.97
6.5	294	316.9	92.21	521.4	601.9	84.56
7.0	305	339.9	88.56	548.0	749.1	63.30
6.6	309	321.5	95.95	602.6	629.4	95.55
6.6	304	321.5	94.24	577.8	629.4	91.07
6.2	301	303.1	99.30	531.9	523.6	98.44
7.0	311	339.9	90.71	412.0	749.1	19.18
6.0	311	293.9	94.50	529.4	475.4	89.80

II. LOWER MANDIBLE

C. Based on Crest Length

CL	ML meas.	ML calc.	Accuracy %	WE meas.	WE calc.	Accuracy %
7.2	209.	196.4	93.97	156.6	133.4	86.19
8.9	212	229.3	91.84	190.1	220.3	94.63
9.3	215	237.1	89.72	187.3	244.5	69.46
9.8	218	246.7	86.83	199.8	276.7	61.51
7.4	211	200.2	94.88	141.1	142.4	99.08
9.5	213	240.9	86.90	178.2	257.0	55.78
9.0	226	231.2	97.70	208.1	226.2	91.30
9.6	228	242.9	93.46	173.0	263.5	47.69
9.4	227	239.0	94.71	185.4	250.7	64.78
8.4	229	219.6	95.90	181.8	192.2	94.28
9.9	221	248.7	87.47	226.1	283.4	74.66
9.8	236	246.7	95.47	254.4	276.7	91.23
9.0	230	231.2	99.48	206.0	226.2	90.19
9.7	237	244.8	96.71	199.8	270.1	64.81
9.1	235	233.2	99.23	245.1	232.2	94.74
9.5	267	240.9	97.53	268.8	257.0	95.61
8.7	240	225.4	93.92	247.2	208.8	84.47
9.7	245	244.8	99.92	234.8	270.1	84.97
11.5	242	279.7	84.42	273.5	404.0	52.29
11.0	251	270.0	92.43	312.1	363.7	83.47
10.3	250	256.4	97.44	388.3	311.2	80.14
10.3	252	256.4	98.25	392.5	311.2	79.29
11.5	254.	279.7	89.88	347.1	404.0	83.61
10.6	263	262.2	99.70	220.4	333.2	48.82
10.4	266	258.4	97.14	365.7	318.4	87.07
10.2	276	254.5	92.21	374.9	304.1	81.11
12.3	278	295.2	93.81	384.2	473.7	76.70
10.9	274	268.1	97.85	434.1	355.9	81.99
11.5	278	279.7	99.39	402.2	404.0	99.50
11.0	281	170.0	96.09	330.6	363.7	89.99
12.0	280	289.4	96.64	350.7	446.9	72.57
11.6	281	281.6	99.79	423.3	412.5	97.45
12.1	288	291.3	98.85	450.1	455.7	98.76
12.2	287	293.3	97.80	496.6	464.7	92.50
11.9	299	287.4	96.12	427.5	437.9	97.57
12.6	291	301.0	96.56	476.9	501.6	92.72
11.9	291	287.4	98.76	421.3	437.9	96.06
14.1	309	330.1	93.17	602.6	654.1	91.45
11.0	301	270.0	89.70	531.9	363.7	68.38
13.8	311	324.3	95.72	412.0	621.9	49.05

II. LOWER MANDIBLE

D. Based on Lower Lateral Wall Length

LWL	ML meas.	ML calc.	Accuracy %	WE meas.	WE calc.	Accuracy %
11.9	210	215.9	97.19	176.8	179.8	98.30
11.3	212	207.1	97.69	190.1	157.2	82.69
11.3	215	207.1	96.33	187.3	157.2	83.93
11.0	213	202.7	95.16	152.4	146.6	96.19
10.0	212	188.1	88.73	170.7	114.4	67.02
13.9	226	245.1	91.55	208.1	269.5	70.49
13.7	228	242.2	93.77	173.0	259.5	50.00
12.0	229	217.4	94.93	181.8	183.8	98.90
13.0	221	232.0	95.02	226.1	226.4	99.87
12.9	238	230.5	96.85	265.7	221.9	83.52
13.7	237	242.2	97.81	199.8	259.5	65.62
12.0	240	217.4	90.58	259.6	183.8	70.80
12.5	240	224.7	93.63	247.2	204.5	82.73
13.8	240	243.6	98.50	257.0	264.6	97.84
14.4	242	252.4	95.70	273.5	295.5	91.96
14.3	247	251.0	98.38	348.1	290.2	83.37
15.8	251	272.9	91.27	312.1	376.4	79.40
14.4	252	252.4	99.84	312.6	295.5	94.53
14.7	250	256.8	97.28	388.3	311.7	80.27
16.1	252	277.3	89.96	392.5	395.1	99.34
15.9	266	274.3	96.88	224.5	382.4	29.67
15.2	262	264.1	99.20	405.8	340.1	83.81
14.7	262	256.8	98.02	316.2	311.7	98.58
16.4	278	281.6	98.71	384.2	414.5	92.11
16.5	276	283.1	97.43	441.7	421.2	95.36
15.9	278	274.3	98.67	402.2	382.4	95.08
15.5	270	268.5	99.44	363.1	357.8	99.09
16.4	280	281.6	99.43	350.7	414.5	81.81
17.2	281	293.3	95.62	423.3	469.2	89.16
17.8	282	302.1	92.87	430.5	513.1	80.81
18.3	288	309.4	92.57	450.1	551.6	77.45
16.7	285	286.1	99.61	435.7	434.6	99.75
16.4	290	281.6	97.10	415.1	414.5	99.86
17.3	299	294.8	98.60	484.1	476.3	98.39
17.9	294	303.5	97.77	521.4	520.8	99.88
16.7	291	286.1	98.32	421.3	434.6	96.84
19.0	305	319.6	95.21	548.0	608.3	89.00
17.3	304	294.8	96.97	577.8	476.3	82.43
18.0	301	305.0	98.67	531.9	528.4	99.34
18.8	303	316.7	95.48	628.3	591.7	94.17