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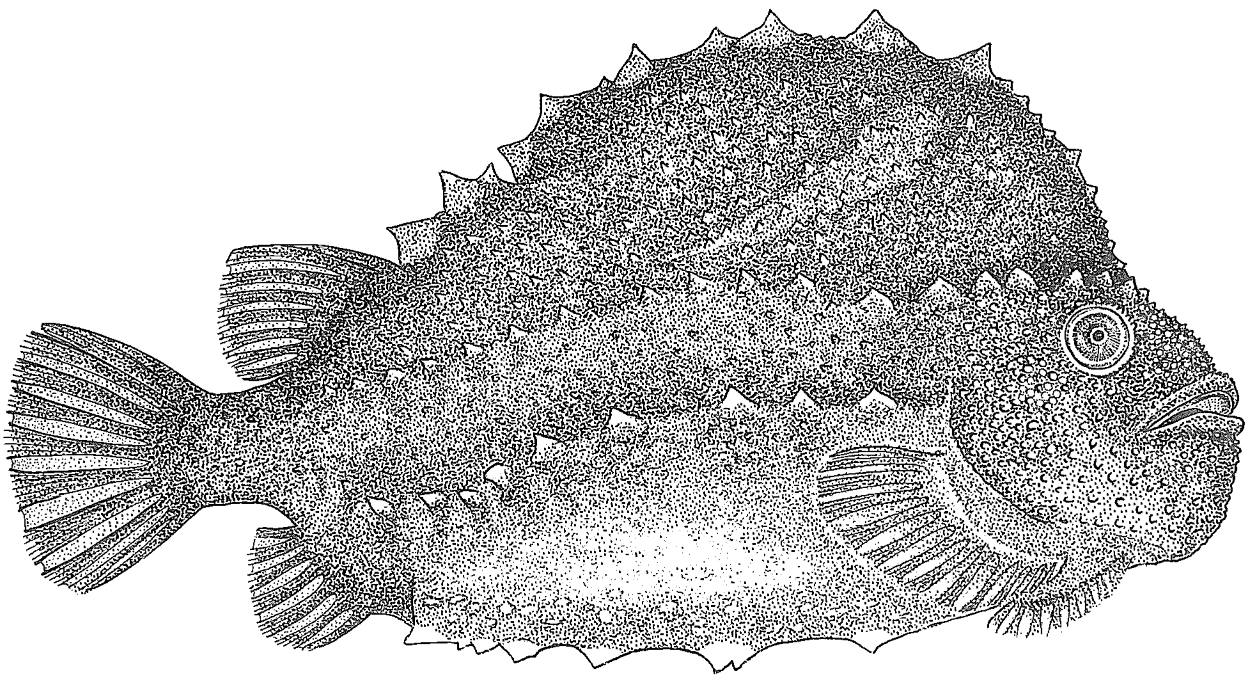
SYNOPSIS OF BIOLOGICAL DATA ON THE LUMPSUCKER
Cyclopterus lumpus (Linnaeus, 1758)



FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

SYNOPSIS OF BIOLOGICAL DATA ON THE LUMPSUCKER

Cyclopterus lumpus (Linnaeus, 1758)

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PREPARATION OF THIS SYNOPSIS

This synopsis has been prepared in view of the importance of *Cyclopterus lumpus* in the fisheries of the Eastern North Atlantic.

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ABSTRACT

This synopsis compiles and reviews the presently available information on identity, distribution, bionomics, life history, population structure and dynamics, exploitation, aquaculture and weed control potential of the lumpsucker, *Cyclopterus lumpus* (Linnaeus, 1758).

Distribution:

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FAO Fisheries Department
FAO Regional Fisheries Officers
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1. IDENTITY

1.1 Nomenclature

1.1.1 Valid name

Cyclopterus lumpus Linnaeus, 1758; Figure 1.

1.1.2 Objective synonymy

Cyclopterus lumpus Linnaeus after Artedi (1738)
Cyclopterus lumpus Linnaeus, 1758
Cyclopterus minutus Pallas, 1769
Cyclopterus lumpus var. *hudsonius* Cox, 1920
After Ueno (1970).

1.2 Taxonomy

1.2.1 Affinities

- Suprageneric

Kingdom Animalia
Phylum Chordata
Subphylum Vertebrata
Superclass Gnathostomata
Class Osteichthyes
Subclass Actinopterygii
Infraclass Teleostei
Division Euteleostei
Superorder Acanthopterygii
Series Percomorpha
Order Scorpaeniformes
Family Cyclopteridae
Subfamily Cyclopterinae

- Generic diagnosis

Body compressed anteriorly and posteriorly, somewhat polygonal in transverse section at the middle of the body. Head short and thick, subquadrangular in cross section. Snout blunted, rounded. Mouth terminal, opening slightly upwards. Teeth simple, small, conical, and arranged in several rows anteriorly. Eye moderate in size, laterally. The first dorsal fin covered by thick skin, forming a high and long crest with large compressed tubercles on the front and top of the crest in adult fish. Height of crest increases with age, the back is much humped in old specimens, so the depth of body changes with growth stage; in large specimens it is nearly equal to half the whole length of the body, but is much less than half the length in small young specimens. There are three longitudinal rows of large compressed tubercles on the side of the body; the uppermost row begins above the eye and continues behind the gill opening to the base of the caudal fin without interruption; the middle row begins above the pectoral fin, runs backwards in parallel with the upper row, and also reaches the base of the caudal fin; the lower row runs along the lower edge of the body from behind the pectoral fin to the front of the anal fin. There are 2-3 pairs of tubercles between the first and second dorsal fins forming a square structure. The sucker is slightly longer than wide and about 1/5-1/6 of the body length. Sensory canals on the head are well developed; there is a pore between the postorbital and suprabranchial pores. There are 5 pores on the infraorbital and 6 on the opercular-mandibular canals.

The preorbital bone is larger than the first suborbital bone; the second suborbital comparatively large. The suborbital stay is trapezoid in form with subequal upper and lower edges. The hyomandibular bone is broad, its width greater than half its length. The metapterygoid lamina bears a braod projection on its inner surface, the tip of this projection closely fits the lateral side of the hyomandibular process, and makes an oblong interrosseous space between the hyomandibular and the posterior margin of the metapterygoid lamina. The opercular bone is triangular, with a wide base and a high wing on the outer edge. The subopercular bone is broad anteriorly, but very slender posteriorly; a projection extends to the middle of the inner edge of the opercular bone, ending in a sharp tip. The interopercular bone is wide and slightly concaved. The outer edge of the prefrontal bone is short and slightly notched on the anterior margin. The frontals are as long as wide, and are nearly square in form; each sends out a thin projection which overhangs the greater part of the eye. The hyper- and hypo-coracoids are small; the actinosts somewhat separated from each other and without distinct foramina between them. The ventral spine has a sharp, strong hook on its back.

The intestine is long, being more than twice the length of the body in adult fish, with many bends. There are numerous pyloric caecae (36-79). Vertebral number ranges from 29-30. (slightly modified by the author from Ueno, 1970).

- Specific diagnosis

An Atlantic lumpsucker with a large, humped dorsal crest which overgows the first dorsal fin so that no free rays are visible. Three longitudinal rows of compressed tubercles on the side of the body and large gill slits extending below the upper corner of the pectoral fin bases.

Dorsal spines 6-8, dorsal rays 9-11, anal rays 9-10, pectoral rays 19-20, caudal rays 11-12, vertebrae 29-30 (11+18 to 19). (Smitt, 1892; Ueno, 1970).

1.2.2 Taxonomic status

Cyclopterus lumpus is a unique species, well established on morphological grounds (see Ueno, 1970 for review), with no close relatives. It is the only species of the genus *Cyclopterus*.

1.2.3 Subspecies/races

Lumpsuckers from cold and/or low salinity areas (e.g., Baltic Sea, Barents Sea, Hudson Bay) tend to show a reduction or absence of skin tuberculation, together with reduced sharpness of the dermal lumps. This led Cox (1920) to

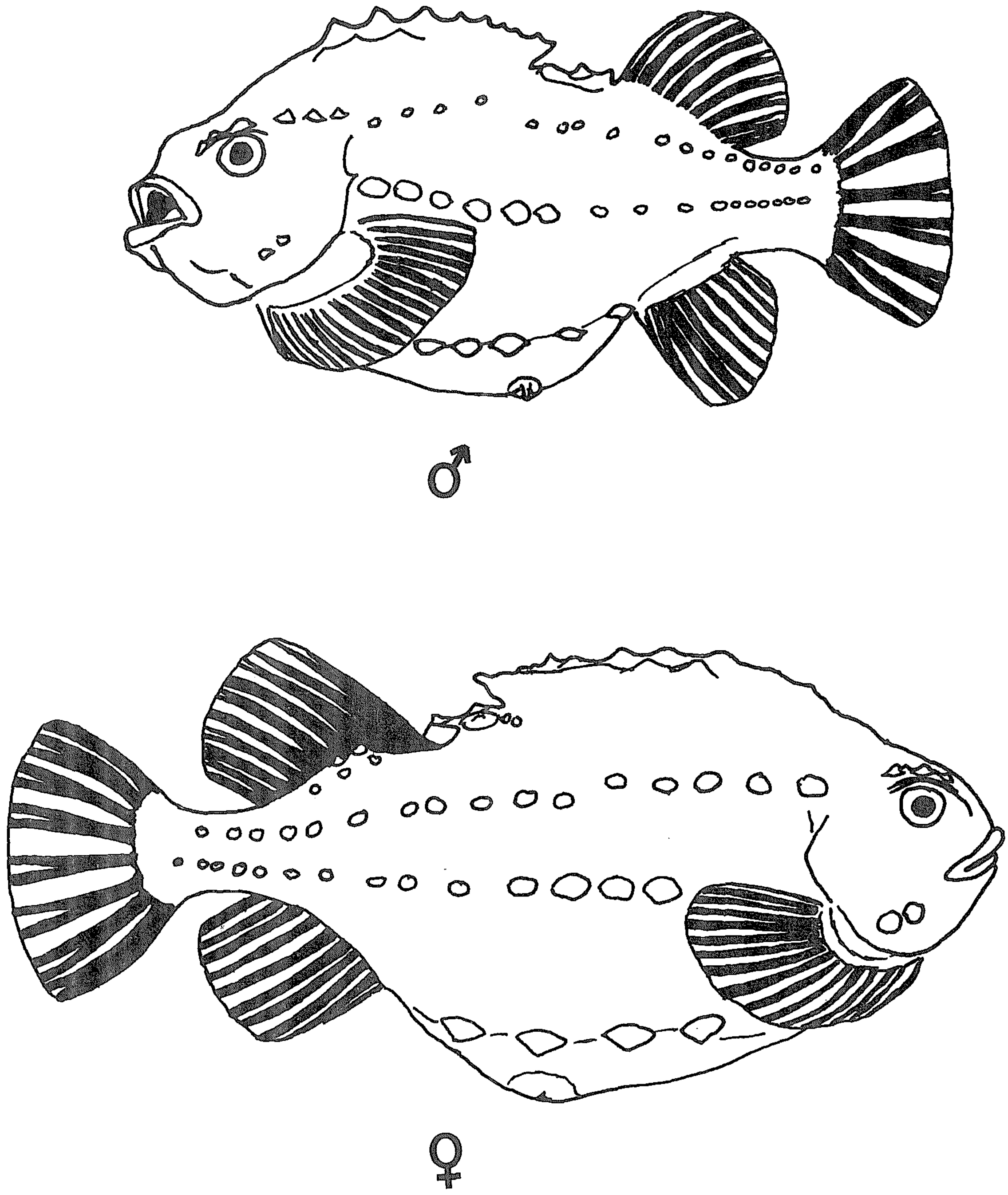


Figure 1 Male and female lumpsuckers
(Redrawn by the author from plates in Smitt, 1892)

propose separate variety status (*C. lumpus* var. *hudsonius*) for the Hudson Bay population, but no subspecies or varieties are currently recognized. No biochemical/electrophoretic genetic studies appear to have been performed upon the species.

1.2.4 Common names

The strange appearance of the lumpsucker, coupled with the marked sexual dimorphism of the species, has led to the use of an unusually large number of common names, often different ones for each sex.

1.2.4.1 Standard names

Standard names in current use are given in Table I.

Table I

Common names of the lumpsucker

Language	Common name
English	Lumpsucker, Lumpfish
German	Lumpfisch, Seehase
French	Lompe
Norwegian	Rognkjeks (♀), Rognkull (♂)
Swedish	Sturygg, Stenbit, Kvabbso
Danish	Stenbider, Kulso (♀)
Icelandic	Hrognkelsi, Rauomagi, Grasleppe
Greenlander	Nepisa, Arnardlok (♀), Angusedlok (♂)
Dutch/Flemish	Snotdolf
Portuguese	Galuha-do-mer
Italian	Ciclottero
Japanese	Dango-uo

1.2.4.2 Vernacular/localized/ obsolete names

Seahen, Seacock, Henfish, Paddle-cock, Red Lump, Blue Lump, Stone-clagger, Sea Owl, Cock-paidle, Hen-paidle, Jar For, Pattle-hush, Poule de Mer, Le gras Mollet, Havpaddle, Steenbider, Seebulle.

1.3 Morphology

1.3.1 Anatomy

Anatomical and morphological studies of *Cyclopterus lumpus* have been made by numerous authors (Rathke, 1822; Hilgendorf, 1878; Guitel, 1890, 1891, 1896; Garman, 1892; Borckert, 1889; Franz, 1907; Gill, 1907; Hase, 1911; Schmidt, 1913; Uhlman, 1921; Gregory, 1933; Jensen, 1944; Ueno, 1970; Davenport and Lönning, 1983; Davenport and Kjørsvik, in press; Davenport, in press).

Interest in lumpsucker anatomy has centered upon the pronounced sexual dimorphism of the species (size, colour during spawning season, proportion of subcutaneous gelatinous tissue, size of urinary bladder, etc.), the cartilagenous nature of the skeleton (which led Linnaeus to classify the species with the elasmobranch fish), the peculiar skin structure (studied in great detail by Hase, 1911), and the structure of the prominent sucking disk (Baudelot, 1868; Buckland, 1881; Gill, 1907; Davenport, in press) (see Figure 2).

1.3.2 Cytomorphology

Li and Clyburne (1977) performed the only lumpsucker cytomorphic/chromosome study when they grew a cell line from fin tissue of *Cyclopterus lumpus*. They studied the growth, cellular morphology, viral susceptibility and chromosome characteristics. Average chromosome number 2N = 50.

1.3.3 Protein specificity

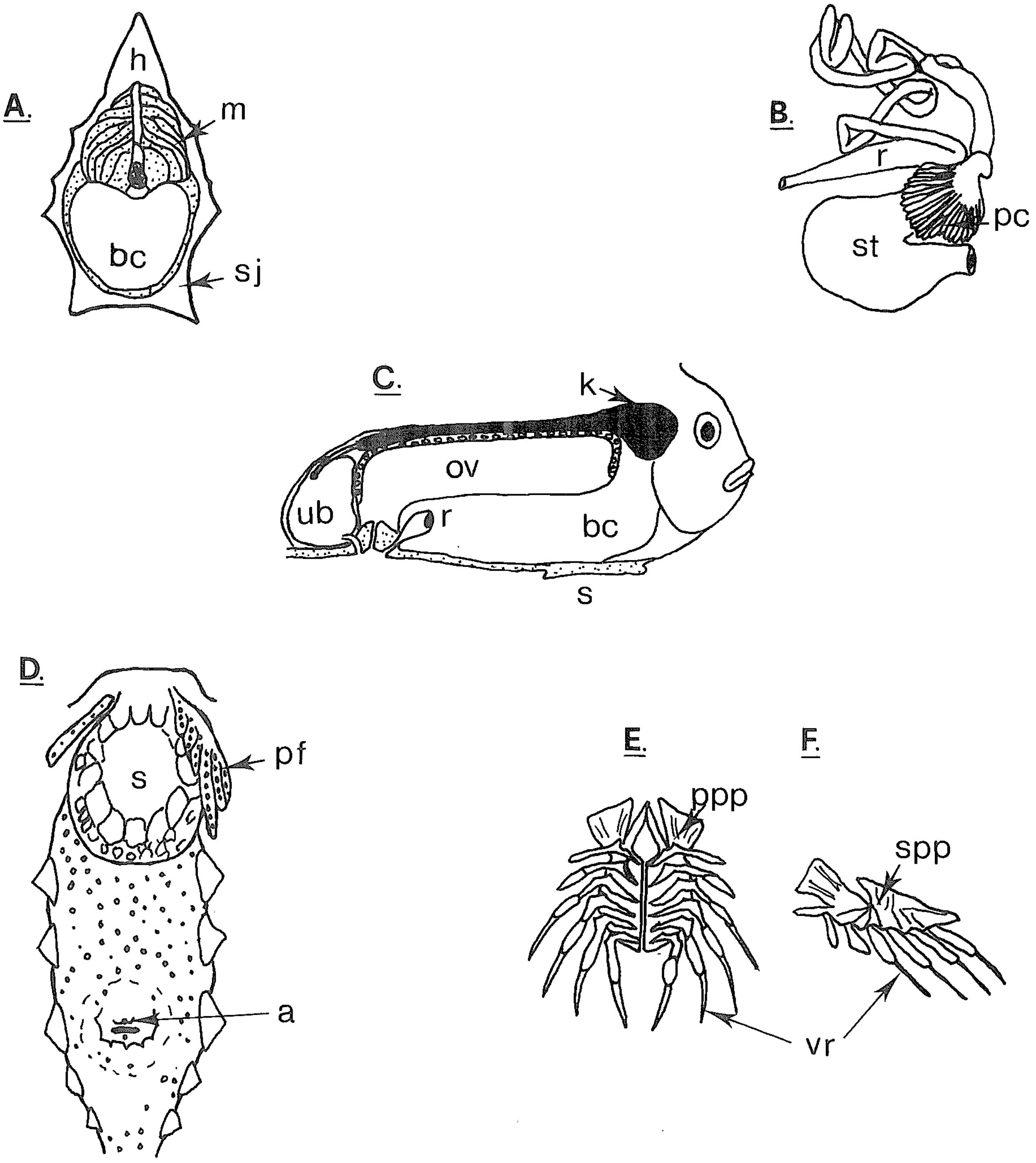
No information available to the author.

2. DISTRIBUTION

2.1 Total Area

There is a fundamental problem in the accurate assessment of the total area occupied by *Cyclopterus lumpus*. Although several studies over many years have shown that the lumpsucker is in fact a semipelagic species spending much of its life far from land (Cox and Anderson, 1922; Saemundsson, 1926, 1949; Andriyashev, 1964; Bagge, 1964; Schopka, 1971, 1974; Blacker, 1983; Daborn and Gregory, 1983), most workers have assumed that its distribution is near shore, and that it does not have to migrate far to its coastal breeding areas. With few exceptions, therefore, the following distributional data apply solely to the coastal breeding zones (see Figure 3).

Cyclopterus lumpus is widely distributed in the boreal region of both sides of the North Atlantic. On the western side of the Atlantic it has been recorded over a wider range of latitude than on the European coast. Bean (1879) reported the most northerly occurrence of the species on the island of Disko (70°N off northwestern Greenland), while Gill (1907) indicated that the southernmost limit was the mouth of Chesapeake Bay (37°N) although lumpsuckers are rarely found south of Cape Cod (Storer, 1864; Gill, 1873; Bean, 1903; Fowler, 1914; Nichols and Gregory, 1918; Gordon, 1960). The species is widely distributed in southwestern Greenland (Fabricius, 1780; Dresel, 1885; Jensen, 1944) and extends into the low salinities of Hudson Bay (Cox, 1920; Cox and Anderson, 1922; Vladykov, 1933). It is common in Newfoundland waters (Jeffers, 1932), the Gulf of Saint Lawrence, New Brunswick and Nova Scotia (Fortin, 1864; Cornish, 1907; Halketh, 1913; Cox, 1921; Huntsman, 1922; Leim 1960; Leim and Scott, 1966).



A. Transverse section through body of lumpsucker (redrawn from Cox, 1920a)

h = hump
m = muscle
bc = body cavity
sj = subcutaneous jelly

B. Alimentary canal of *Cyclopterus* (redrawn from Ueno, 1970)

st = stomach
pc = pyloric caecae
r = rectum

C. Urogenital system of lumpsucker (simplified and redrawn from Davenport and Lønning, 1983)

k = kidney
bc = body cavity
r = rectum
ub = urinary bladder
ov = fused ovary/oviduct

D. Underside of female lumpsucker (redrawn from Davenport and Lønning, 1983)

s = sucker
pf = pectoral fin
a = anus

E, F. Skeleton (cartilagenous) of sucker from below and from left side respectively (redrawn from Ueno, 1970)

ppp = propelvic processes
spp = suprapelvic processes
vr = ventral rays

Figure 2 Anatomical features of *Cyclopterus lumpus*

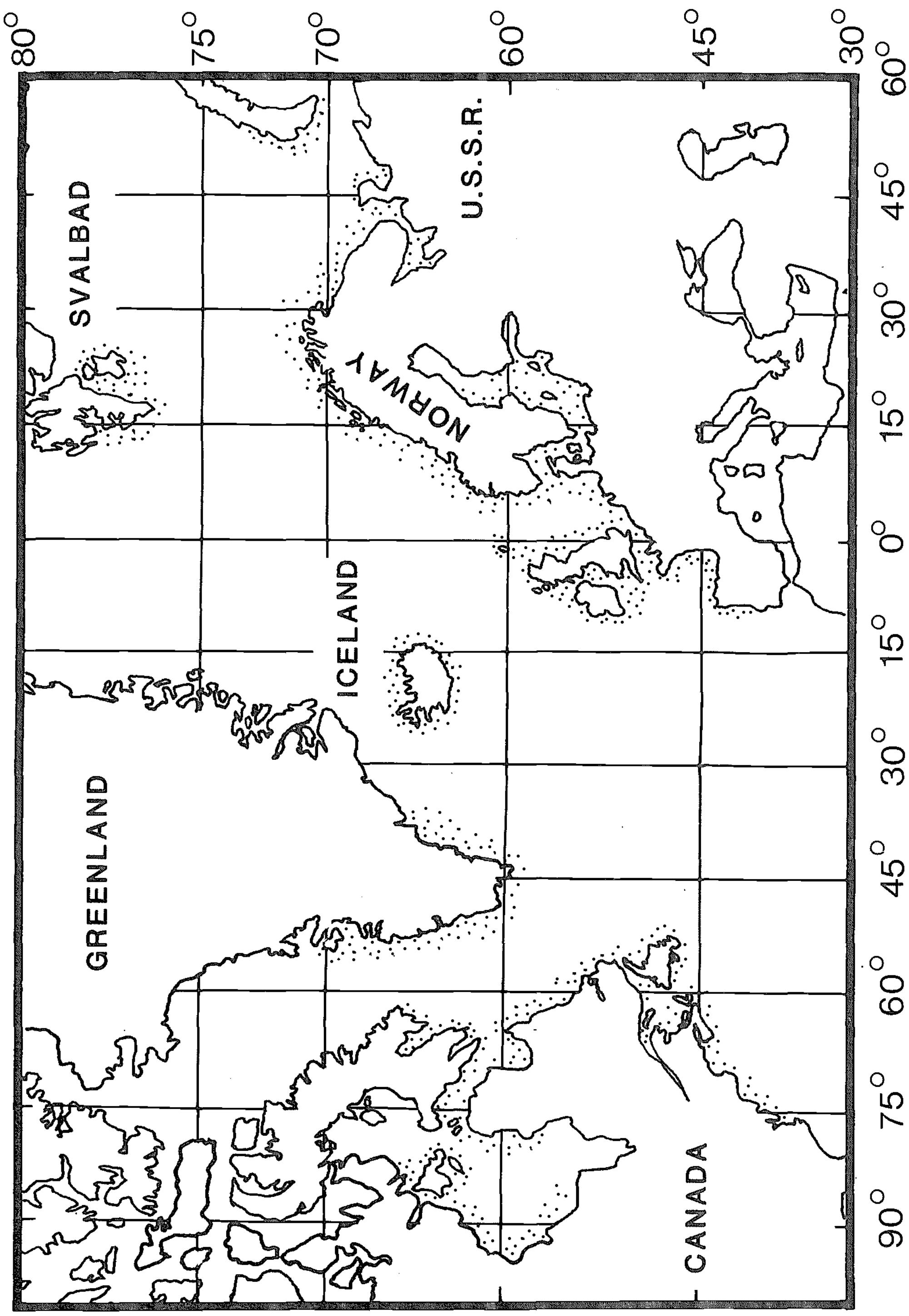


Figure 3 Map of the distribution of *Cyclopterus lumpus*. Dotted areas indicate spawning grounds

Cyclopterus is very common around Iceland (Günther, 1861; Saemundsson, 1926, 1949). Myrseth (1971) discussed lumpsuckers from Jan Meyen (an island north of Iceland), while the archipelago of Svalbad (= Spitzbergen) and the island of Nova Zemlya are amongst the most northerly recorded breeding areas (Lönnberg, 1899; Knipowich, 1926), though the occurrence on Svalbad was disputed by Jensen (1944). Lumpfish are common in the Barents Sea and White Sea (e.g., Derjugin, 1915; Knipowich, op. cit.), stretch along the Norwegian, Danish, Dutch, Belgian, French and Spanish coasts (e.g., Day, 1880; Smitt, 1892), and have a southern limit on the northern coast of Portugal (Nobre, 1935; Albuquerque, 1956; Almaca, 1965). The lumpsucker is well known from all coasts of the UK and Ireland (e.g., Yarrell, 1841; Couch, 1878) although it is more common in the north and is particularly abundant in the Orkneys and Shetlands. Jensen (1944) reported that it occurred in the Faroes too.

A population of rather small lumpsuckers (similar in form to the Hudson Bay fish - see Ueno (1970) for discussion) lives in the Baltic Sea, penetrating the Gulf of Bothnia (Reuter, 1883; Andersson, 1942; Bruun and Pfaff, 1950; Halme, 1954).

As Cox and Anderson (1922) stated, *Cyclopterus* "occupies an enormous range of littoral", perhaps 20 000 mi of coast in total on both sides of the Atlantic. It must therefore be regarded as a most abundant fish, the abundance masked by its rather solitary, territorial breeding habit.

2.2 Differential Distribution

2.2.1 Spawn, larvae and juveniles

Lumpsuckers lay their eggs (as sizeable masses) in near-shore shallow water, usually subtidally, but occasionally at or just above low water spring tide level (e.g., Yesipov, 1937). The egg masses are guarded by males for 6-10 weeks. There has been some dispute about the behaviour of the larvae immediately after hatching (see Section 3), but within a short period the larvae are dispersed by water currents. Early workers stressed that newly hatched larvae remain in shallow water, often attached by their suckers to weed. Growing larvae and juveniles are certainly to be found in intertidal pools throughout the summer after spring spawning, but there is evidence that some larvae are recruited to the open sea neustonic community (Daborn and Gregory, 1983). These workers found juvenile lumpsuckers (<55 mm length) from July to September in neuston samples collected from the Bay of Fundy (North America). The largest juveniles appeared to be about one year old (Cox and Anderson, 1922), and it appears that older juveniles adopt the semipelagic habit of the adult fish. The neustonic phase apparently involves an association with floating weed, since juveniles feed upon harpacticoid copepods (*Harpacticus chelifer*) characteristic of shoreline algae.

2.2.2 Adults

Adult lumpsuckers were once thought to live a benthic existence in nearshore deep water (except during the breeding season). Observations of gut contents by many workers, coupled with the tagging results of Bagge (1967) and Schopka (1971, 1974) and the numerous pelagic records reviewed and augmented by Blacker (1983) have revealed that adults are substantially pelagic, living in the upper 50-60 m of oceanic water, often over abyssal depths. Bagge (1964) and Schopka (1974) found that adults remained pelagic until the winter before spring spawning. A gradual switch to the demersal habit occurred during that winter.

3. BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.1.1 Sexuality

Lumpsuckers are heterosexual and the sexes are readily identifiable. Male fish are much smaller than females (see Figure 4 - Thorsteinsson, 1981), possess relatively much larger suckers (Davenport, in press) and, in the breeding season, are richly coloured, being pink or red on the under surfaces (in contrast to the blue-green colour of females). Outside the breeding season, both sexes lose colour and separation of the sexes is less easy, though the dorsal hump of males is less prominent. It is not possible to strip eggs or sperm from lumpsuckers; artificial rearing requires gametes to be collected by killing and dissection (Davenport, 1983; Lønning, Kjørsvik and Davenport, 1984).

3.1.2 Maturity

Cox (1920a) reported spawning lumpsuckers to be five-seven years old (aged by vertebral rings). Saemundsson (1926) also believed that lumpsuckers had to be at least five-six years old to spawn. Bagge (1964, 1967) described the age composition of *Cyclopterus* in the North Sea and Baltic. North Sea spawners included age groups IV-IX, but were dominated by groups V and VI. Only male fish spawned at the age of four years (at a mean length of about 31 cm). Male fish dominated group V too, so it would appear that North Sea males mature one-two years earlier than females. Baltic specimens examined by Bagge were in groups III-VI, but included some immature fish, so further deductions cannot be made.

Tagged Icelandic lumpsuckers collected by Schopka (1974) were all reported to be four years old, but Thorsteinsson (1981), in a detailed consideration of ageing validation and age composition, found that spawning female lumpsuckers caught commercially between 1976 and 1979 had the age composition shown in Figure 5. He found that female lumpsuckers were recruited to the spawning

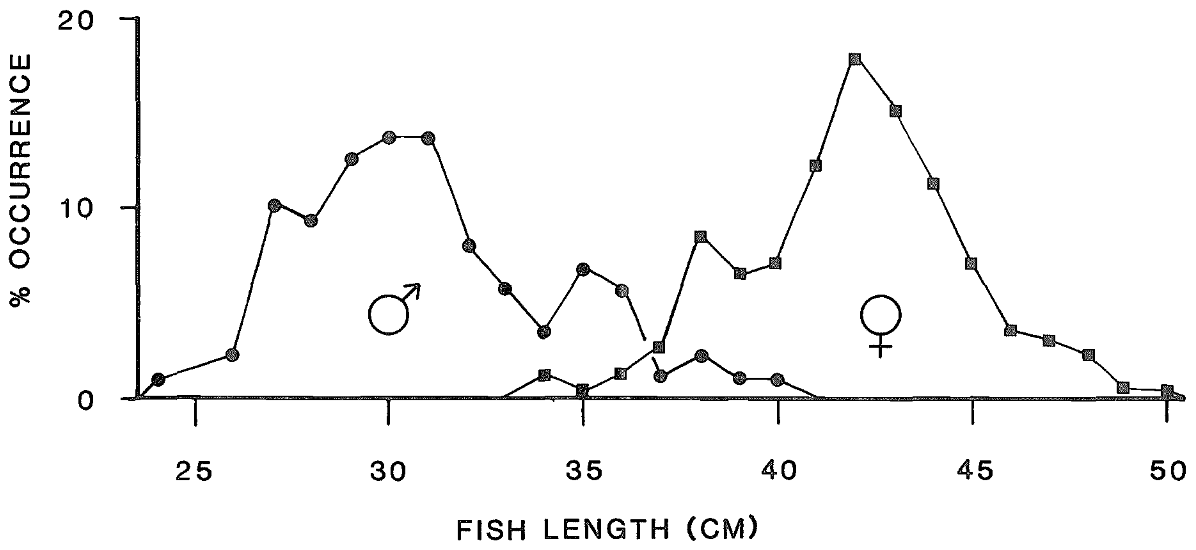


Figure 4 Size of male and female lumpsuckers trawled in Icelandic waters (Redrawn from Thorsteinsson, 1981)

stock at the age of 5 (with good agreement between growth curves and otolith analysis), with less than 1% spawning at the age of 4. Most spawners were 5-8, though specimens of 9-10 were not uncommon. The oldest females were 12-13 years old. Five-year old female Icelandic lumpsuckers had a mean length of 39 cm. This is rather smaller than equivalent North Sea fish which had a mean length of 45 cm (Bagge, 1964). On the other hand, Baltic females were only about 17 cm in length at age 5, demonstrating the stunted nature of this low salinity population.

3.1.3 Mating

Mating takes place in shallow water on rocky shores, particularly in areas overgrown with kelp (Cox, 1920a). Male fish arrive in the spawning areas before females and establish territories. Mochek (1973) reported that lumpsuckers laid eggs on stones and amongst *Laminaria* beds, but not on exposed rock.

Although there are numerous accounts of the male guardianship of eggs after mating, the author has been unable to trace a detailed account of courtship behaviour before mating. Partly this seems to be because spawning in aquaria or laboratories occurs at night (Fulton, 1907; pers. obs.), although Mochek (1973), who apparently observed mating (without describing it), stated that spawning was associated with high tide. Mochek worked with cages set at low water, and with sublittoral containers, so was dealing with fairly natural conditions. He reported rivalry between lumpsucker males, and that females in cages attracted the attentions of males. The author (Davenport, unpublished data) noted that if seawater from a bucket which had contained a male fish was added to a tank containing quiescent ripe females, the hen fish became agitated and swam vigorously for some minutes. Possibly both sexes locate each other by olfactory means. The author also attempted to film mating in a large, well-lit aquarium, and observed several hours of courtship, in which both sexes showed their flanks to one another, interspersing episodes of tail fanning (more vigorous in the male) with long periods of sucker attachment in close proximity to one another. The fishes did not mate in the aquarium, but did so shortly afterwards in a dark holding tank.

Females do not release all their eggs in one batch, but lay two or three masses of eggs at intervals of 8-14 days (Ehrenbaum, 1904; Andriyashev, 1954). Many workers have demonstrated that females play no part in rearing the eggs.

3.1.4 Fertilization

Fertilization is external with sperm and ova shed freely into the water. On contact with sea water, the eggs adhere to one another to form large masses (up to 26 cm x 10 cm x 10 cm according to Zhitenev (1970)) which tend to be ovoid in form.

3.1.5 Gonads

The following description is taken from Davenport and Lønning (1983). The anatomy of the abdominal cavity of ripe females is dominated by the pink roes which can fill two thirds of the body cavity in some fish (see Figure 6). The ovaries and oviducts are fused to form a single sac which is strongly bifurcated anteriorly. The left horn of the structure is rather smaller than the right, thus leaving room for stomach and liver. The oviduct, which opens posteriorly to, and separately from, the rectum is very wide and guarded by a substantial and powerful sphincter. The dorsal and dorso-lateral portions of the

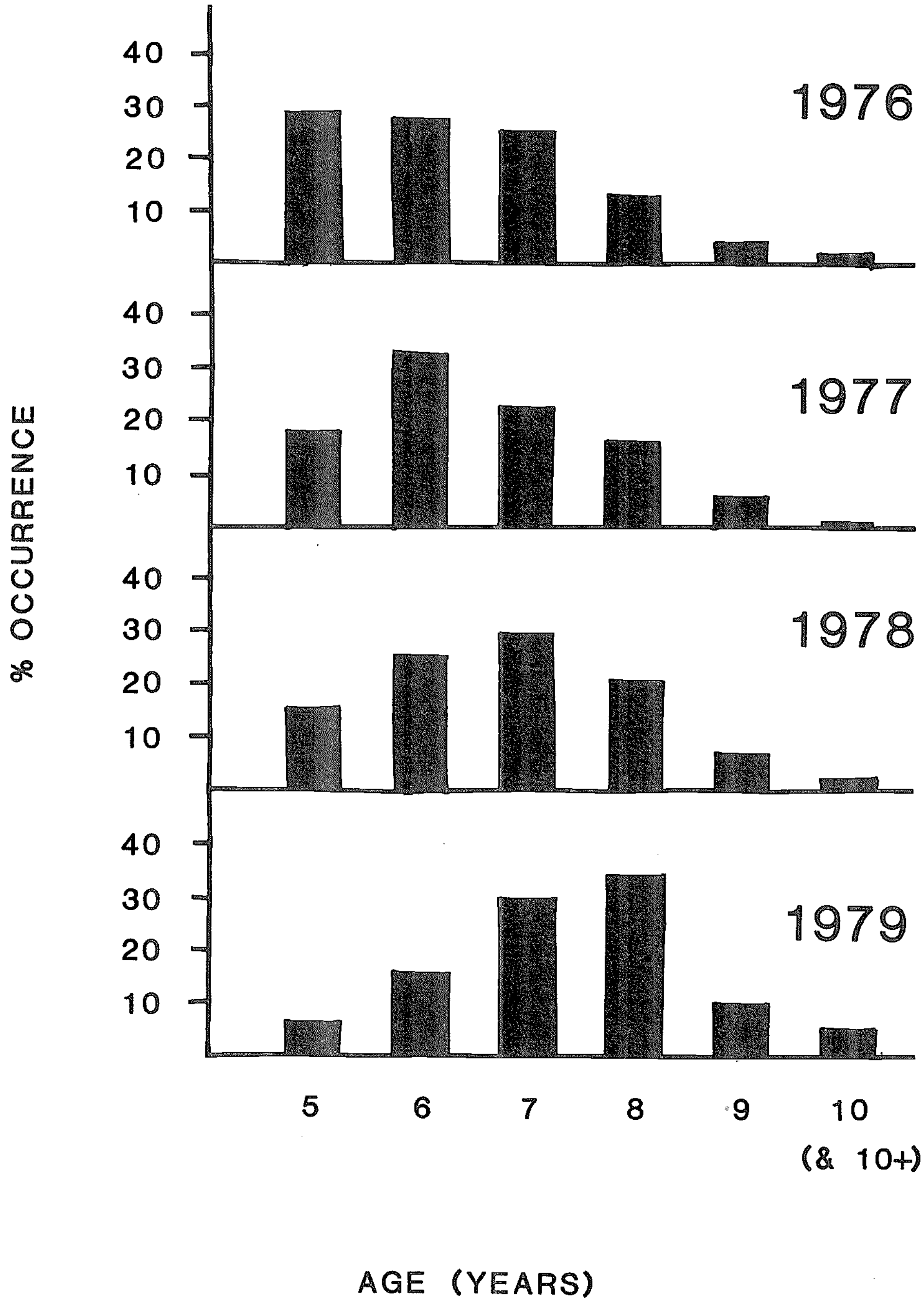
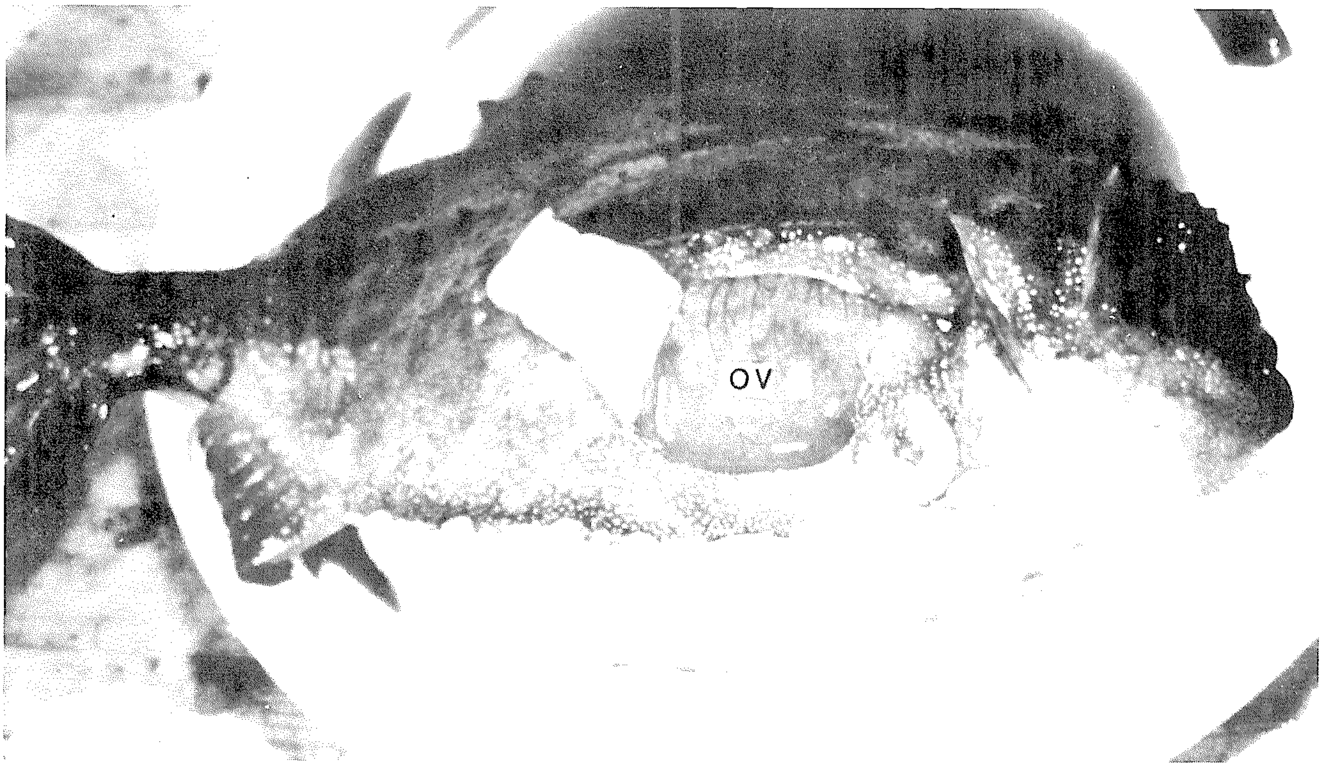
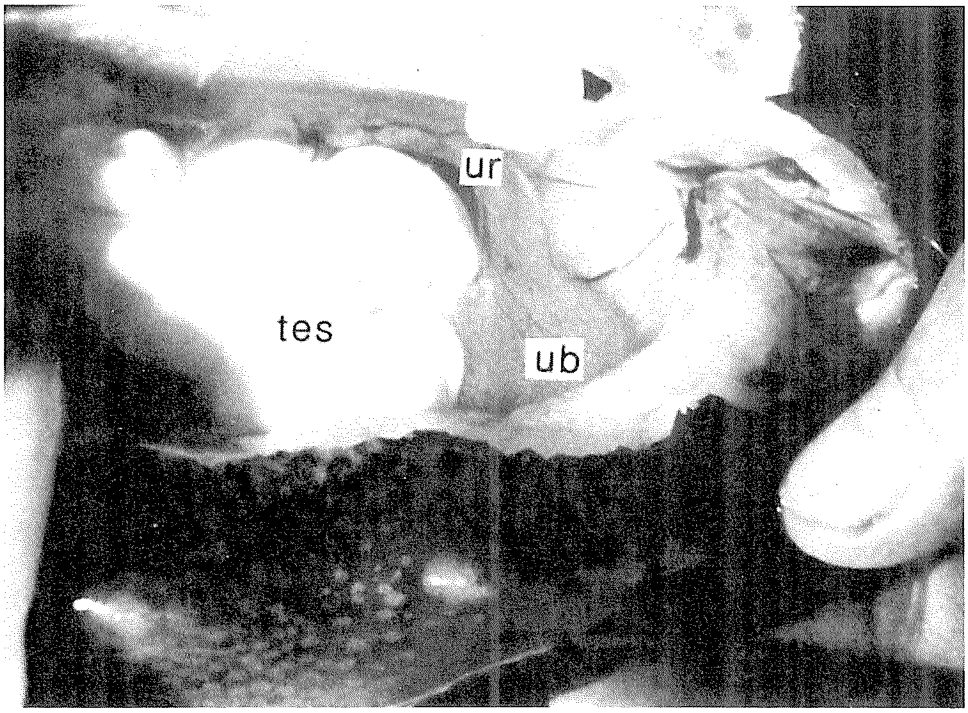


Figure 5 Age composition of female lumpsuckers caught in Skjálfandaflói (1976-79) (Redrawn from Thorsteinsson, 1981)



A. Female



B. Male

tes = testes; ub = urinary bladder; ur = ureter; ov = ovary/oviduct

Figure 6 Photographs of female and male lumpsuckers, dissected to demonstrate gonads
(Davenport and Lønning, 1983)

ovary-oviduct are lined by a thick, viscous layer which contains whiteish opaque, unripe eggs in most females. Ripe eggs, which are clear and rose pink, fall from this layer into the lumen of the structure, which is filled with a copious ovarian fluid (for composition see Table II). This fluid has low divalent ion concentrations, essential because lumpsucker eggs harden and stick together in the presence of divalent ions (Lønning, Kjørsvik and Davenport, 1984).

The ovarian fluid volume was estimated by Myrseth (1971) who found 200-400 ml in whole roes. Davenport and Lønning (1983) estimated that a 40 cm female would contain 500 ml of ovarian fluid. They suggested that the copious ovarian fluid acted as a barrier during spawning to prevent reflux of sea water into the oviduct (where it would cause subsequent egg batches to harden and adhere to one another).

Fecundity in the lumpsucker is very high for a fish laying demersal, brooded eggs. The weight of the eggs may be up to one-third of the total fish weight (Fulton, 1891; Thorsteinsson, 1983). The eggs are fairly small (approx. 2.3 mm overall diameter) so egg numbers may be as high as 400 000 in the largest fish, though 100 000 would be more realistic for most spawning females. Myrseth (1971) considered fecundity in lumpsuckers from West Greenland, Iceland, Hordaland (a Norwegian county around Bergen) and Troms (North Norway) in some detail (see Figure 7). These studies revealed significant differences between populations, with Icelandic and Greenland lumpsuckers having more eggs than Norwegian populations.

The gonads of the male lumpsucker have attracted little attention. They are bulky pure white structures (see Figure 6), but are otherwise unremarkable save that viable sperm may be obtained from testes for several days after removal from the fish (Davenport, 1983).

3.1.6 Paternal guardianship of egg masses

Fabricius (1780) is usually credited with being the first to note that *Cyclopterus* egg masses were guarded during development by the male parent, though Jensen (1944) remarked that Glahn (in Grantz, 1771) had describe the phenomenon a little earlier.

During the nineteenth century several biologists refused to believe Fabricius' story (e.g., Couch, 1878), but it was eventually confirmed (McIntosh, 1886; Ehrenbaum, 1904; Fulton, 1907). Fulton's account is particularly comprehensive, but further information has been provided more recently by Zhitenev (1970) and Mochek (1973).

First, the male fish moulds the egg masses while the eggs are soft and sticky; he creates funnel shaped depressions in the mass which are believed to aid mass ventilation (Zhitenev, 1970). One male may guard egg masses from several females; even when these touch one another they do not adhere (Zhitenev, *op. cit.*), probably because inter-egg adhesion is only possible for a few hours after spawning (Davenport, Lønning and Kjørsvik, 1983).

The male vigorously fans the eggs during the first few hours of development: this is believed to drive off the ammoniacal by-products of inter-egg adhesion (Davenport, Lønning and Kjørsvik, *op. cit.*). Thereafter, egg mass ventilation is intermittent (by blowing water through the mouth and by pectoral fin action), with "fanning" spells lasting for periods ranging from a few seconds to about an hour (Mochek, 1973). Continuous ventilation is resumed shortly before hatching (Fulton, 1907) when oxygen demand becomes high (Davenport, 1983).

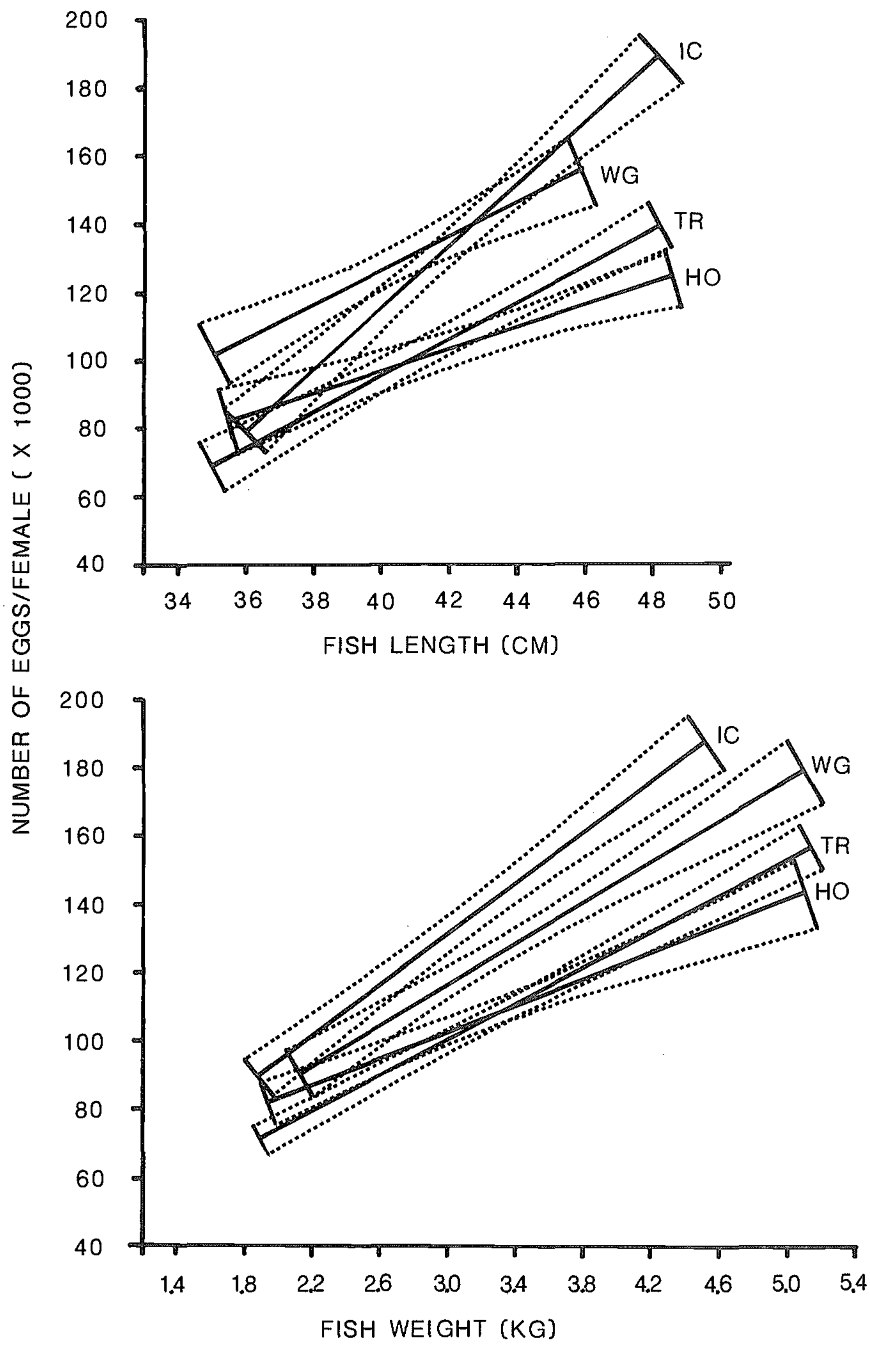
During brooding the male is very aggressive, not only to other lumpsuckers, but also to potential egg predators. Fabricius (1780) remarked that it would even attack the wolffish *Anarhichas lupus*, while Jensen (1944) recorded that it would tackle the conger eel *Conger vulgaris*. It seems to be generally agreed that the male does not feed during the brooding period (which may last 6-10 weeks); only Mochek (1973) recorded feeding (on gammarid amphipods), and that in an aquarium (where the prey could not escape from the vicinity of the egg masses).

Yesipov (1937) claimed that male lumpfish had been observed to spout water (from the mouth) over egg masses exposed to air by low tides. This has been decried by some workers, but is consistent with the findings of McIntosh (1886) who observed a male lumpsucker and its spawn in extremely shallow water between the tidemarks at Saint Andrews, Scotland. On each tide (for 5-6 weeks) the male

Table II

Ovarian fluid composition in *Cyclopterus lumpus* (from Davenport and Lønning, 1983)

Fluid	Osmolarity mOsm	pH	mM urea	mM NH_4^+	mM Na^+	mM K^+	mM Ca^{2+}	mM Mg^{2+}	mM Cl^-	protein g l^{-1}
Ovarian fluid	356	7.65	1.90	0.059	176	9.2	1.45	0.65	170	0.92
Blood plasma	359	7.40	1.80	0.098	182	3.4	5.30	0.99	166	28.50
Sea water	980	8.10	0.05	0.001	484	10.6	8.80	52.60	520	0.00



IC = Iceland
WG = West Greenland
TR = Troms (North Norway)
HO = Hordaland (around Bergen)

Figure 7 Lumpsucker fecundity
(Redrawn from Myrseth, 1971)

was forced to lie on its side with one operculum out of water in order that it could guard the egg mass.

For well over a century it has been suggested that newly hatched *Cyclopterus* fry attach themselves to the male fish and are guarded by them. McIntosh (1886) was clearly aware of this hypothesis (but in his view the larvae dispersed immediately on hatching), although Mochek (1973) inaccurately attributes the original description to Brem (1895). Fulton (1907) and Mochek (1973), the latter working in near natural conditions, confirmed that newly hatched larvae did not attach to the male, but rapidly dispersed. However, the attractive concept of the "peripatetic nursery" (Cox, 1920a) is quite durable. As recently as 1984 the author was told that SCUBA divers had observed the phenomena in fjords near Tromsø, North Norway.

3.1.7 Spawn

Lumpsucker eggs are small, and apparently of uniform size throughout the species' range. Fulton (1907) recorded 2.2-2.6 mm overall diameter for Scottish specimens, Cox (1920a) 2.4-3.0 mm for Canadian eggs, Andriyashev (1954) 2.2-2.5 mm for White Sea material; Davenport and Lønning measured Norwegian lumpsucker ova at 2.3 mm. When in the ovary-oviduct, the eggs are invariably rose pink in colour, but after discharge to the environment they change to a variety of yellow, green, purple, violet, blue and grey colours (each mass bein of fairly homogenous colour). The colours are gradually lost during development, and are apparently due to the presence of carotenoid pigments in the copious fatty yolk. As the embryo develops, the pigments are withdrawn from the yolk into the body of the embryo where they are concentrated in the chromatophores (Zhitenev, 1970).

Newly released lumpsucker eggs are soft and extremely sticky (Davenport, Lønning and Kjørsvik, 1983). The transparent adhesive material is secreted by the ovary, and coats all of the eggs within the oviduct. The material is not sticky until exposed to the divalent ions of sea water, when it forms a viscous elastic material which binds the eggs together (Walther and Davenport, unpublished data). The eggs remain sticky for about an hour (at 5°C), then the "glue" condenses to form an electron-dense layer which surrounds the eggs, but is particularly thick at the circular inter-egg junctions which make up 30-40% of the egg surface in eggs within the mass (Zhitenev, 1970). During the first 48 hours of development lumpsucker eggs harden, reaching a resistance to bursting of about 2 000 g. The hardening process is dependent on divalent ions also, particularly calcium, but the ions appear to activate an enzymatic process, since they are not deposited in the hardened chorion (Lønning, Kjørsvik and Davenport, 1984). The eggs are relatively heavy (density approx. 1.06 g ml^{-1}; Davenport and Kjørsvik, in press) as would be expected given their demersal position.

3.2 Pre-adult Phase

3.2.1 Embryonic phase

No detailed description of the stages of development of lumpsucker eggs appears to have been published. Some attention has been paid to the effects of temperature on development time; Ehrenbaum (1904) reported that development to hatching in the North Sea took 70 days at the beginning of the breeding season, but dropped to only 14 days later on. Andriyashev (1954) recorded a development time of two months in White Sea lumpsucker eggs. Collins (1978) reported that eggs did not hatch at 3.8°C but hatched after 31 days at 6.4°C and 25 days at 9.8°C. Davenport (1983) recorded a development time of 40 days at 5°C, and noted that the earliest stages of development were particularly drawn out; 24 hours after fertilization some eggs were still at the four-cell stage, and late gastrulae could be as much as 9-10 days old. Zhitenev (1970) noted that the vascular system of the yolk sac was formed at the same time as segmentation of the embryo begins; he also noted that eggs deep within the egg masses developed more slowly than superficial eggs (Figure 8), presumably because of less effective ventilation and consequent exposure to low oxygen tension.

Davenport (1983) investigated the effect of low oxygen tension on lumpsucker eggs. He found that unfertilized eggs were exposed to low oxygen tensions in the oviduct prior to spawning (approx. 40% air saturation levels were recorded in ovarian fluid). Early stage eggs (11 days old, just post gastrula) could withstand completely anoxic conditions for at least 30 minutes (after exposure for many hours beforehand to falling oxygen tensions). However, sensitivity to oxygen depletion increased during development. Even so, 36-day old eggs (four days before hatching) could still extract oxygen from water of only 10-20% air saturation.

There are a few records of lumpsuckers entering water of low salinity (Smitt, 1892) (other than the populations living permanently in low salinity areas (e.g., Hudson Bay and Baltic)). Kjørsvik *et al.* (1984) studied development at different salinities in eggs and larvae of *Cyclopterus* from Norway. They found that development was normal only between 20.4 and 34‰; death occurred at lower or higher salinities. This finding tends to suggest that the Baltic Sea and Hudson Bay lumpsuckers may be physiological races, since they certainly encounter salinities below 20.4‰.

The metabolism of embryos has been studied by Zhitenev (1970), Davenport (1983) and Davenport, Lønning and Kjørsvik (1983). The initial metabolic rate of newly fertilized eggs at 5°C is extremely low (0.0109 µl O_2 mg dry wt^{-1} h^{-1}), roughly 10% of the rate measured for cod eggs by Davenport and Lønning (1980). This appears to reflect the initally slow rate of embryonic development since lumpsucker eggs about to hatch consume 0.258 µl O_2 mg dry wt^{-1} h^{-1} (approx. 32% of the corresponding cod egg rate).

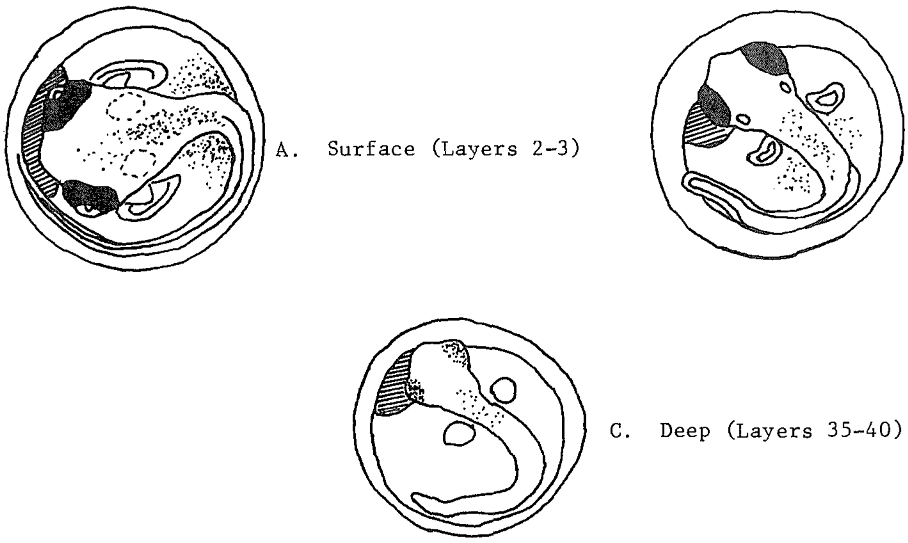


Figure 8 Effect of ventilation. Development of lumpsucker embryos at different levels in the egg mass
(Redrawn from Zhitenev, 1970)

Davenport, Lønning and Kjørsvik (1983) found that newly spawned lumsucker eggs apparently gave off great amounts of ammonia (68 ng NH_4 mg dry wt^{-1} h^{-1}) but this output decreased rapidly, the decrease appearing to be correlated with the declining stickiness of the eggs (see Table III). It would appear that the ammonia is given off by the proteinaceous adhesive as it "cures", and is not excreted by the egg themselves. Two-three days after fertilization, ammonia output was only 5.4 ng NH_4 mg dry wt^{-1} h^{-1} and rose little during development: shortly before hatching it was only 9.8 ng NH_4 mg dry wt^{-1} h^{-1}, about 7% of the equivalent cod egg value. From the O:N consumption:excretion ratios shown in Table IV it is quite clear that the nitrogen output in the first 12 hours of development cannot be of metabolic origin (since the theoretical minimum for the ratio is about 8 for animals metabolizing pure protein - see Conover and Corner (1968) for discussion). During most of egg development the O:N ratio comfortably exceeds 20, indicating that fat is being broken down.

3.2.2 Larval/adolescent phase

The larval/juvenile stages shown in Figure 9 are taken from Cox (1920a). He reported that newly hatched larvae were about 5.5 mm in length, which is close to the 6 mm value recorded by Cowan (1926). Newly hatched lumpsuckers have a continuous fin running along the back, round the tail and on the underside to the vent. Pectoral fins are rudimentary at this stage, and no ventral fins ever appear since the sucker is present at hatching and allows immediate attachment to weeds or stones (Fulton, 1907; Cox, 1920a; Cowan, 1926). The median fin breaks up into separate fins by the length of about 8-9 mm, and fin rays are visible in all fins. At this stage the lumpfish has a perfectly normal first dorsal fin, but this is gradually overgrown by the characteristic dorsal "hump", and a 32-mm specimen is essentially a miniature of the adult fish.

Cowan (1926) monitored growth rate in captive larvae which hatched on the 8th May 1924 (at 6 mm length). By July they were 11 mm long and by September 16-34 mm. By the end of October 35-42 mm had been attained, but during the subsequent winter the larvae did not grow despite feeding regularly on crab digestive gland. In the Spring they grew again and were 40-80 mm at the age of 1 year. This growth pattern is consistent with the data of Cox (1920a) and the proposition of Daborn and Gregory (1983) that 1 year old Bay of Fundy lumpsuckers are about 55 mm length. Few of Cowan's fish survived longer, but she reported that a 2-year old specimen had a length of 174 mm. Myrseth (1971) measured the length:weight relationship of lumpsuckers in the range 15-60 mm lenght (from North Norway) and found the relationship
$W = 2.309\ L^{3.053}$ g (L measured in mm).

Newly hatched lumpsucker larvae show much greater oxygen uptake rates than eggs about to hatch (Zhitenev, 1970; Davenport, 1983). In this they are similar to the herring *Clupea harengus* (Holliday, Blaxter and Lasker, 1964; Eldridge, Echeverria and Whipple, 1977). Volodin (1956) and Fry (1957) suggested that the chorion (egg shell) of teleost eggs hindered gaseous exchange, and that this resulted in late stage embryos being exposed to a low oxygen tension environment

Table III

Stickiness of lumpsucker eggs
(modified from Davenport, Lønning and Kjørsvik, 1983)

Egg stage	Stickiness index[a/] 1	2	3 (replicates)
A. Unfertilized eggs in ovarian fluid	1	1	1
B. Unfertilized eggs after 2 min in s.w.	10	10	10
C. Fertilized eggs			
after 15 min in s.w.	10	8	10
after 30 min in s.w.	6	10	10
after 60 min in s.w.	4	2	6
after 6 h in s.w.	1	2	1
after 24 h in s.w.	1	1	1

a/ Maximum 10; all eggs of a sample adhere to one another after separation

Minimum 1; no eggs adhere to one another after separation.

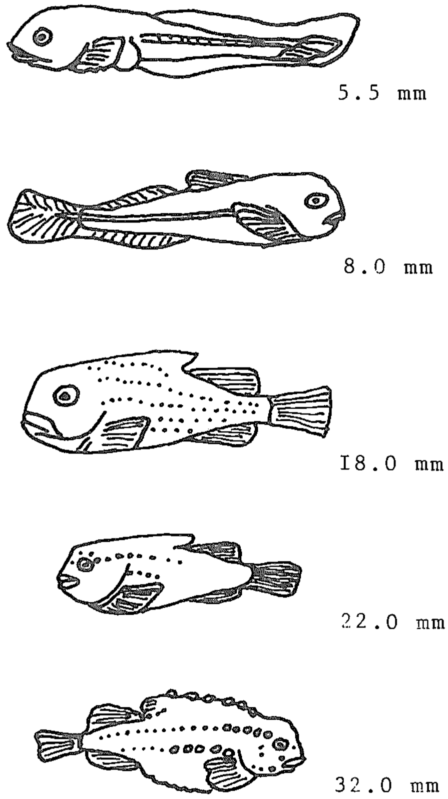


Figure 9 Larvae and juveniles *Cyclopterus lumpus*. (From Cox, 1920a) (Not to scale)

Table IV

O:N ratios for lumpsucker eggs and larvae
(modified from Davenport, Lønning and Kjørsvik, 1983)

Time after fertilization	O:N ratio[a/] (by atoms)
A. Eggs	
30 min	0.24 } affected by adhesive process
90 min	0.37 } affected by adhesive process
4.5 h	0.48 } affected by adhesive process
12.0 h	1.19 } affected by adhesive process
3 days	18.4
7 days	75.2
11 days	25.6
18 days	32.4
22 days	107.6
37 days	38.4
B. Larvae	
40 days	44.8 (newly hatched)
43 days	111.6
45 days	96.3
55 days	67.5
75 days	28.3

a/ i.e., ratio of oxygen uptake to nitrogen excreted

which depressed their oxygen uptake. Nitrogen excretion also rose sharply on hatching (Davenport, Lønning and Kjørsvik, 1983), but the O:N ratios (Table IV) indicated that larvae with yolk sacs still broke down fat.

3.3 Adult Phase

3.3.1 Longevity

Apstein (1910) suggested that female lump-suckers could be up to 70 cm in length, but most later workers agree on a maximum length of 60-61 cm for both American and European fish (Gordon, 1954; Leim and Scott, 1966). Only two substantial analyses of age and size within lumpsucker populations appear to have been performed, one on North Sea and Baltic specimens (Bagge, 1964; 1967), and a more comprehensive study of Icelandic lumpsuckers by Thorsteinsson (1981, 1983).

Bagge (1964) recorded one female of 57 cm and found that its age (from otolith rings) was 9 years; he found no males older than 8. Thorsteisson (1981, 1983) found a few females of 12-14 years, but these were not normally the largest fish. His growth curves became asymptotic at about 50 cm, so the age of 60 cm lumpsuckers remains obscure.

3.3.2 Hardiness

Ueno (1970) described *Cyclopterus lumpus* as an Atlantic-boreal species (by the criteria of Ekman (1953) and remarked that the southern and northern limits of distributional range agreed with the 20°C and 0°C August surface water isotherms, indicating that the lumpsucker is fairly eurythermal. No experimental data for tolerance of temperature, salinity or oxygen tension by adult fish appear to have been published.

3.3.3 Competition

No information available to the author.

3.3.4 Predators

Little is known of predation upon adult lumpsuckers during the pelagic phase of their life history, although there is some evidence that they are taken by sharks (Aflalo and Marston, 1904) and by the sperm whales *Physeter catodon* (Roe, 1969). Thorsteinsson (1983) states that seals, Greenland sharks and sperm whales are the main predators of Icelandic lumpfish. However, during the breeding season, when they move into shallow water, they are preyed upon by a variety of birds and mammals. Gulls and fish eagles eat them in Norway (pers. obs.), while otters catch them in the Shetland Islands (BBC television film). Some of the early workers remarked upon predation by seals which apparently strip away the skin and subcutaneous jelly to obtain the underlying flesh (Couch, 1878).

Males guarding egg masses are particularly vulnerable to bird predation, as the eggs are sometimes laid intertidally, or only slightly below low water spring tide level. McIntosh and Masterman (1897) reported that they were preyed upon by rooks and carrion crows (Corvidae).

Egg masses are eaten by cod and blennies when under water (McIntosh, 1886), and by rates, starlings and crows if laid intertidally or stranded by bad weather (McIntosh and Masterman, *op. cit.*).

3.3.5 Parasites

Lumpsuckers are known to be hosts of several parasitic copepods: *Holobomolochus confuscus*, *Caligus elongatus*, *Lernaeocera branchialis*, *Shyrion lumpi* (Kabata, 1960; Boxshall, 1974; Templeman, Hodder and Fleming, 1976).

Boxshall (*op. cit.*) found that 36% of North Sea adult lumpsuckers were infested with *H. confuscus*. Templeman, Hodder and Fleming (1976) demonstrated that *Cyclopterus* is the common intermediate host of larvae of *L. branchialis* in Newfoundland waters, with adult copepods infesting Atlantic cod (*Gadus morhua*). Larvae of *L. branchialis* were attached near the tips of the branchial filaments (mainly on the first two branchial arches) of *Cyclopterus*. No records of deleterious effects of these copepods on lumpsuckers appear to have been recorded.

The records of the British Museum of Natural History show that lumpsuckers may also be infested by a wide variety of helminths, but no information about the relative frequency of infection appears to be available.

3.3.6 Pollution

In the wake of the mercury poisoning epidemics of Japan in the late 1960s/early 1970s (caused by contamination of seafood in the locality of certain industries) there was disquiet about possible contamination of food fishes by mercury. Freeman *et al.* (1974) measured mercury levels in a range of Canadian Atlantic coast fish; these included *Cuclopterus lumpus*. Dorsal muscles of lumpsuckers contained 0.06 ± 0.05 ppm Hg, well below the allowable limit of 0.5 ppm Hg for fish of commerce in North America. This value was amongst the lowest recorded.

3.4 Nutrition and Growth

3.4.1 Food

Both male and female lumpsuckers appear not to feed before and during the breeding season, so that fish caught at this time rarely exhibit gut contents beyond a copious, clear gut fluid (for composition of the gut fluid, see Davenport and Lønning, 1983). This led the earliest writers to speculate wildly about the species' eating habits (some thought it subsisted on fish faeces), though by the time of Smitt's description (1892) it was generally agreed that the species ate weak benthic animals (annelids and molluscs). McIntosh (1885) reported that a large female caught near Saint Andrews (UK) in March had a stomach distended by "fine specimens of *Nereis pelagica*".

The first extensive study of feeding in *Cyclopterus* was carried out by Apstein (1910) who investigated 101 lumpsuckers from the North Sea and Baltic. He reported on gut contents from both sexes, although in most cases the guts were empty (69 fish) or contained unidentifiable detritus. Most identifiable prey organisms were either mysids or ctenophores (*Mysis mixta*, *Pleurobrachia* spp.). Additionally he reported an amphipod from one fish and 27 young sandeels (*Ammodytes*) from another. Seagrass (*Zostera*?) was recorded from one fish.

Cox and Anderson (1922), working upon Canadian material, found specimens of the euphausid *Meganyctiphanes norvegica* and the medusa *Aurelia flavidula* (complete with associated hyperiid amphipods) in the stomach of their lumpsuckers. One small *Cyclopterus* contained many specimens of the weed/hydroid dwelling amphipod *Caprella* spp.

Myrseth (1971) examined the stomachs of a large number (424) of lumpsuckers caught at Malangen in Troms (North Norway). He found that 80% of the fish had empty stomachs, and that euphausids dominated the contents of the remaining 20%. Amphipods, isopods and *Nereis pelagica* were also found.

Garrod and Harding (1981) reported ctenophores and euphausids from lumpsucker stomachs, but also found fish eggs and larvae (mainly of the plaice *Pleuronectes platessa*). The overall impression therefore, is of a fish which subsists mainly on large planktonic organisms living in surface/mid waters, but which sometimes browses upon benthic organisms, particularly those dwelling upon weed.

Only one study of the food of young lumpsuckers appears to have been performed (Daborn and Gregory, 1983). These workers studied fish below 55 mm in length, and found that these also fed upon near surface plankton, eating harpacticoid copepods (associated with drifting weed) when small, and shifting to the amphipods *Calliopus laeviusculus* and *Parathemisto gaudichaudi* as they grew.

3.4.2 Growth

The earliest consideration of growth appears to be that of Cox (1920a) who constructed the length:weight relationship presented (after conversion to metric units) in Figure 10. Unfortunately, the original data on which the curve is based are not available, but weight varies (approximately) with the cube of the length (which is also the case with the pre-adult stages - Myrseth, 1971); this suggests that lumpsucker proportions change little during growth. Cox (*op. cit.*) aged a few fish by vertebral rings (visualized by staining and clearing), but with the exception of a large male (34 cm length) in its eighth year, the data were not assigned to either sex so are of little value.

Bagge (1964) measured length and age of spawning North Sea and Baltic lumpsuckers (see Table V). These data are limited, but indicate that lumpsucker growth in length is slow in the spawning population, and confirm the smaller size of male fish. The results also demonstrate the much smaller size of Baltic lumpsuckers, which are less than half the length (and presumably an eighth of the weight?) of their North Sea relatives. It would appear that most growth in length occurs before maturity.

Thorsteinsson (1981, 1983) carried out the most comprehensive growth study so far performed (on Icelandic fish between 1974 and 1981), though still had problems in obtaining year classes II to IV which appear to be totally epipelagic in habit. Ageing was carried out on otoliths (sagittae) which are very small (rarely above 2 mm

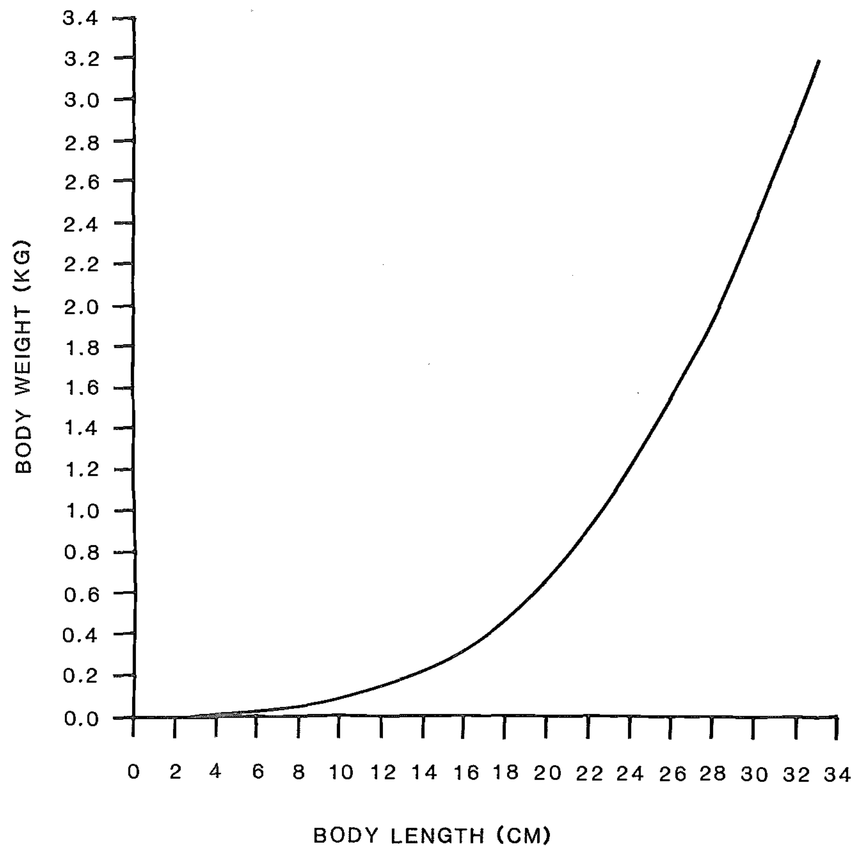


Figure 10 Length-weight relationship of adult lumpsuckers from Newfoundland waters (Redrawn from Cox, 1920a)

Table V

Mean length (cm) of lumpsuckers (estimated by the author from Bagge, 1964)

	AGE GROUP								
	I	II	III	IV	V	VI	VII	VIII	IX
North Sea males	-	-	-	31.6	35.9	37.0	38.0	39.6	-
North Sea females	-	-	-	-	44.6	45.4	47.0	-	-
Baltic males	-	-	13.5	14.2	15.4	-	-	-	-
Baltic females	-	-	15.0	15.6	17.0	15.6	-	-	-

in length). These were read directly under oil, or indirectly by acetate peel. Otolith year ring radius (between the otolith centre and the rostrum) is plotted against age in Figure 11. Female fish length at various ages is also plotted in Figure 11.

Both Schopka (1974) and Thorsteinsson (*op. cit.*) carried out tagging exercises in which some fish were captured after a year at liberty. Thorsteinsson aged all his fish at recapture, whereas Schopka only aged some. Growth data for aged fish are shown in Table VI. There is an obvious major problem in considering the data in this table; the size of the lumpsuckers recorded by Schopka (1974) appears to be much too large for their reported age (e.g., mean length at age 4 = 41.1 cm) given the subsequent (and very detailed) age/size investigations of Thorsteinsson (which predict a length at age 4 in female lumpsuckers of about 30 cm) on the same populations. The earlier studies of Bagge (1964), although on different populations, tend to support Thorsteinsson's age values too. It would probably be wisest therefore to ignore the ages given in Schopka's data (they are accompanied by a question mark in the table presented here). If this is done, and attention paid solely to the growth increments, then the mean growth increment for all spawning females studied by both authors was 3.6 cm, indicating a slow rate of growth after recruitment to the spawning stock.

No information is available concerning the effects of environmental or biotic factors on growth rate of lumpfish, beyond the finding of Cox (1920) and Bugge (1964) that the lumpsuckers of low salinity seas grow to a much smaller maximum size than the lumpfish from areas of near oceanic salinity.

3.4.3 Metabolism

No information about the metabolism of adult lumpsuckers appears to have been published, not least because spawning populations are non feeding.

3.5 Behaviour

(For reproductive behaviour see 3.1.5 and 3.1.6).

3.5.1 Migrations and local movements

Tagging experiments to study migrations were initiated in April 1966 in the southern part of the Kattegat (Denmark) by Bagge (1967). Great white Petersen discs (diameter 25 mm) were used as tags. Two discs were attached to each fish with titanium wire on either side of the "hump". All fish (1 122 females, mean length 42.3 cm; 446 males, mean length 36.0 cm) were mature and in age groups V and VI. In 17 months after release 10,3% of tagged fish were recaptured (13.2% of males, 8.8% of females). The sexual difference in recapture was statistically significant and Bagge suggested that natural mortality is greater in females than males during the spawning season. He noted that dead females were often collected in bottom trawls during Spring. However, he recognized that males probably spend far longer periods in shallow water than do females (mainly in nest guarding) so may be exposed to a greater risk of recapture [the author finds this point rather unconvincing as there appears to be no feeding and little movement of the male during nest guarding]. Recapture of lumpsuckers in April and May 1966 (i.e., shortly after tagging) was almost always in shallow water around the eastern Danish coast, indicating local movements and dispersal. Few were caught in June, July and August, but in September 1966 one specimen was caught in a surface herring drift net in the Skagerrak (north of Denmark) over a depth of 300 m of water. Other specimens were caught in bottom trawls in the same area in March 1967. Bagge interprets these data as indicating a return to an epipelagic feeding ground after spawning, followed by a resumption of the benthic habit in the winter before the spawning migration into shallow water, a hypothesis also supported by Schopka (1974).

A full year after tagging, specimens were recaptured very close to the original tagging locality, indicating a strong homing ability.

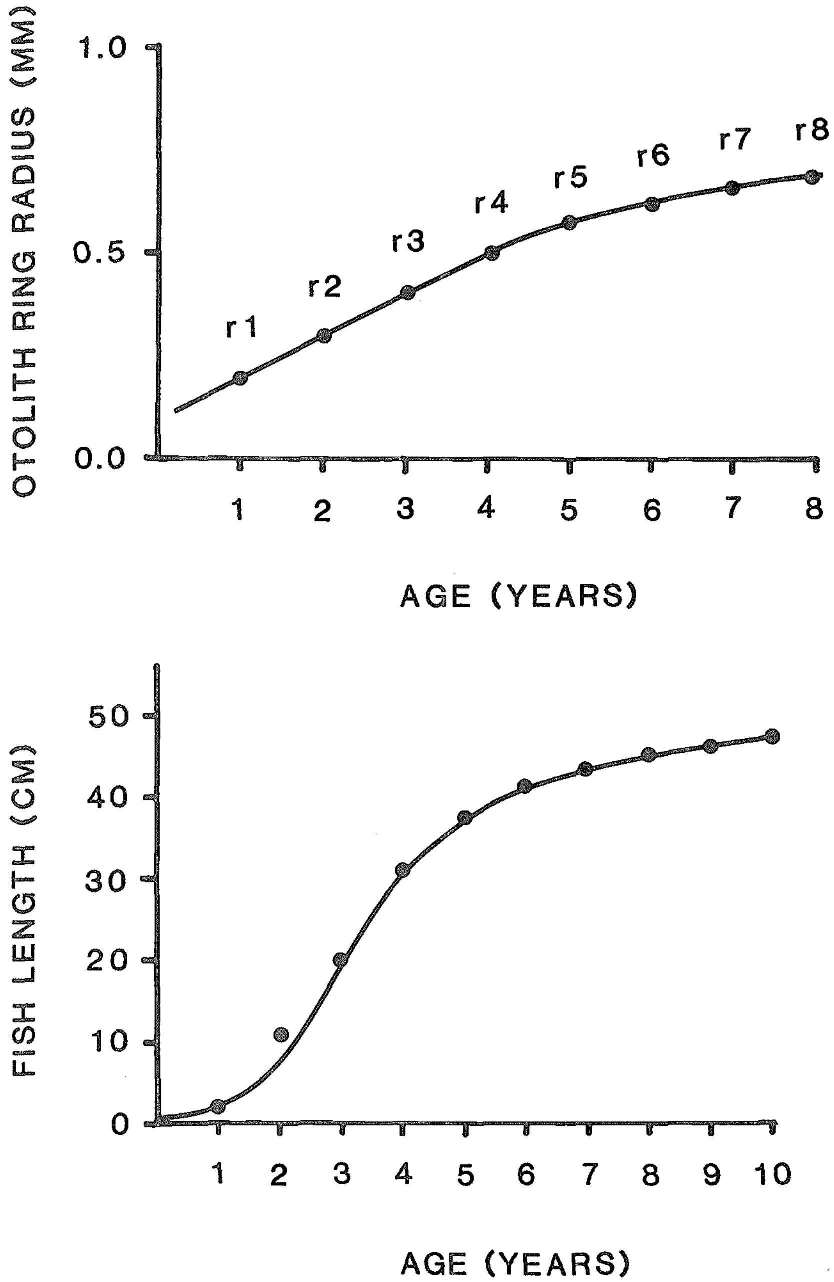


Figure 11 Growth in female Icelandic lumpsuckers.
(Redrawn from Thorsteinsson, 1983)

Table VI

Growth increment data for tagged Icelandic lumpsuckers recaptured after 1 year at liberty (taken from Schopka, 1974 and Thorsteinsson, 1981)

Init. length (cm)	Recap. length (cm)	Growth increm. (cm)	Sex m/f	Age y
A. Schopka				
43	44	1	f	4?
38	48	10	f	4?
43	47	4	f	4?
38	39	1	f	4?
41	42	1	f	4?
44	47	3	f	4?
41	46	5	f	4?
41	43	2	f	4?
39	44	5	f	4?
41	46	5	f	4?
43	49	6	f	4?
42	46	4	f	5?
40	45	5	f	5?
B. Thorsteinsson				
35	35	0	f	6
34	40	6	f	6
39	40	1	f	7
42	44	2	f	8
28	30	2	m	7
28	31	3	m	8

Schopka (1974) tagged a much larger number of lumpsuckers (6 665) in 1971-73 and recaptured 10.2%. Most were tagged in the spawning season (April-July), but a few were tagged offshore in autumn and winter from research vessels. Such fish, tagged in their feeding areas, were recaptured in a wide variety of spawning sites on the coasts of Iceland during the following Spring. This suggests that fish "home in" to specific spawning sites rather than migrating to the nearest area of shallow water.

Fish tagged in spawning area were generally recaptured in the locality of tagging within three weeks. This indicates that spawning of individual fish is accomplished in two-four weeks, after which they leave the spawning ground and are replaced by new ripe females. This scenario is consistent with the finding of Ehrenbaum (1904) that hen fish lay two-four batches of eggs at intervals of 8-14 days. As in Bagge's study, Schopka found that all fish captured after a year at liberty were caught at the original tagging locality, indicating a very strong homing instinct (and also confirming that fish spawn more than once).

3.5.2 Territoriality/schooling

Cyclopterus appears to be a basically solitary rather than schooling fish; certainly it appears not to aggregate during its epipelagic feeding phase. During the spawning season, males apparently set up territories and show aggression to one another (Fulton, 1907; Mochek, 1973). The concentrations of fish in the shallow water spawning grounds have been referred to as spawning schools (e.g., Andriyashev, 1958), but this is probably incorrect; the concentrations are likely to be the inevitable result of large numbers of fish entering a small area containing suitable spawning sites, rather than a process involving social interaction.

4. POPULATION

4.1 Structure

4.1.1 Sex ratio

The sex ratio of lumpsuckers is obscure, principally because current fishery practices are aimed at the capture of female fish, but also because of the pronounced size dimorphism of the species which means that the gillnet mesh size which traps ripe females allows some males to escape. Since the male is apparently capable on occasion of brooding egg masses from more than one female simultaneously (e.g., Mochek, 1973), it is tempting to speculate that males outnumber females. Certainly all scientific collections appear to have netted far fewer male lumpsuckers than females. In the author's experience (with small mesh gillnets) four-five females were caught for every male. However, males are more powerful swimmers than females (Davenport and Kjørsvik, in press) so may be better able to avoid currents which sweep females into nets. Also, there is some evidence from tagging trials that female mortality is higher after spawning than is the case for males (Bagge, 1967), though this is offset to some extent by ageing measurements which have revealed females as old as 14, but no males older than 9 (Bagge, 1964; Thorsteinsson, 1981, 1983).

4.1.2 Age composition

(see 3.1.2)

4.1.3 Size composition

The bulk of spawning females (V-XIII) caught in commercial gillnets are between 35 and 50 cm in length (roughly 2-5 kg). There is a peak of net selection (in the Icelandic fishery) of 42-44 cm (Thorsteinsson, 1983). Age classes II-IV have been very poorly studied because of their exclusively epipelagic lifestyle. This is unfortunate because growth after maturity (at V and above) is very slow (Bagge, 1964; Thorsteinsson, 1983).

4.2 Abundance and Density of Population

No sensible estimates of abundance and density of population appear to be feasible at present, even in the Icelandic area where knowledge is most detailed. Lumpsuckers occupy an enormous range of rocky coastline during the spawning season, but it is not known whether they are evenly distributed or otherwise. Exploitation is normally only carried out within small boat range of communities, which are fairly sparse in the northerly portions of the distribution (e.g., Canada, Greenland) and there may well be unfished/unknown stocks in these areas.

4.3 Natality and Recruitment

4.3.1 Reproduction rates

The number of eggs produced by a female during a single spawning (i.e., in one egg mass) appears not to have been considered very often, although Zhitenev (1970) counted 38 600 eggs in one mass and 52 700 in another. However, the total laid during a spawning season (as 2-4 batches) is usually assumed to correspond to the total number of ripe and unripe eggs found in a ripe female (around 80 000-200 000; Fulton, 1891; Myrseth, 1971 - see Figure 7). Fertilization in the field and in the laboratory appears to be close to 100% (Zhitenev, 1970; pers. obs.), but Zhitenev reported that the outermost layer of eggs in White Sea egg masses invariably died during development and became coated in algae.

No reliable data for field mortality between fertilization and hatching are available. In aquaria, egg masses often become anoxic and black at the centre (e.g., Fulton, 1907; Zhitenev, 1970) but it is not clear whether this happens in nature.

4.3.2 Factors affecting reproduction

There is some evidence that storms cause lumpsucker egg masses to be swept away from spawning sites (e.g., McIntosh, 1886) and deposited in the intertidal zone.

Temperature is known to have a strong direct effect on egg development time (Ehrenbaum, 1904; Collins, 1978; Davenport, 1983) and there are probably indirect effects too (e.g., longer development times may involve increased mortality due to predation or bacterial attack).

Low salinity areas (Hudson Bay, Baltic) are characterized by much smaller spawning adult lumpsuckers than occur in the open sea (Cox, 1920; Bagge, 1964). There is no evidence that egg size is smaller, so presumably fecundity is also much reduced in these populations - a common feature of brackish water populations of basically marine animals (Kinne, 1971).

4.3.3 Recruitment

Thorsteinsson (1983) carried out the only extensive study of recruitment (and then only to the spawning stock). His ageing validation studies have already been described (3.4.2). To determine the age at which fish first spawned he inspected otoliths for an abrupt reduction in the yearly increments of the otolith (a generally accepted technique - see Blacker, 1974). By back calculation (using known otolith radius/fish length data) it was possible to calculate fish length at first spawning as well. Thorsteinsson found that the age structure of spawning lumpsuckers was complex. Some fish grew quickly and spawned first at the age of 5 or 6. Others grew slowly and did not spawn until 8-10 years of age. This meant that fish of a given size varied greatly in the number of times they had spawned (see Table VII). In contrast, size at first spawning was quite constant, indicating that maturity and recruitment to the spawning (and therefore fishable) stock depends upon size rather than age (see Table VIII).

4.4 Mortality

4.4.1 Egg, larval and juvenile mortality

Egg masses are eaten by invertebrates, fish and some terrestrial and avian predators (e.g., McIntosh, 1886; McIntosh and Masterman, 1897). There is some evidence that the central layers of some egg masses are doomed because of inadequate ventilation (Fulton, 1907; Zhitenev, 1970). Virtually nothing is known of influences on larval and juvenile mortality.

4.4.2 Adult mortality

The results of Thorsteinsson (1983) show that mortality in adult fish is size dependent. Within recruitment groups (cohorts) mean length increases with age until a certain length interval (approx. 42-44 cm in Icelandic females) is reached, after which mean length falls with age, indicating the death of larger fish. The source of this size-dependent mortality is obscure. It could be due to fishing mortality (the peak selection of the commercial nets also occurs at 42-44 cm), but trawl catches (which include unfished as well as fished populations) show a similar decline in abundance beyond the 42-44 cm interval. Predatory pressure on adults in Icelandic waters is mainly from seals, sharks and sperm whales, and there seems to be no reason to postulate an increased vulnerability when this particular size is reached. Thorsteinsson postulates that the reproductive process (including gonad production, spawning migration and the associated prolonged starvation) becomes progressively more expensive with increasing size, and that eventually large fish do not recover from spawning.

4.5 Population Dynamics

At present, knowledge of the population dynamics of *Cyclopterus* is limited, not least because of the extremely widespread spawning grounds, combined with a general lack of knowledge about the biology and distribution of the species between spawnings. Thorsteinsson (1983) points out that no allozyme studies have yet been performed despite the strong homing abilities which make localized subpopulations likely. These deficiencies, combined with the complex age/size structure of the spawning populations (see 3.3.1, 3.4.2, 4.3.3) make population modelling impossible at present.

Table VII

Age of recruitment to the spawning stock of various age classes of 4 samples of Icelandic lumpsuckers (from Thorsteinsson, 1983)

Age class	Number of fish recruited at age						Samples
	5	6	7	8	9	10	
5	8						
6	9	6					Sample 1
7	8	6	4				
8	2	3	3	1			
Total	27	15	7	1			
7	13	2	2				
8	3	8		5			
9	6	10	3	5	2		Sample 2
10	2	2	3	3	1	3	
11		2	1	1	1	1	
12	1	1	1	1			
13				1	2		
Total	24	25	10	16	7	4	
6	1	2					
7	6	3	3				
8	7	10	5	6			
9	4	9	4	4	5		Sample 3
10		4	4	6		1	
11		3		5		1	
12			1	1	1		
13				3			
Total	18	31	17	25	6	2	
6	1						
7	5	1	1				
8	8	3	2	4			
9	2	6	4	3	2		Sample 4
10	3	5	2	4	1	1	
11	1		4	2	1	1	
12		1	1	3		1	
13			2	1		2	
14				1	2		
Total	20	16	16	18	6	5	

5. EXPLOITATION

5.1 Fishing Equipment

Lumpsuckers have almost certainly been exploited at a local level for centuries. Much of the catch was presumably incidental to other fisheries (particularly for herring and salmon), but the vulnerability of nesting males encouraged shore-based exploitation which persisted into this century. Cox (1920a) reported that the fishermen of Helgoland (a small island in the North Sea) collected lumpsuckers by gaffing them at low tide (with iron hooks attached to poles). Between 1905 and 1908 some 14 000 kg of lumpsuckers were exported to ports on the West German mainland from Helgoland from this simple fishery, which was essentially identical with that practised by Greenlanders at the time of Fabricius (1780).

Present fishing is overwhelmingly by gillnet (see Table IX), though reasonable numbers are caught by trawling (particularly off Newfoundland - Collins, 1976) and longlining as incidental catches. Herring drifters often caught substantial numbers of lumpsuckers in the past. In Iceland the lumpsucker fishery is aimed almost entirely at the female fish, which are much larger than the males (see Figure 4). The mesh size of the majority of gillnets is therefore 27-29 cm whereas males are caught in nets of mesh size 17-19 cm (Thorsteinsson, 1981).

5.2 Boats

Some lumpsuckers are caught by offshore trawlers (particularly in the Newfoundland fishery), but most boats involved in setting gillnets are small general purpose inshore vessels.

Table VIII

Total length (mean and range) at recruitment age in Icelandic lumpsuckers (from Thorsteinsson, 1983)

Recruitment Age (y)	Mean length (cm)	Length range (cm)
A. Females		
5	37.8	36-40
6	38.8	37-40
7	40.9	39-43
8	40.1	36-43
9	40.4	35-45
B. Males		
4	28.0	24-29
5	28.4	26-32
6	28.2	27-28
7	28.0	27-29

Table IX

Norwegian methods of lumpsucker capture (1978) (from Norges offisielle statistikk B162)

Method	Tons catch	% Total catch
Total catch (live weight)	3 137	100.0
Gillnet catch	2 489	79.3
Handline catch	144	4.6
Longline catch	4	0.1
Trawl catch	103	3.3
Other	397	12.7

5.3 Fishing Areas

In the nineteenth century, when lumpsuckers were fished primarily for their flesh, usually by subsistence fishermen, *Cyclopterus* was fished for throughout its range. Today, when it is fished mainly for roe, substantial fisheries are limited to Norway, Iceland, Greenland, Denmark and the USSR, although Collins (1976) reported that a fishery initiatied off Newfoundland in 1969 was becoming of some commercial importance. In all cases, fisheries are based upon the capture of female fish in inshore shallow waters during the breeding season.

5.4 Fishing Seasons

The lumpsucker fishery is highly seasonal, being concentrated into the short period when fish perform their breeding migrations. This is generally in the late spring and early summer (April-July) and appears not to vary significantly with geography. Examples of recent monthly catches in the Norwegian fishery are given in Figure 12.

5.5 Fishing Operations and Results

Obtaining information about lumpsucker fisheries is difficult, partly because lumpsucker catches are often incidental to fisheries of greater commercial importance (herring, flounder, mackerel and salmon), and partly because the major product (salted roe) is marketed as a sturgeon caviare substitute/alternative, and the source of the roe is virtually unknown to the general public. In Denmark the fish has retained a wider market (it is still sold fresh through the retail trade, a practice long abandoned in the UK for example). The Danish authorities recognized the lumpsucker as a staple food fish in the early part of this century, so statistics were kept. Between 1903 and 1907 an average of 491 851 kg fresh weight of lumpfish were caught per year by Danish fishermen (Cox, 1920a), mainly from the North Sea and Kattegat (roughly 9% were caught in the Baltic proper). The sales were believed to be extremely profitable because of their largely incidental nature.

Swedish and Norwegian statistics prior to, and immediately after the Second World War are extremely difficult to obtain, either because the fish themselves formed part of a "mixed fish" category, or the roe quantities were not separated from the roe of other fish (e.g., cod, herring). Cox (1920a) estimated that several million kilos of lumpsuckers were taken by the Swedes each year.

Recognition of the possibility of using lumpsucker roe (dyed black) as a substitute caviare appears to have taken place shortly in Europe shortly before the Second World War. Initially a minor usage, it progressively became dominant and "lumpfish caviare" has become a recognized product in its own right.

Norwegian statistics before 1956 are not available, but thereafter were increasingly well documented, and form the basis of Figure 13 (prepared by the author). From 1956-64 the catch was expressed solely in terms of weight of roe (which makes up about 15% of live fish weight). From 1965 onward live weight values became available, but roe weights were abandoned in 1979. From this figure it would seem that there was a gradual rise in quantity of fish taken until the mid 1970s, since when the catch has remained relatively stable. Interestingly, this increased catch (common to Iceland and Denmark as well) is not widely appreciated in the fishing community of Norway. Fishermen not directly involved in the trade will remark that far more lumpsuckers were caught by previous generations. The author believes that this reflects the shift from the visible exploitation of the flesh of the fish for home/local consumption, to the less obvious processing for exported imitation sturgeon caviare.

A breakdown of utilization of Norwegian lumpsuckers in a typical year is given in Table X.

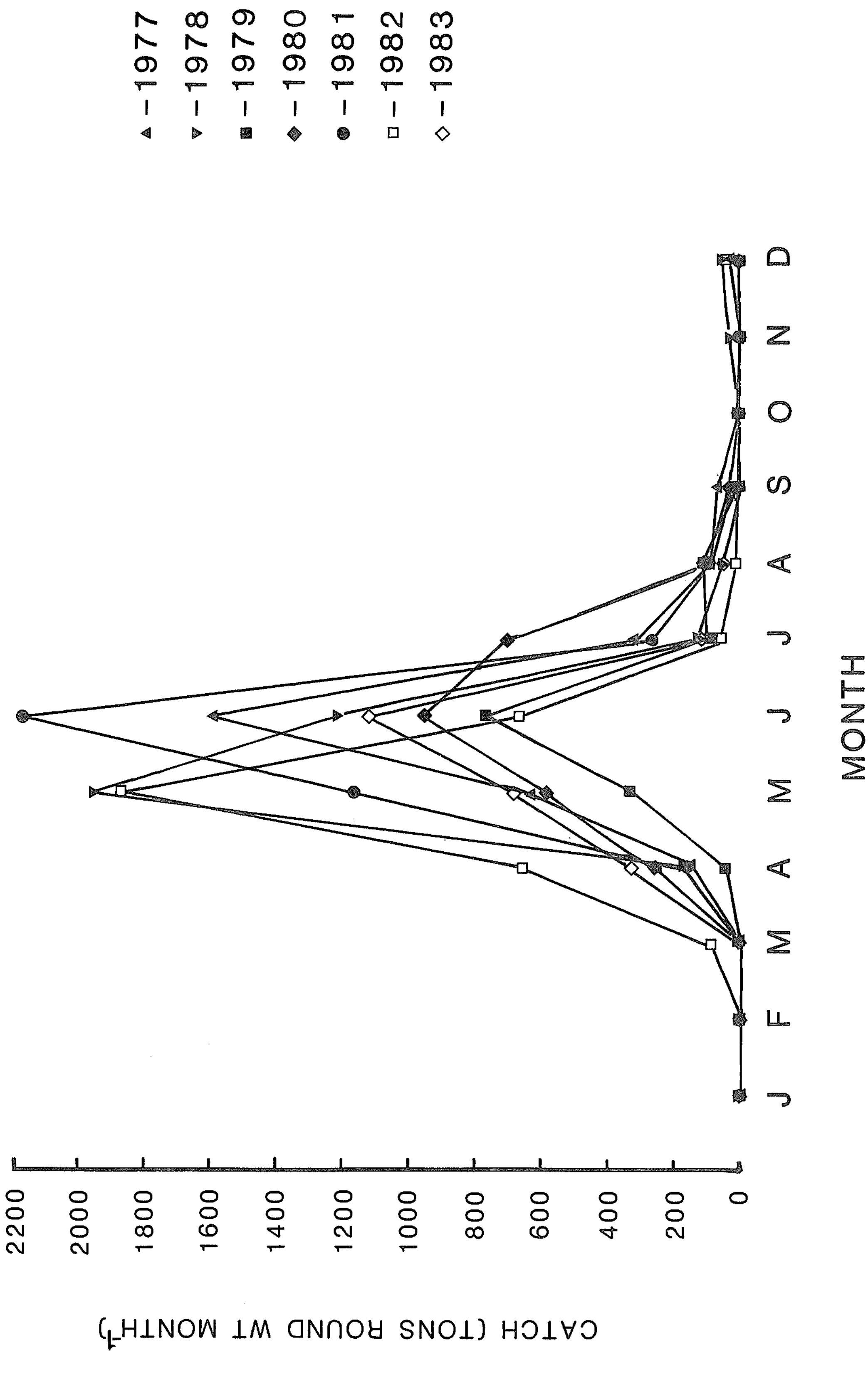


Figure 12 Seasonality of Norwegian lumpsucker fishery

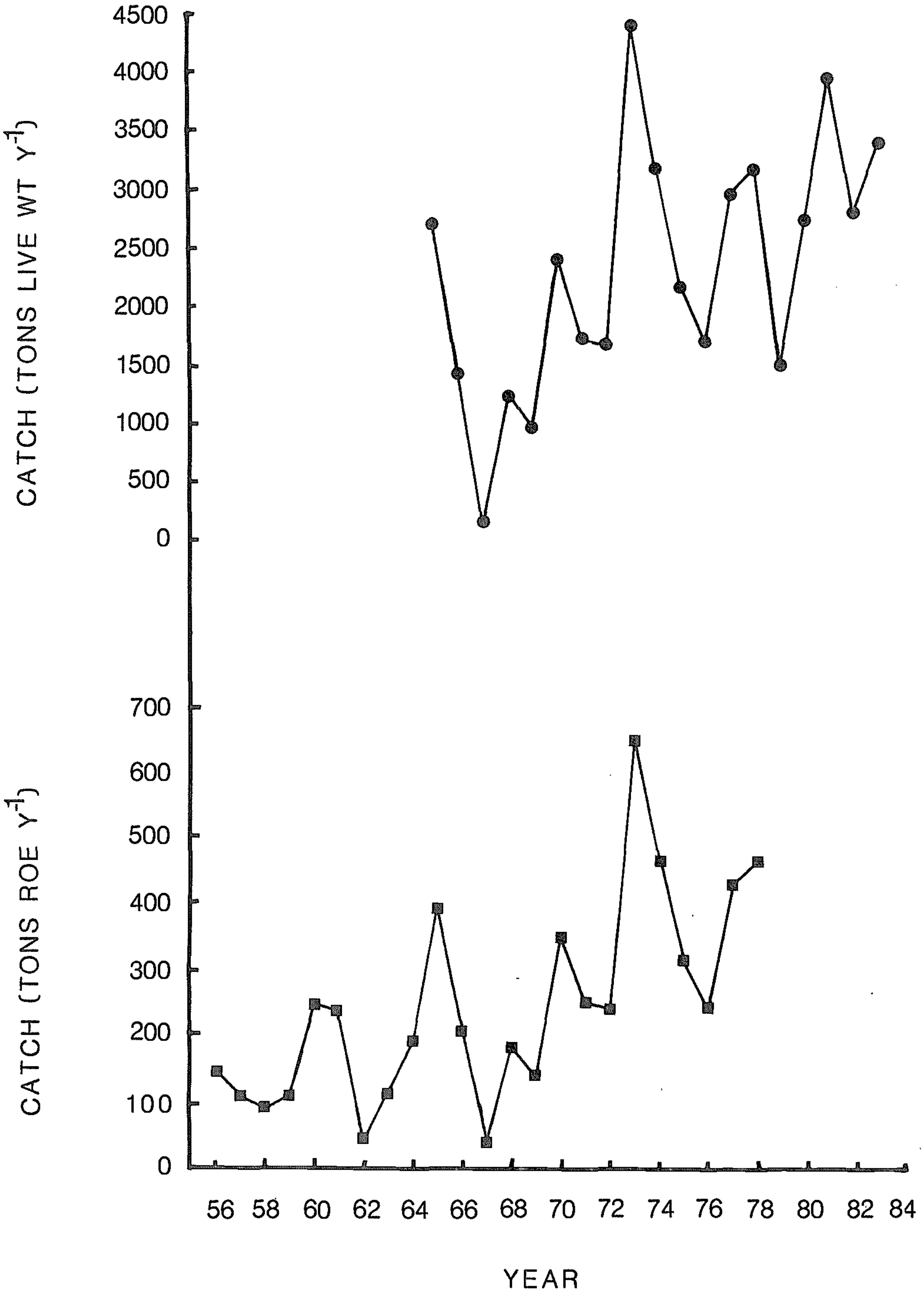


Figure 13 Norwegian lumpsucker catches (1956-83)

Table X

Utilization of Norwegian lumpsucker catch (1978)

	Tons	% total
Total live weight catch	3 137	100.0
Sold fresh	102	3.3
Sold frozen	-	-
Canned	-	-
Processed for salt roe	2 980	95.0
Fish meal/oil/animal feed	55	1.7

Saemundsson (1949) reported that 93 000-675 000 lumpsuckers were caught annually by gillnetting in the kelp-fringed bays of Iceland between 1922 and 1937 when the fish was caught for home consumption (fresh, dried, salted or smoked) rather than roe export (which started on a small-scale in 1945 shortly after World War 2). The current Icelandic fishery is very much greater in size, and supplies about 70% of the world market for lumpfish roe (Thorsteinsson, 1981). Thorsteinsson (personal communication) reports that the average annual roe catch from 1974 to 1984 was about 1 600 t, so that the fishery is three-four times larger than that of Norway. As about 0.7 kg of cured roe is derived from each individual caught, this quantity of roe represents about 2 200 000-2 300 000 individuals - perhaps four times the maximum prewar fishing intensity. Many Icelandic fishermen are dependent upon the lumpsucker fishery (Thorsteinsson, 1981).

The fishery of the USSR, although apparently undocumented, is probably comparable with the Norwegian one. It is certainly sizeable, since Altukhov *et al.* (1958) stated that the lumpsucker catch in the White Sea was only slightly smaller than the herring catch in those years when the *Cyclopterus* year class was strong. With the decline of the Russian and Iranian sturgeon fisheries, more attention has been paid to the exploitation of White Sea lumpsuckers (Nadezhin, 1970).

In contrast to the primary usage for human consumption in Europe, Greenland and Iceland, lumpsuckers caught in North America have largely been discarded or treated as trash fish, despite the efforts of the Canadian authorities to create commercial interest in the species (e.g., Cox, 1920). Collins (1976) reported that lumpfish had been used to bait lobster traps, and also as pig or dog feed. However, in Newfoundland a survey (1968-69) by the Newfoundland Department of Fisheries and Agriculture showed that a few local communities valued the flesh of the male fish, and that sufficient quantities of lumpsuckers were available to merit a commercial fishery (for roe and fresh fish). This was initiated in 1969 and apparently continues, stimulated by the decline in world sturgeon fisheries during the 1970s. In 1972 about 200 t of roe were collected (Wells in Pinhorn, 1976), although this was said to be from around 500 t live weight of fish. The 200 t value would make the Newfoundland fishery about half the size of the Norwegian fishery at the same date. However, unless the roe:liveweight ratio is much higher in Canadian than European fish, one would expect 200 t of roe to correspond to about 1 200 t of live fish.

An interesting feature of the lumpsucker fisheries lies in the unusual difference in utilization of the two sexes. Obviously the modern trade in roe relies exclusively on the female fish, but formerly it was the male fish that was preferred. In the early nineteenth century fishermen did not appreciate that red coloured fish were male and blue/green fish female. Instead, they believed that "red" lumpfish were ripe, edible fish with firm flesh, while "blue" lumpsuckers were exhausted from spawning, flabby and worthless. Paradis *et al.* (1975) and Davenport and Kjørsvik (in press) have analysed muscle tissues from both sexes of *Cyclopterus* and found that there is indeed a marked sexual dimorphism in tissue composition, with the male fillets having a much higher fat (and lower water) content (see Table XI).

Cox (1920a) reported that around 40% of the live fresh weight of a lumpsucker was made up of saleable flesh (compared with 50% in cod). Given the fat, protein and energy content of male fillets, it is evident that lumpsuckers have a high food value. It is therefore rather surprising that the fish no longer enjoys the esteem that it did in the eighteenth century when Sir Walter Scott implied in his writings that the inhabitants of Edinburgh preferred lumpsuckers to all fish except the turbot! Even today, Newfoundlanders from some communities perceive it as a greater delicacy than herring, mackerel or salmon (Collins, 1976).

No information about fishing effort or selectivity of nets appears to be available beyond a note by Wells (in Pinhorn, 1976) that 2 300 kg of lumpsuckers were caught in each of three 30-minute trawl tows off Newfoundland in 1973, and the statement by Thorsteinsson (1983) that Icelandic gillnets show peak selectivity for 42-44 cm fish.

5.6 Processing

Paradoxically there is little published information about processing of lumpsuckers in Europe, Greenland or Iceland (where substantial fisheries exist); smoking, drying and salting of fish has been performed as for other fish such as cod, herring and mackerel. Roe processing itself is very simple, as eggs are simply cured in brine (and usually dyed black). However, an intractable problem has been the utilization of wastes from roe harvesting operations. This has been considered in some detail by the Canadian authorities, who considered lumpsucker

Table XI

Composition of tissues of lumpsuckers
(simplified from Davenport and Kjørsvik, in press)

Mean values, with standard deviations in parentheses.
Values are calculated for samples of 100 g wet weight.

Tissue	Water (g)	Dry wt. (g)	Fat (g)	Protein (g)	Ash (g)	Energy content (kcal)
Female fish						
A. Dorsal muscle	86.2(0.6)	13.8	7.76(1.10)	4.94(1.88)	1.89	85.28 (4.42)
B. Tail muscle	87.7(0.8)	12.3	4.34(1.48)	6.16(1.50)	1.37	69.62 (3.94)
C. Subcutaneous jelly	93.3(0.8)	6.7	2.21(1.47)	1.47(0.58)	1.35	28.48 (1.61)
D. Eggs	83.5(0.7)	16.5	3.27(1.35)	7.51(1.30)	2.29	92.07 (4.13)
Male fish						
A. Dorsal muscle	64.1(1.4)	35.9	19.57(1.69)	13.82(5.46)	1.87	219.35(18.31)
B. Tail muscle	77.3(1.3)	22.7	11.78(0.87)	10.40(3.34)	1.75	149.60 (5.68)
C. Subcutaneous jelly	88.6(0.4)	11.4	2.91(1.89)	3.72(0.56)	1.17	49.36 (8.55)

exploitation rather abortively for over half a century before the initiation of the Newfoundland fishery in 1969. Dewar, Lipton and Mack (1971), Jangaard (1972) and Paradis *et al.* (1975) have all investigated processing and/or waste utilization (the latter problem still not dealt with satisfactorily even in Iceland, where the largest current fishery exists).

Fish meals prepared from lumpsucker waste (head, skin, subcutaneous jelly, muscles, viscera) were found to be relatively low grade, but comparable with meals prepared from menhaden (*Brevoortia tyrranus*) caught in Nova Scotian waters. Attempts to manufacture photoengravers' glue from lumpsucker skins were technically successful, but the yield was lower than for cod skins, and the unusually thick, collagenous skin made processing difficult and expensive in the absence of machine skinning gear. Oil production was judged not worthwhile because of the low yield (0.2 kg of oil from 80 kg fish). Paradis *et al.* concluded that specific by-product use of lumpsucker wastes was impractical (though Jangaard, 1972 thought there might be economies of scale if the lumpfish roe industry in Newfoundland was expanded). Development of markets for consumption of flesh by humans or pets (as in happening in Iceland) was thought to be more promising.

6. PROTECTION AND MANAGEMENT

6.1 Regulatory Measures

Although Cox (1920a) reported that the Baltic Sea lumpsucker catch was declining "due, presumably to overfishing by Germans and Swedes", the only regulatory measures applied to *Cyclopterus* appear to be those introduced fairly recently (1976) by the Icelandic Government.

Thorsteinsson (1981) reported that fishing time, boat size, gillnet mesh size and number of nets per boat had all been limited. Lumpsucker fishermen are required to apply for a licence each year and send in a catch report at the end of the fishing season. The shallow water fisheries of Iceland are divided into 6 regions; fishing in each is only allowed for 3 months in each year, with the starting date varying from region to region.

6.2 Management

Little management of lumpsucker fisheries beyond the prudent regulatory mechanisms (described in 6.1) appears to have taken place. However, Thorsteinsson (1983) reports the establishment of an informal scheme in Iceland for the prediction of abundances of spawning females in future years, based upon the regular linear measurement of samples of spawning females (by the lumpsucker fishermen) throughout the spawning season. This is seen as the first step toward effective management.

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