FAO Fisheries Synopsis No. 82 FIRM/S82
(Distribution restricted)

SAST - *Ammodytes tobianus* - 1.72(04),002,02
Ammodytes dubius - 1.72(04),002,05
Ammodytes americanus - 1.72(04),002,06
Ammodytes marinus - 1.72(04),002,07

SYNOPSIS OF BIOLOGICAL DATA ON NORTH ATLANTIC SAND EELS OF THE GENUS AMMODYTES

A. tobianus, A. dubius, A. americanus and A. marinus

Prepared by

P. J. Reay

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ROME, 1970

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Special groups of synopses are identified by symbols followed by classification numbers based on indexed code of "Current Bibliography":

- SAST Data concerning certain species and fish stocks.
- MAST Information on methods and subjects.
- OT Oceanographic data.
- IT Limnological data.

and

- CART Information concerning fisheries and resources of certain countries and regions (FID/S).

Des catégories spéciales de synopses sont identifiées à l'aide de symboles suivis des chiffres de classification basés sur le code d'indexation de la « Current Bibliography »:

- SAST Données sur certaines espèces et populations de poissons.
- MAST Renseignements sur des méthodes et des sujets.
- OT Données océanoprаphiques.
- IT Données limnologiques.

et

- CART Renseignements sur les pêcheries et les ressources de certains pays et régions (FD/S).

Grupos especiales de sinopsis se distinguen con las siglas siguientes, seguidas por números de clasificación que se basan en las claves de los índices de la « Current Bibliography ».

- SAST Datos relativos a ciertas especies y poblaciones.
- MAST Sinopsis sobre métodos y materias.
- OT Sinopsis sobre oceanografía.
- IT Sinopsis sobre limnología.

y

- CART Información sobre los recursos acuáticos vivos de algunos países y regiones (FID/S).

FAO Fisheries Technical Paper — FR/T (No.)

Special groups of Technical Papers are identified by:

- RE Indexed lists of experts and institutions drawn from Registers maintained by the Fishery Resources Division.
- CB Lists of periodicals, special sections of "Current Bibliography for Aquatic Sciences and Fisheries," special bibliographies and papers concerning documentation problems.
- MFS Provisional editions of "FAO Manuals in Fisheries Science."

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Des catégories spéciales de documents techniques sont identifiées à l'aide des symboles suivants:

- RE Listes indexées d'experts et institutions tirées des registres tenus à jour par la Division des ressources halieutiques.
- CB Listes de périodiques, des sections spéciales de la « Current Bibliography for Aquatic Sciences and Fisheries », des bibliographies particulières et des articles sur les problèmes de documentation.
- MFS Editions provisoires des « Manuels FAO de science halieutique ».

Certains documents portent parfois d'autres numéros d'identification, par exemple, s'ils ont été préparés pour une réunion dont les documents ont été marqués à l'aide d'un autre système.

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- RE Listas índices de expertos y de instituciones tomadas de los registros que se llevan en la Dirección de Recursos Pesqueros.
- CB Listas de periódicos, secciones especiales de la « Current Bibliography for Aquatic Sciences and Fisheries », bibliografías especiales y trabajos relativos a los problemas de documentación
- MFS Ediciones provisionales de los « Manuales de la FAO de Ciencias Pesqueras ».

Algunos documentos tienen también otra identificación si, por ejemplo, son contribuciones a una reunión cuyos documentos han sido marcados con arreglo a otros sistemas.

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SYNOPSIS OF BIOLOGICAL DATA ON NORTH ATLANTIC SANDEELS OF THE GENUS AMMODYTES

(*A. tobianus*, *A. dubius*, *A. americanus* and *A. marinus*)

Prepared by

P.J. REAY

Marine Resources Research Unit
Portsmouth Polytechnic
Portsmouth, U.K.

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, October, 1970

PREPARATION OF THIS SYNOPSIS

This Synopsis is concerned with the biology and exploitation of *Ammodytes* species in the North Atlantic. The inclusion of four species within the same Synopsis is justified by their close similarity, and by the relatively small amount of available information on them; some data from the related Pacific species have also been included, but only in sections where no information was available on the Atlantic species.

Sandeels are currently of considerable importance as a fishmeal resource in the North Sea, and such exploitation is likely to develop in other North Atlantic areas in the near future; inshore species are less important and their present use is mainly as bait.

The author wishes to acknowledge the advice and information received from A. Wheeler (British Museum (Natural History)) and C.T. Macer (Fisheries Laboratory, Lowestoft) during the preparation of this Synopsis.

Distribution

FAO Department of Fisheries
FAO Regional Fisheries Officers
Regional Fisheries Councils and Commissions
Selector SM
Author

"Current Bibliography" entry

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Synopsis of biological data on North Atlantic sandeels of the genus *Ammodytes* (*A. tobianus*, *A. dubius*, *A. americanus* and *A. marinus*)

ANW. ANE. Ammodytidae. Taxonomy, nomenclature. Morphology. Distribution. Bionomics and life history. Behaviour. Population. Exploitation. Protection. Management. Pond fish culture. Selected bibliography.

CONTENTS

* As no information was available to the author, these itens have been omitted from the text.

1. IDENTITY

1.1 Nomenclature

1.11 Valid names

The following are the original combinations under which the species were first described:

Ammodytes tobianus Linnaeus, C., (1758). Systema naturae. I: 123. Ammodytes. (Ed. Decima): 247-8.

Ammodytes dubius Reinhardt, J., (1838). K. danske Vidensk. Selsk. Skr.nat. og math. 7 (54): 131-2.

Ammodytes americanus DeKay, J.E., (1842). Zoology of New York, or the New York fauna, Pt. IV. Genus Ammodytes, 317-8.

Ammodytes marinus Raitt, D.S., (1934). J. Cons. perm. int. Explor.Mer., 9: 365-72.

TABLE I

Meristic and morphological features used to distinguish A. tobianus and A. marinus

	v	A. tobianus	A. marinus	Author
1	Total vertebral number	60-68	65-75	) Raitt (1934)
2	Dorsal fin ray number	49-58	56-63	} Kändler (1941)
3	Anal fin ray number	24-32	29-33	) Soleim (1945)
4	Pectoral fin ray number	10-14	12-16	
5	Plicae (skin fold) number	120-138	140-150	Andriashev (1954)
6	Low ventral median dermal fold	absent	present	Düncker and Mohr (1939) (not recognised by later authors such as Braun (1941)
7	Radialia on lower part of suboperculum	well pronounced	feint	Andriashev (1954)
8	Scales on dorsal surface	extend anterior to and alongside dorsal fin	absent from anterior and alongside dorsal fin	Andriashev (1954)
9	Scales on ventral surface	in tight chevrons	loosely arranged	Andriashev (1954)
10	Scales over musculature at base of caudal fin	present	absent	Corbin (pers. comm.)
11	Pigmentation on head	slight, usually in-conspicuous	conspicuous, & sharply contrast-ing with unpig-mented areas	Present author
12	Larval pigmen-tation:-			
	a) caudal pigmen-tation	none until 15 mm.	appears before 15 mm.	Einarsson (1955) Macer (1967)
	b) pre-anal ventral body pigment	rapidly obscured by the body wall	remains conspic-ous	
	c) dorsal pigment	commences anterior to notochord tip	commences at notochord tip	

1.2 Taxonomy

1.21 Affinities

Suprageneric

Phylum–Vertebrata
Subphylum–Craniata
Superclass–Gnathostomata
Series–Pisces
Class–Teleostomi
Subclass–Actinopterygii
Order–Clupeiformes
Suborder–Ammodytoidei
Family–Ammodytidae

Generic

Genus: Ammodytes, Artedi P. (1738), in Bibliotheca ichthyologica seu historia litteraria ichthyologiae. Genera Piscium. Ichthyologiae pars III. Malacopterygii. Ammodytes: 55–57.

Genotype = A. tobianus Linn.

The genus Ammodytes includes the Pacific species A. hexapterus Pallas., and A. personatus Girard, in addition to the Atlantic species, A. tobianus, A. marinus, A. dubius and A. americanus as listed in Section 1.11, and has the following diagnostic characteristics:–

1. Premaxillae protrusible
2. Vomer without teeth
3. Body covered in scales which on the dies lie in oblique skin-folds (plicae)
4. Lateral-line pores linearly arranged
5. Dorsal and anal fin margins straight.

Characteristics 1–2 distinguish Ammodytes from the genus Hyperoplus Günther., and characteristics 3–5 distinguish both from the genus Gymnammodytes Düncker and Mohr. This generic concept is now adopted by several authors, including Wheeler (1969).

Specific

Diagnosis

The diagnostic features of A. tobianus and A. marinus are listed in Table I; the two species are clearly distinct on both meristic and morphological grounds.

A. americanus and A. dubius both appear to resemble A. marinus rather than A. tobianus on morphological grounds (eg. larval pigmentation patterns; Richards, 1965; Macer, 1967), and the characteristics currently used to distinguish them from each other and from A. marinus are somewhat tenuous (See Section 1.22). Richards et al. (1963) described A. americanus (as A. hexapterus) as an inshore fish with body-depth 7.1 – 9.7% of standard length and with meristic characteristics of V = 61 – 73, D = 51 – 62, A = 23 – 33, and A. dubius as offshore, with a body-depth of 6.8 – 9.2% and V = 65 – 75 (78), D = 56 – 68, and A = 27 – 35. In view of the wide degree of overlap between these two definitions, it is suggested that, until further information becomes available, the restricted concept of A. dubius as used by Leim and Scott (1966), be adopted, and that the remaining NW Atlantic Ammodytes be included as a rather heterogenous assemblage, with polymodal meristic counts, under the name of A. americanus; the meristic features of the two species would then be as described in Table II.

Thus, in the North Atlantic, A. tobianus is clearly distinguishable on both meristic and morphological grounds from the other three species. Of these, A. dubius is probably distinct meristically, but there is a wide overlap and close similarity between A. americanus and A. marinus.

Three other species of sandeel are present in the North Atlantic, Hyperoplus lanceolatus (LeSauv.), H. immaculatus (Corbin), and Gymnammodytes semisquamatus (Jourdain). These are all restricted to European coasts and can be distinguished from the species under consideration by the generic characteristics given above.

TABLE II

Meristic Characteristics of A. americanus and A. dubius

	V	D	A	
A. americanus	61–73	51–62	23–33	Richards et al. (1963)
A. dubius	71–78	61–69	31–36	Leim & Scott (1966); Scott, (1968)

Subjective Synonymy

1. A. tobianus

= A. lancea Curvier, G., (1829) Le Règne Animal distribué d'après son organisation,

......Les Ēquilles. Paris: 360; and Yarrell (1936).

The name A. tobianus was mistakenly used by Cuvier to describe the greater sandeel which LeSauvage (1824) had already named A. (=Hyperoplus) lanceolatus to distinguish it from the lesser sandeel named A. tobianus by Linnaeus (1758). Curvier then gave the name A. lancea to the latter species, believing that Linnaeus had originally been in possession of greater sandeels. Jensen (1941) has however shown that Linnaeus based his work on lesser sandeels, although his type specimens may have included both A. tobianus and A. marinus; on this basis in fact, Jensen advocated retention of the name A. lancea in preference to A. tobianus and it has been used objectively in this way by many authors since. As Andriashev (1954) and Backus (1957) have however pointed out there can be no valid grounds for the use of the name A. lancea, and the situation should be resolved by establishing either a neotype or a lectotype on the basis of Linnaeus' material and retaining the name A. tobianus as used initially by LeSauvage, and later, implicitly, by Raitt (1934).

2. A. marinus

= A. tobianus (ex parte; mixed with A. tobianus and not distinguished by any authors prior to Raitt (1934).

= A. lancea marinus (non Cuvier). Jensen (1941).

= A. dubius (non Reinhardt). Düncker and Mohr (1939).

= A. hexapterus marinus (non Pallas). Lindberg (1937).

3. A. americanus

= A. hexapterus (non Pallas). Richards et al. (1963).

4. A. dubius

= A. lancea dubius (non Reinhardt). Jensen (1941).

Artificial key for sandeels of the genus Ammodytes

A	Present in the North Atlantic............B
AA	Present in the North Pacific.............E
B	Present in the North East Atlantic......C
BB	Present in the North West Atlantic......D
C	Belly-scales in tight chevrons; scales present on the base of the caudal fin; low meristic counts with V = 60-68; inshore..A. tobianus
CC	Belly-scales loosely arranged; scales absent from the base of the caudal fin; high meristic counts with V = 65-75; offshore............ A. marinus
D	Low meristic counts with V = 61-73; up to 22 cm long.........................A. americanus
DD	High meristic counts with V = 71-78; up to 38 cm long...................A. dubius
E	Low meristic counts with V = 56-67..............A. personatus
EE	High meristic counts with V = 64-74.............A. hexapterus

1.22 Taxonomic status

All the species under consideration are morphospecies and none have been established as a result of either breeding experiments, cytomorphology or comparative serology.

A. tobianus is clearly a distinct species on morphological, meristic and physiological (spawning season) grounds, but the remaining species in the genus appear to share a common larval pigmentation pattern (Macer 1967; Kobayashi, 1962) and spawning season, and may, as Lindberg (1937) and others have suggested, be geographical morphological forms of a single polytypic species; in support examination of a small number of preserved specimens of A. dubius, A. americanus and A. personatus by the present author, has indicated that these species are similar to A. marinus in terms of scale-pattern characteristics. Further work is obviously needed, however, and in the meantime it is convenient to adopt the nomenclature and species definitions outlined above.

A. tobianus exists as two distinct but sympatric forms - autumn and spring spawners (Bahr, 1935). In addition to the seasonal differences in gonad maturity and the occurrence and growth of young stages induced by the different spawning seasons, individuals can usually be distinguished by the structure of their otoliths, (Kändler, 1941) and populations in many instances on meristic grounds (Section 1.31 and Table III). In the otoliths of spring-spawning fish, the first opaque ring is separated from the opaque centre by a broad hyaline zone; in those of autumn-spawners the centre and the first ring are usually almost confluent.

1.24 Standard common names, vernacular names

The following list of common names is mainly based on the ICES list of names of fish (Bulletin Statistique Vol. 49).

Danish	-	Tobis
Dutch/Flemish	-	Zandspiering, Smeelte
English	-	Sandeels, Lesser Sandeels
Faerose	-	Nebbasild
Finnish	-	Tuulenkalat
French	-	Equille

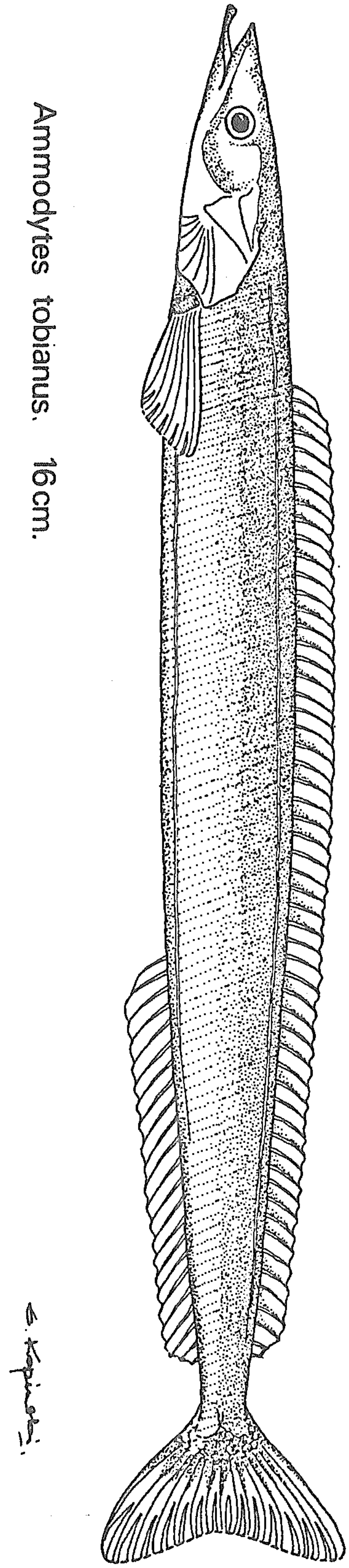

Fig. 1. External morphology of *A. tobianus*.

German	-	Sandaal, Sandspierling, Tobias Fisch
Greelandic	-	Putorutotoq
Icelandic	-	Tronusilli, Sandsili
Irish (Gaelic)	-	Corr
Norwegian	-	Sil, Tobis
Polish	-	Tobiasz, Dobijak
Portuguese	-	Franchão, Agulhae
Spanish	-	Lanzón
Swedish	-	Tobis
U.S.S.R.	-	Peschanka
U.S.A., Canadian	-	Launce, Sand Launce

1.3 Morphology

1.31 External Morphology

The body is elongate, subcylindrical and covered with small cycloid scales which, on the sides of the body, lie on the underside of oblique skin-folds (plicae). The head is pointed and the lower jaw projects anteriorly; the mouth is bordered by the premaxillae which are protrusible, and teeth are absent. The lateral lines run dorso-laterally, and there is a pair of ventro-lateral skin-folds. Pelvic fins are absent, the dorsal and anal fins are elongate and the forked caudal fin is preceded by a well-marked peduncle. There are no spines, but the fin-rays of the dorsal and anal fins are unjointed and unbranched. The gill openings are strongly extended anteriorly, and there are four gill arches with a slit behind the last arch, (Based on Andriashev, 1954).

Ammodytes species are white on the ventral surface, silvery on the sides and light brown to dark grey on the dorsal surface. Generalised external morphology is illustrated in Fig. 1.

Intraspecific morphometric variation has received little attention. Kirillov (1936) found some significant differences in A. marinus between a sample from Novaya Zemblya and one from the Murman coast; in particular, the latter fish had deeper bodies and smaller heads. Body depth was also considered by Richards et al. (1963) in a detailed study of Ammodytes from the east coast of North America; in general, for fish under 75 mm in length, the low meristic count, inshore populations had significantly deeper bodies than the high meristic-count offshore ones. Regression coefficients of depth on length ranged from 0.036 to 0.162 and suggested allometric growth.

Most attention has been paid to meristic characters, and in particular, the total number of vertebrae. In very general terms, there are about ten more vertebrae than there are dorsal fin rays, but the number of anal fin rays is less than half the number of vertebrae; Kändler (1941) in fact found a strong positive correlation between the number of vertebrae and the number of fin rays, with, for example in A. tobianus: $r = + 0.69$ (dorsal rays) and $r = + 0.42$ (anal rays).

Data on vertebral counts are summarised in Tables III and IV; where possible and necessary, standard deviations and confidence limits have been calculated from the original data. In A. tobianus counts are not available over a very wide geographical area, and the most conspicuous intraspecific variation is between the spring and autumn spawning groups. In general, autumn spawners have more vertebrae and show a slightly greater variance but the differences between the groups off the Isle of Man, and at two of the Baltic stations given by Kändler, are not significant at the 95% level. In A. marinus, samples have been examined from stations throughout most of its geographical range, and a clear latitudinal cline in vertebral number is apparent; in addition, samples from the North Sea show a significantly higher vertebral number than those from a similar latitude in the Baltic and Irish Seas.

In the case of NW Atlantic Ammodytes the position is confused by the uncertain relationship between A. americanus and A. dubius (see Section 1.21). However, it is clear from Table III that, as in A. marinus, there are latitudinal clines in vertebral number, and in addition separate high- (offshore) and low- (inshore) meristic groups at the same latitudes. Several of the groups show conspicuously skewed distributions, and variance is typically greater than in A. tobianus and A. marinus. Richards et al. (1963) have pointed out, that A. americanus may be partially divided into a group of small size fish inhabiting semienclosed bays and a group of larger fish with a wide meristic range which are caught along exposed coasts. These authors initially recognised three main groups of Ammodytes in the NW Atlantic with high, intermediate and low meristic counts; mainly on the basis of body-depth, they then divided the intermediate group so that high to intermediate (A. dubius) and low to intermediate (A. hexapterus = A. americanus) groups were formed.

TABLE III

Intraspecific meristic variation; counts of the total number of vertebrae in A. tobianus, A. marinus and A. dubius

Number of vertebrae includes the urostyle

A. tobianus *	GROUP	N.	Range	Mean	95% C.L.	Mode	S.D.
Iceland (Bruun 1941)	O	52	60-65	62.56	±0.28	63	1.01
Faeroes (Bruun 1941)	O	22	63-66	64.52	±0.46	65	1.02
Isle of Man (Cameron 1958)	AS	367	62-66	63.91	±0.10	64	0.90
" " " " "	SS	339	61-66	63.75	±0.12	64	1.10
North Sea, German coast (Kändler 1941)	AS	566	61-68	64.08	±0.08	64	1.04
" " " " " "	SS	274	61-65	63.09	±0.12	63	1.00
Baltic Sea, German coast (Kändler 1941)	AS	584	60-67	63.50	±0.11	64	1.24
" " " " " "	SS	961	60-67	63.17	±0.08	63	1.07
Portsmouth, S.England coast.Original data	AS	100	62-66	63.94	±0.18	64	0.94
" " " " " " "	SS	200	61-65	63.21	±0.09	63	0.82
Dingle, W. Eire coast. Original data	SS	49	60-65	62.96	±0.30	63	1.02
A. marinus							
W. Greenland (Jensen 1941)		38	67-72	69.39		69	
Novaya Zemblya (Kirillov 1936)		100		70.9	±0.27		1.33
Murman coast (Kirillov 1936)		121		71.3	±0.16		0.87
Iceland (Einarsson 1951)		167	69-75	71.97			
Iceland (Bruun 1941)		97	68-73	71.53	±0.23	72	1.15
Faeroes (Bruun 1941)		129	68-72	69.67	±0.17	70	0.17
Tana, N. Norway (Soleim 1945)		89	69-74	71.88	+0.25	72	1.18
Grense, N. Norway (Soleim 1954)		200	69-75	71.78	+0.16	72	1.18
Fosnavag, Norway (Soleim 1945)		200	68-73	70.70	±0.14	71	0.98
Bergen, Norway (Soleim 1945)		200	67-72	69.49	±0.15	70	1.06
Scotland (Raitt 1935)		205	67-72	69.21	+0.16	69	1.18
Isle of Man, Irish Sea (Cameron 1958)		240	66-71	68.71	±0.14	69	1.09
Celtic Sea (Corbin & Vati 1949)		45		68.56	±0.26		0.86
Heligoland, N. Sea (Kändler 1941)		28	68-72	70.11	±0.43	70	1.12
Loreley Bank, N.Sea (Kändler 1941)		39	67-71	69.49	±0.28	70	0.86
Hornsreef, N. Sea (Popp Madsen 1957)		216		70.20			
Jutland Bank, N. Sea (Popp Madsen 1957)		100		69.92			
Kolberg, Baltic Sea (Kändler 1941)		217	65-72	68.51	+0.16	68	1.21
A. dubius							
W. Greenland (Jensen 1941)		179	73-78	75.10	±0.16		1.10
W. Greenland (Einarsson 1951)		66	73-78	75.25			
W. Greenland (Scott 1968)		39	73-78	75.03	±0.36		1.11
Nova Scotia (Scott 1968)		146	71-78	74.60	±0.20		1.23

* O = spawning group not stated (most counts in this category have been omitted)
AS = autumn spawning group
SS = spring spawning group

TABLE IV

Intraspecific meristic variation; counts of the total number of vertebrae in Ammodytes recorded by Richards et al. (1963)

Number of vertebrae includes the urostyle

LOCALITY			N	Range	Mean	95% C.L.	Mode	S.D.
Hudson Bay	D	*	7	71-74	72.29	±1.07	71	1.20
" "			35	64-70	67.45	±0.45	68	1.31
Labrador Coast			59	64-72	68.27	±0.36	68	1.38
" "	D	*	12	71-75	73.50	±0.91	75	1.45
Lake Melville, Labrador		*	9	62-65	63.20	±1.38	62	1.30
Maqdalen Islands, Perce, Quebec			82	61-70	66.73	±0.37	68	1.70
Maine			65	65-70	67.91	±0.29	68	1.18
Massachusetts Bay	D	*	34	64-72	69.27	±0.69	70	1.98
Tarpawlin Cove, Mass.	D	*	14	67-71	69.36	±0.66	70	1.15
" " "		*	23	61-67	64.48	±0.65	64,66	1.50
Menemsha Bight, Mass.	D		14	70-73	71.21	±0.56	72	0.97
" " "		*	86	62-68	65.87	±0.36	68	1.66
Woods Hole, Mass.	D		51	67-73	70.51	±0.35	70,71	1.25
" " "			115	61-68	64.66	±0.30	65	1.64
Montauk Pt. LongIsland, N.Y.	D		19	69-72	70.32	±0.43	71	0.89
" " " " "			45	63-72	64.84	±0.35	65	1.17
Long Island Sound			301	61-69	65.18	±0.19	65	1.69
Island Beach, New Jersey	D		98	65-73	69.48	±0.37	69	1.85
Perlmutter's data:-								
North of Cape Cod			87	63-71	68.32	±0.28	69	1.34
" " " "	D		76	72-78	74.46	±0.28	74	1.21
South of Cape Cod		*	94	60-71	66.50	±0.36	67	1.78
" " " "	D		79	68-75	71.00	±0.25	71	1.13

* Strongly skewed distributions

D These samples were referred by the original authors to A. dubius, the remainder to A. hexapterus (= A. americanus)

2. DISTRIBUTION

2.1 Total area

In the North Atlantic, Ammodytes species have a boreal/boreo-arctic distribution, and are generally common, often abundant, over the shallow sandy areas of the continental shelf within the approximate latitudinal limits of 36°N and 73°N. The total distribution of the genus is shown in Fig.2, and the distribution of individual species in relation to adjacent land areas in Table V. On account of their association with coastlines and shallow water (eg. Henderson 1961) distribution in relation to natural regions of the oceans is probably of less significance; Suffice it is to say that the N.W. Atlantic species, A. americanus and A. dubius, are both to be found in Labrador waters (5.1.3.) Baffin Bay (5.1.4.), Hudson Bay (5.1.5.) and Newfoundland waters (5.2.1.) with the former, in addition, in Gulf Stream waters (5.3.2.); both the N.E. Atlantic species, A. tobianus and A. marinus are present in the Barents Sea (5.1.2.), the Irminger-Gyral (5.2.2.), the Norwegian Sea-Faeroese waters (5.2.3.), the North Sea, Irish Sea and English Channel (5.2.4.) and the Baltic Sea (5.2.5.), with A. tobianus also in Atlantic Drift Current waters (5.3.3.) and A. marinus probably in East Greenland waters (5.1.1.).

The recorded latitudinal range limits of A. tobianus are at 69°N (Murman coast; Andriashev, 1954) and at 36°N (Spain; De Buen, 1935). To the west, the species is present at Iceland, but only along the south and west coasts (Einarsson, 1951); to the east it is present throughout most of the Baltic (Kändler, 1941), but does not appear to extend into either the White Sea or the Mediterranean. Insufficient data is available to determine whether spring- and autumn- spawning groups have different ranges; both are present in the Baltic and North Sea (Kändler, 1941), in the Irish Sea (Cameron, 1958) off the west coast of Ireland (Fives, 1967), and in the English Channel (present author), but Einarsson (1951), recorded only a spring spawning from the species at Ireland and Smitt (1893) referred only to an autumn spawning-season from the Norwegian coast.

With a distribution ranging from 73°N (Novaya Zemblya; Kirillov, 1936) to 49°N (western end of English Channel; Corbin and Vati, 1949), A. marinus is seen to have a similar, but more northerly range compared with A. tobianus. In addition, it is present around all Icelandic coasts (Einarsson, 1951), but is absent from the Gulfs of Bothnia and Finland in the Baltic (Düncker, 1960). Whether the low meristic-count sandeels recorded from West Greenland to 72°N are to be regarded as A. marinus (Jensen, 1941) or as A. americanus will remain unresolved until the taxonomy of these fish is fully reviewed (see Section 1.22).

Jensen (1941) recorded A. dubius from West Greenland between the latitudes of 61°N and 70°N. The most southerly populations are over the Nova Scotia Banks at 43°N (Scott, 1968), although Richards et al. (1963), using a wider concept of the species, indicated a southerly limit of 39°N. Richards et al. gave the latitudinal limits of A. americanus along the mainland coast of North America as 36°N and 60°N. Both A. dubius and A. americanus occur in Hudson Bay (Vladykov, 1933; Richards et al., 1963).

2.2 Differential Distribution

2.21 Spawn, larvae and juveniles

Spawn

Insufficient data is available on the demersal eggs for an assessment of their distribution to be made.

Larvae

On hatching, the larvae become planktonic, resulting in a potentially wider distribution than the adults; even so, Corbin and Vati (1949) failed to find post-larvae of any sandeel species further than 100 km from the coast in the Celtic Sea area, and records from the North Sea and Scottish waters revealed a distribution more conveniently to be described in terms of an association with coastlines and shallow water than with water masses (Henderson, 1961).

Larvae of A. tobianus were not found in the Celtic Sea area by Corbin and Vati (1949) - their 'A. tobianus' larvae were later shown by Einarsson (1951) to be those of Hyperoplus lanceolatus (Le Sauv.) - and Cameron (1958) noted their scarcity around the Isle of Man in spite of the abundance of juveniles inshore in the area. Fives (1967) however located larvae in both spring and autumn off the Galway coast of Ireland, and Einarsson (1951) found then in spring off the west coast of Iceland within the 50 metre depth contour, and mainly at 15-20 metres below the surface. In the North Sea, Macer (1965) distinguished concentration of spring larvae off the Thames, Wash, Humber and Dutch coastal areas, from autumn larvae which were mainly off the Dutch and French coasts; most of these larvae were well offshore, and over areas from which the adults are rare or absent.

It is the larvae of A. marinus which form the abundant concentrations of sandeel larvae in the North Sea area in early spring as recorded by Bowman (1914), Kändler (1941), Henderson (1953), Ryland (1964), and Macer (1965).

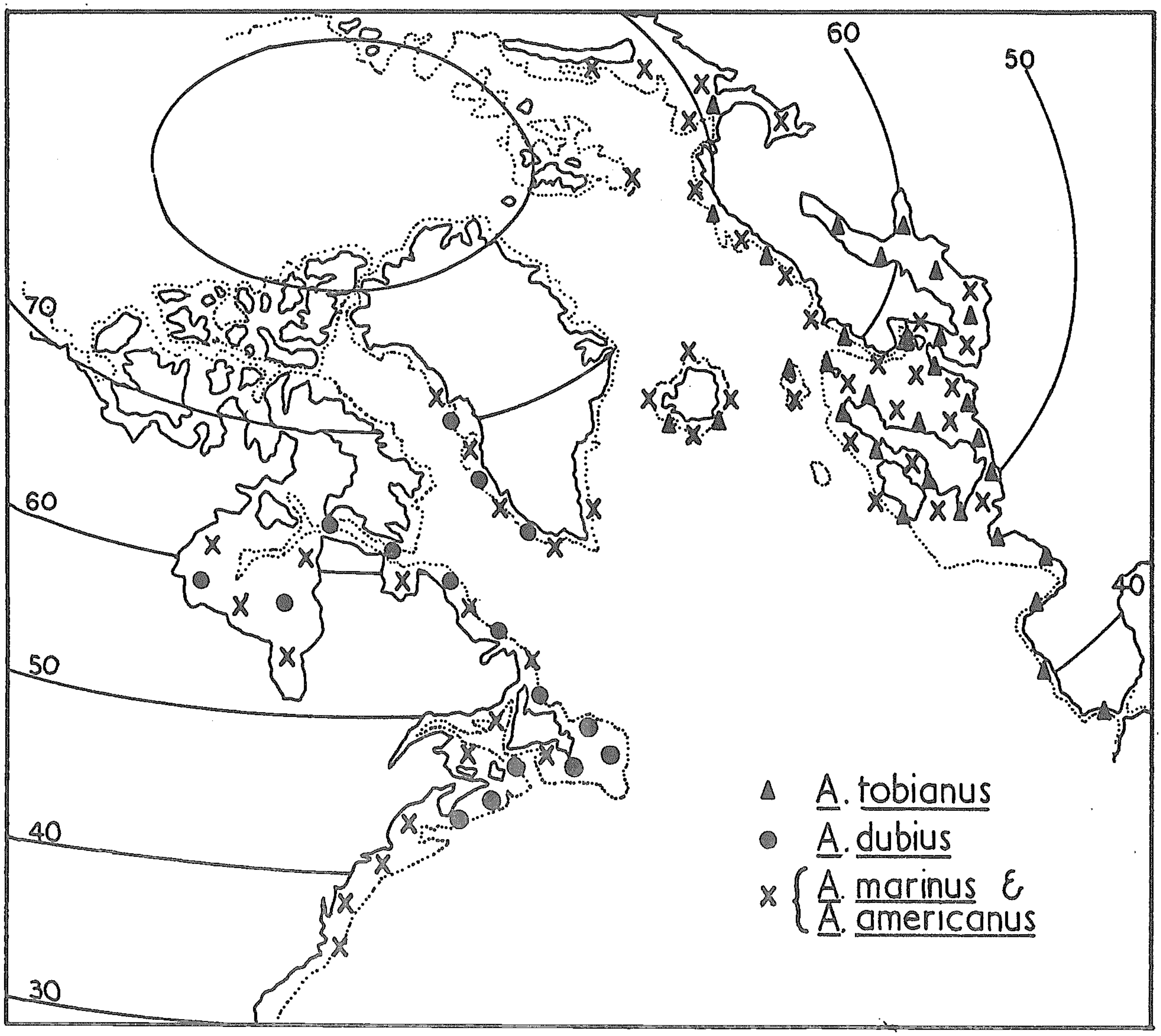

Fig. 2. Probable distribution of Ammodytes species in the North Atlantic, (Boundary between A.marinus and A.americanus is at Greenland; see Section 2.1).

TABLE V

The distribution of Ammodytes species in relation to land areas in the North Atlantic

		A. tobianus	A. marimus	A. dubius	A. americanus	
211,13,14	N.W. Territories, Manitoba and Ontario			+	+	Vladykov (1933) Richards et al. (1963)
215	Quebec			+	+	Leim and Scott (1966)
216	Newfoundland, Labrador			+	+	Leim and Acott (1966)
217	New Brunswick, Nova Scotia			+	+	Scott (1968)
236	New England				+	Richards et al. (1963)
237	Mid-Atlantic States				+	Norcross et al. (1961) Richards et al. (1963)
250	Greenland		+?	+	+?	Jensen (1941)
511	Denmark	+	+			Jensen (1941)
512	Faeroes	+	+			Bruun (1941)
513	Iceland	+	+			Bruun (1941)
514	Norway	+	+			Smitt (1893) Soleim (1945)
515	Spitzbergen, Bear Island, Jan Mayen		+			Andriashev (1954)
516	Sweden	+				Smitt (1893)
517	Finland	+				Düncker (1961), Valtonen (1964)
521	Netherlands	+	+			Roessingh (1957)
522	Belgium	+	+			Poll (1947)
524	France	+	+			Furnestin (1939) Forest (1950)
531	Ireland	+	+			Molloy (1966) Fives (1967
533	England, Wales	+	+			Corbin & Vati (1949) Macer (1965)
534	Scotland	+	+			Raitt (1934)
535	N. Ireland	+	+			
536	Channel Isles	+	+			Present author
537	Isle of Man	+	+			Cameron (1958)
541	Portugal	+				Gonçalves (1942)
542	Spain	+				De Buen (1935)
561	Germany	+	+			Kändler (1941)
572	Poland	+				Kändler (1941)
716	Arctic Soviet Isles		+			Kirillov (1936)
720	Finno-Karelia	+	+			Andriashev (1954)
731-33	Estonian, Latvian, & Lithuanian S.S.R.	+				Kändler (1941)

Macer also found large concentrations of young larvae in the Dowsing area and in the Dover Straits (also recorded by Furnestin, 1939), and there were larger larvae to the south of the Dover Straits which, it was suggested, were from an unlocated spawning ground in the English Channel. Within the southern part of the North Sea, Macer (pers. comm.) recognises three main centres of larval distribution; a) the south-west Dogger b) the eastern North Sea (in both of which, swirls minimise net dispersal) and c) the Southern Bight, where a residual current of up to 4km per day carries the larvae to the north-east.

According to Corbin and Vati (1949), larvae of A. marinus are absent from the Lands End/Ushant area of the English Channel, but are present in the Celtic Sea. Cameron (1958), and Fives (1967) recorded the larvae from the Isle of Man and west coast of Ireland, respectively, and Einarsson (1951) found the largest numbers in Faeroese waters in the fjords and between the islands where the depth ranged from 50-150 metres. In the southern North Sea, Ryland (1964) found the larvae nearer the surface (concentrated at about 10 metre depth) in daytime than at night.

In the N.W. Atlantic, Serebryakov (1965) recorded large concentrations of sandeel larvae (as A. americanus) over the Newfoundland Grand Banks, the Nova Scotia Banks and in the Gulf of Maine; it is likely that the majority of these larvae - the most abundant fish larvae in the I.C.N.A.F. area - belong to A. dubius. Richards (1965) recorded larvae (as A. hexapterus and A. dubius) from Chesapeake Bay to West Greenland, and Wheatland (1958) and Norcross et al. (1961) have provided more detailed accounts of the distribution of larvae in Long Island Sound and Chesapeake Bay respectively; in the latter area the larvae were most abundant further than 45km offshore.

Off West Greenland, Einarsson (1951) found the newly hatched larvae of A. dubius mainly within 20-30 metres of the surface and predominantly well within the 150 metre depth-contour.

Juveniles

Young sandeels assume the demersal habit of the adults at about 30-40 mm; post larvae of this size become rare in the plankton and A. tobianus begins to appear in beach-seine catches at about this length. (Cameron, 1958).

Juveniles appear to be found in the same general areas as the adults, although in A. marinus (Cameron 1958) and in offshore populations of N.W. Atlantic Ammodytes (Richards et al, 1963), they may be present in inshore areas from which the adults are absent. There are, however, no indications of separate nursery areas, and any differences between the distribution of juveniles and adults can probably be accounted for by the greater abundance and initial wide dispersal of the former.

2.22 Adults

A. tobianus is typically found close inshore (i.e. accessible to beach seines) over sandy areas in bays and estuary mouths, although Macer (1966) has recorded occasional individuals 60km offshore in the North Sea. The species also occurs in intertidal sands. Autumn and spring spawning populations show some differences in distribution, but both appear to occupy a wide range of habitats and there is, as yet, no evidence of any differential habitat selection. Along the south coast of England, spring-spawning fish are dominant in the Isle of Wight/ Portsmouth area, whereas only autumn-spawning fish are present along the Devon and Cornwall coasts (present author), and Kändler (1941) located the spawning grounds of spring-spawners in the mouth of the Elbe estuary, whilst those of autumn-spawners were on the lorely Bank (Heligoland).

A. marinus is a widely distributed and common species usually associated with offshore banks. It is abundant in areas of the southern North Sea, and Macer (1966; and pers. comm.) distinguishes three main stocks: a) eastern (15-37 metre depth), b) western (27-37 metre depth over the S.W. Dogger, 12-22 metre depth over the Norfolk Banks) and c) southern Bight. Molloy (1967) found large concentrations on the Kish and Bennet Banks in the Irish Sea, and off Scotland, stocks are present off the west coast, around the Shetland Islands and in the Moray Firth and Aberdeen Bay areas (Raitt, 1934; N.P. Langham, pers. comm.).

Scott (1968) has located considerable quantities of A. dubius over the Nova Scotia Banks, although they were less common on the more north-easterly banks. It is likely that the abundant stocks of sandeels on the Newfoundland Grand Banks (Templeman, 1966) also belong to this species. A. dubius is exclusively an offshore species (Backus, 1957; Richards et al., 1963; Leim and Scott, 1966).

A. americanus is found close inshore, but there are also offshore components. It would appear to be particularly abundant along the New England coast and is present in estuaries, bays, and along exposed coasts (Richards et al., 1963, Leim and Scott, 1966).

2.3 Determinants of Distribution

Ecological

Sandeels are mainly to be found in

association with the sandy substrates into which they burrow (Masterman, 1895; Popp Madsen, 1963; and many others), and although Kirillov (1936) encountered A. marinus over weed and gravel areas, it appears in general, that rocky, muddy and coarse gravel areas are usually avoided. Several authors (such as Macer 1966) have described the most favourable substrates as clean, coarse sands or fine gravel, but no attempt has been made to determine quantitatively the role of different types of sandy substrate on distribution. Populations of sandeels along the south coast of England have been found by the present author, to be associated with substrates ranging from mean particle size 0.35 mm (Ø quartile deviation 0.55) to 1.30 mm (Ø quartile deviation 1.0). It is possible that the total particle composition and the way in which it affects water circulation and thus oxygenation within the substrate, is a more important parameter than mean particle size, per se.

The main concentrations of sandeels appear to be in shallow water; in the southern North Sea A. marinus is most abundant in depths of 20-40 metres (Macer, 1966), and A. tobianus and A. americanus are usually in much shallower water than this. The greatest depth recorded is the isolated occurrence of A. dubius over the Nova Scotia Banks at 400 metres (Scott, 1968) although most were taken between 40 and 100 metres.

Popp Madsen (1963) has suggested that in the southern North Sea, whilst sandeels are present in most places where the bottom is suitable, the largest concentrations are restricted to the edges of the larger banks and to the tops of the smaller ones - particularly where the current speed exceeds 0.5 knots; Macer (pers. comm.) has however been unable to confirm such a relationship between distribution and tidal strengths.

Scott (1968) concluded that A. dubius over the Nova Scotia Banks was eurythermal; fish could be taken from water ranging from -2°C to 11°C although the largest quantities were taken from waters with a temperature between 3°C and 6°C. Similarly, the present author has found A. tobianus active between 6°C and 18°C along the south coast of England, but inactive below 6°C in December, January and February; around the Isle of Man where the winter temperature does not fall below 6°C, Cameron (1958) apparently found this species active throughout the year. Holmquist (1958) recorded A. dubius larvae from pools in floating ice-blocks off West Greenland.

No information exists on the relationship between distribution and salinity, but a wide tolerance in A. tobianus is inferred from its present in the Gulf of Bothnia, and in estuarine situations elsewhere (eg. a spawning population exists in the River Fowey, S. England at a point where salinity ranges from 15% to 32%). Norcross et al. (1961) referred to records of larvae of A. americanus in salinities from <1.8% and to suggestions that as the sandeel grows it becomes less tolerant of low salinity. For A. americanus and A. dubius (see Section 1.21) Richards et al. (1963) gave environmental salinities of 26-32% and 30-36% respectively.

Behavioural

Sandeels have neither swim-bladder, nor fins capable of compensatory movements, and in order to remain clear of the bottom the normal myotomic swimming movements must be maintained. Effective energy conservation and some degree of escape from predation is accomplished by burrowing into and resting within, the substrate. Since considerable periods of time may be spent within sand and since no inhalent opening is maintained between the buried fish and the surface of the sand, it is essential that the substrate be well supplied with O_2, and strong currents flowing over a substrate with large interstitial spaces would enable such aeration to take place. Sandeels are thus able to alternate between periods of inactivity within the substrate and periods of activity (feeding) in the overhead water masses.

3. BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

All species are bisexual and there are no published records of hermaphroditism. The sexes cannot be distinguished by any obvious external characteristics.

3.12 Maturity

Sexual maturity is attained as follows:-

A. tobianus; at two years according to Cameron (1958) but the present author has found maturity at one year to be common in both spring- and autumn- spawning fish in the English Channel. This involves fish as small as 83 mm, and 60-70% of those reaching early maturity are males.

A. marinus; according to Cameron (1958) and Macer (1966) mainly at two years, but the largest individuals in a year class may mature at one year. Macer gave 5%, 80% and 98% as the proportions spawning at one, two and three years respectively, in the North Sea. Kirillov (1936) considered that A. marinus from Novaya Zemblya first matured at three years.

A. dubius; one to two years (Scott, 1968).

3.15 Gonads

Macer (1966) has provided the following regression equation based on 35 A. marinus from the North Sea and the Faeroes:

Fecundity = 2.046 x (Length 3.055)

Other fecundity data are shown in Table VI together with the equivalent fecundities calculated from the above equation. All are a measure of annual egg production.

The intraseasonal pattern of gonad maturation and the duration of the different stages is to some extent dependent upon the time of year at which spawning takes place; according to Kändler (1941) the ova of spring-spawning A. tobianus take seven months to mature, those of A. marinus (winter spawning) takes five months; and those of autumn spawning A. tobianus take only three months. In A. tobianus (Kändler, 1941), A. marinus (Macer, 1966) and A. dubius (Scott, 1968) the testes have been found to reach a state of maturity (in terms of size in relation to the body cavity) before the ovaries.

TABLE VI
Fecundity data; A. tobianus, A. marinus

	Length (cm)	N	FECUNDITY x 10^2 Mean	Range	Equivalent fecundity calculated from Macer's (1966) equation (see Section 3.15)
a)	A. tobianus, southern North Sea (Kühl and Lumann, 1965)				
	10.5	1	3.2	-	2.5
	11.6	2	4.1	3.7- 4.5	3.4
	13.6	6	6.5	4.3-10.0	5.8
	14.5	10	7.2	4.0-13.3	7.4
	15.6	14	6.0	2.5- 9.6	9.1
	16.6	10	8.1	4.1-16.3	10.9
	17.3	3	8.1	6.4- 9.5	12.4
	18.1	1	8.3	-	14.3
b)	A. marinus, Novaya Zemblya (Kirillov, 1936)				
	12.0	6	4.4	-	3.9
c)	A. marinus, Murman coast (Kirillov, 1936)				
	12.0	6	2.6	-	3.9

3.16 Spawning

The unimodal distribution of ovarian eggs and the absence of redeveloping gonads in A. marinus (Macer 1966) suggests that individuals spawn only once during each spawning season; this is probably also true for the other species.

A. tobianus (Thomopoulos, 1954). Thomopoulos also suggested a lunar/tidal determination of spawning, for he found that peaks were reached 3-4 days before full moon - mainly in October, but also in September and November.

TABLE VII

The occurrence of larvae and condition of the gonads as an indication of spawning season in Ammodytes species

\+ occurrence of larvae less than 10 mm in length
R " " ripe/running adults

Months	J	F	M	A	M	J	J	A	S	O	N	D
A. tobianus												
Baltic Sea (Kändler, 1941)			R	R	R			R	R	R		
North Sea (Kühl and Lühmann, 1965)			R	R							R	R
North Sea (Macer, 1965)	+	+		+	+	+			+		+	+
Irish Sea (Cameron, 1958)				+	+				+			
Ireland, west coast (Fives, 1967)		+	+	+					+	+	+	
English Channel (Thomopoulos, 1954)									R	R	R	
" " (present author)		R	R						R	R	R	R
A. marinus												
Faeroes (Einarsson, 1951)			+	+	+							
North and Baltic Seas (Kändler, 1941)		+	+	+							R	R
North Sea (Macer, 1965,66)	R	+	+	+							R	R
Irish Sea (Cameron, 1958)	R	R	+	+								
Ireland, west coast (Fives, 1967)		+	+	+								
Celtic Sea (Corbin and Vati, 1949)	+	+	+									
English Channel (Furnestin, 1939)	+	+	+									
A. americanus/A. dubius												
West Greenland (Einarsson, 1951)						+	+					
Nova Scotia Banks (Scott, 1968)	R	R									R	R
Long Island Sound, N.Y. (Wheatland, 1956)	+	+	+	+								+
Chesapeake Bay (Norcross et al. 1961)	+	+	+									

The occurrence of ripe and running gonads and the occurrence of small larvae in the plankton are summarised in Table VII, to indicate the spawning seasons. Although both methods have obvious limitations, which preclude more detailed analysis, it is clear that A. marinus, A. americanus, and A. dubius spawn in the winter months, and that there are two spawning seasons in A. tobianus, in spring and autumn. It can be shown from otolith studies in the latter species (Cameron 1958; present author) that fish spawn at the same time of year as they were initially spawned, thus indicating separate spawning populations. (see Section 1.22)

What effect any sequence of spawning of individuals has on the length of the spawning season is unknown, but in any one area spawning takes place over a period of about three months in

Spawning in A. tobianus has been recorded close inshore (Fullarton 1894; Thomopoulos, 1954; Kändler 1941), and Kändler found that spawning occurred in spring in the mouth of the Elbe estuary (5 metres depth), and in autumn off Heligoland (10 metres depth). Cameron, however, (1958) was unable to locate spawning grounds of this species around the Isle of Man, in spite of the abundance of young fish. According to Furnestin (1939), the spawning of A. marinus takes place in depth of 20-40 metres, but Andriashev (1954) has referred to depths of 25-100 metres. In general it appears that spawning takes place within and not outside, the general area inhabited by a population; that is there are no indications of migration to specific spawning grounds. It is not known to what extent spawning takes place within the sand substrate.

The sex-ratio of A. marinus at the time of spawning is for A. marinus over the Dogger area of the North Sea and has been recorded by Macer, (1966); it was found that males comprised 67% of a sample of 120 fish, and this ratio applied to both mature and immature fish; this was in contrast to the combined sex-ratio for all cruises between March and August in which males comprised 45% of 2252 fish (x^2test, p<0.0001; significantly different from a 1:1 ratio.

3.17 Spawn

The eggs are demersal and normally deposited within or on the surface of the substrate where they attach to sand-grains (Ehrenbaum 1904; Williams et al. 1964). In addition, Soleim (1945) has recorded an instance of attachment to algae.

Thomopoulos (1954) has given the density, of the eggs as 2-3 times that of seawater, and has described the egg of A. tobianus as being slightly sub-spherical and adhesive, with a conspicuous micropyle, a dull, pale yellow yolk, and a large yellow oil globule (170-330μ) sometimes accompanied by smaller ones. Similar descriptions of the eggs of A. marinus and A. americanus have been given by Furnestin (1939) and Williams et al. (1964) respectively. According to Williams et al., the mean diameter of A. americanus eggs was 825μ(670μ- 910μrange) and according to Thomopoulos, that of A. tobianus was 750μ.

3.2 Pre-Adult Phase

3.21 Embryonic phase

In A. americanus, the embryo remains colourless until its body extends nearly twice around the yolk. Following myomere formation, the eye turns brown, its pigment darkening simultaneously with the appearance of body pigment, (Williams et al., 1964).

3.22 Larval phase

According to Masterman (1895), larvae of A. marinus, after hatching, undergo a period of quiescence within the sand until the yolk is exhausted and they have reached a length of 4-5 mm; at this stage they appear at the surface of the sand but remain near the bottom until a length of 10 mm is reached and only then do they move towards the surface. However, larvae smaller than 10 mm and even smaller than 5 mm are commonly taken in plankton samples (Kändler, 1941; Einarsson, 1951; Norcross et al., 1961; Macer, 1965), indicating that, in contrast to the eggs, the newly hatched larvae move or are moved away from the bottom. Diurnal differences in depth distribution suggest that the larger larvae are capable of a vertical migration (Norcross et al., 1961) and this may reduce the importance of a particular system (eg. surface currents) in determining the distribution of the larvae. In the southern North Sea, Ryland (1964) found that during the day, larvae of A. marinus were concentrated at 8 metres depth, but at night were more generally distributed between 0 and 40 metres. On the other hand, Norcross et al. (1961) found daytime concentrations of A. americanus in deeper water than they were at night, although a clear pattern was obscured by seasonal variation.

Metamorphosis is usually complete at 30-40 mm (Cameron 1958; Macer 1965) and Norcross et al., (1961) have suggested that the "average growth rate" for A. americanus larvae in Chesapeake Bay is 11.7 mm per month. It is, however, very difficult to know how long it takes individual larvae to proceed from hatching to metamorphosis - that is the duration of the larval phase. On theoretical grounds, Macer, pers. comm.), has calculated a period of 24-28 days for A. marinus in the southern North Sea, but for autumn-spawning A. tobianus where at least some populations appear to overwinter as larvae (Kändler, 1941) the duration of the larval phase must be of the order of 3-5 months.

The development of A. americanus/dubius larvae has been described by Richards (1965); oil-globule absorption occurred at a length of 5-7 mm, median fin rays first became visible at 9-16 mm, with dorsal fin rays anterior to the vent visible at 15-25 mm. Development in general was slower in offshore regions and in northern latitudes. The development and features of larvae are shown in Fig. 3.

The importance of the larvae of A. marinus (up to 5 cm long) as a spring food for herring (Clupea harengus L.)in the North Sea, was emphasised, by Hardy (1924); he found that the larvae formed 41.72% (adjusted weight index) of the adult herrings annual diet, and were eaten between March and June.

Both Covill (1959) and Ryland (1964) noted the importance of diatoms and dinoflagellates in the diet of the smallest larvae of A. americanus and A. marinus, and the change to a diet consisting mainly of copepods and their nauplii from a length of about 10 mm. Ryland also noted that appendicularians were an important food for A. marinus larvae in the North Sea as indeed they were for the less abundant plaice (Pleuronectes platessa L.) larvae in the same area; he suggested that whilst the available prey was sufficient to meet the needs of these larval predators, the standing crop only represented three days

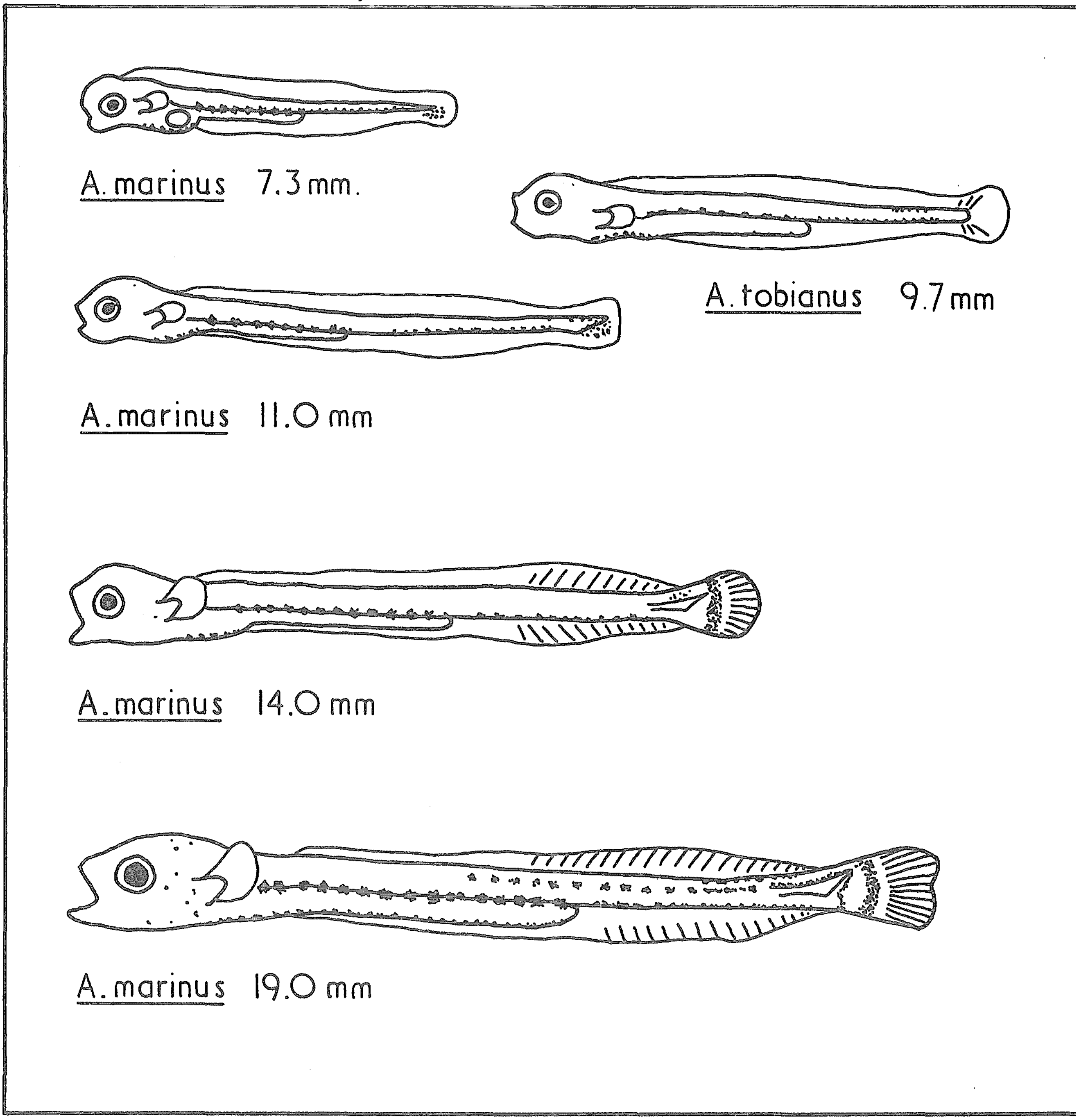

Fig. 3. Pre-metamorphic stages of A. marinus and A. tobianus (adapted from Macer 1967).

ration, and thus, in this instance, the rate of appendicularian recruitment would have determined the reality of a state of interspecific competition between plaice and sandeels. Covill calculated that 10-16 times the weight of food actually found in the average stomach (0.3% of body weight) of A. americanus would be necessary to supply the energy needed for growth and maintenance, and that there would be no difficulty in fulfilling these requirements even at the low copepod densities prevalent in Long Island Sound between January and March.

The larvae do not appear to feed at night. Covill (1959) found that in A. americanus, stomach contents were minimal in early morning, and after an increase towards mid-day, diminished slowly into late afternoon. Ryland (1964) concluded that for A. marinus larvae in the North Sea, there was an intensive 2-3 hour feeding period beginning at first light followed by a diminished intensity throughout the day and cessation at the onset of darkness.

3.23 Adolescent phase

After metamorphosis at about 40 mm, the demersal habit is assumed and the fish become adoloscent. This period may be of short duration in for example those spring-spawning A. tobianus which metamorphose in July and whose gonads begin to ripen in November (present author) but it is probably normally of about 1½ years. Adolscent fish occur in the same areas as adults, and although those of A. marinus (Kändler, 1941; Cameron, 1958) may, unlike the adults, be present inshore, there is no evidence to suggest the existence of specific nursery areas.

Adolescents have a more rapid growth-rate (Section 3.43) and eat smaller food items (Section 3.42) compared with adults.

Adolescence in A. marinus begins in May in both the North Sea (Macer, 1966) and the Irish Sea (Cameron, 1958). Cameron recorded influxes of newly-metamorphosed A. tobianus in May-July and November at the Isle of Man, corresponding to the spring and autumn broods respectively; from localities along the south coast of England, the equivalent influxes have been recorded in July and April by the present author.

3.3 Adult Phase

3.31 Longevity

Assuming an annual mortality rate of 70% (see Section 4.41), the average expectation of further life is about 0.9 years.

The maximum age groups (T max) encountered as a result of otolith reading are as follows:-

A. tobianus	VII	Original data; English Channel
A. marinus	IX	Macer, 1966; North Sea
A. dubius	IX	Scott, pers. comm.; Nova Scotia

Insufficient data is available to determine whether there is any intraspecific variation in T max (see also Section 4.12)

3.32 Hardiness

A. tobianus and A. marinus can easily be kept alive in aquaria for periods of several months, and P. Winslade (pers. comm.) has reported the spawning of A. marinus under these conditions at Lowestoft. A. tobianus can be kept alive in wet sand for at least six hours (Cameron, 1958). Thomopoulos (1954) considered that male A. tobianus were hardier than females, judging by their survival in captivity. Ammodytes species are much less susceptible to injury from handling than are for instance clupeoids, and are usually alive on capture from trawl and seine. When used as live bait, they can remain alive in floating keeps ('courges') for periods of over a week. Sandeels may survive ingestion to the extent of being able to penetrate the gut, enter the body cavity and become encysted in the liver of their predators (Breder, 1956).

No critical work has been carried on the limits of tolerance to environmental factors, but the way in which these may influence distribution is discussed in Section 2.3. Observations on captive sandeels and inference from field results suggests that these fish may respond to periods of food scarcity by remaining within the sand for longer periods than when food is abundant, and conditions more favourable.

3.33 Competitors

Other plankton feeding fish, such as clupeoids are frequently caught with Ammodytes species (for example with A. marinus in the North Sea; Macer, 1966) but there is no evidence for food competition in such instances. The four species of Ammodytes in the North Atlantic are separated either geographically or by virtue of inshore/offshore habitat selection, thus precluding the possibility of competition. In the N.E. Atlantic, another plankton feeding sandeel, Gymnammodytes semisquamatus may occur with A. marinus as in the North Sea: Macer (1966) has suggested that potential competition for food between these two species may be minimised by the fact that the latter are concentrated on the tops of banks, whereas the former are mainly found between the banks.

3.34 Predators

From a review of the literature it is apparent that, throughout their range, sandeels are heavily exploited by a wide variety of vertebrate predators. Because however, such information results almost entirely from trophic studies of the predators themselves, it is impossible to draw any quantitative conclusions on the influence of predation in controlling the size, density, and size composition of the sandeel populations. Sandeels have been occasionally recorded in the diet of pinnipedes and small cetaceans (Bigelow and Schroeder, 1953), and such predation may be heavy locally, for example in grey seals (Halichoerus grypus (Fab.)) off S.W. Shetland Isles (Rae 1968). Particularly heavy predation by breeding seabirds in the summer months will be significant for sandeel populations within the feeding range of colonies; Pearson (1968) has reviewed the literature on seabird feeding and described the trophic ecology of the Farne Island seabird colonies off the east coast of England; Ammodytes species were the dominant food and it was estimated that 943 metric tons were consumed within the colony in a single season. The size of sandeels taken ranged from 25–175 mm and thus included larvae, adolescents and adults, but most were adolescents of 50–75 mm; the major predators were the surface feeding terns (Sterna species), and kittiwake (Rissa tridactyla (L)), and the diving auks (Alcidae) and shag (Phalacrocorax aristotelis (L)). Predation by other fish has led to concern over potential competition for sandeel resources between the industrial fisheries and stocks of food-fish species (for example Roessingh, 1957). There is no evidence to suggest that this is happening, however, and both Macer (1966) and Rae (1967) have noted the relative unimportance of sandeels as a food resource in the southern North Sea - the major area where industrial fishing for sandeels has taken place. In other areas, such as the Nova Scotia Banks,(Scott, 1968) Faxe Bay, Iceland (Brown and Cheng, 1946; McIntyre, 1952) and off the north coast of Scotland (Holden 1966; Rae, 1967) predation on sandeels is undoubtedly heavy, particularly in the summer months. Cod (Gadus callarias L.) eat sandeels over a wide area (Scott, 1968; Rae, 1967; Brown and Cheng, 1946) and often intensively - as off the north coast of Scotland where, according to Rae, 70 - 85% of cod of all sizes eat sandeels throughout the year. Whiting (Odontogadus merlangus (L), (Jones, 1954), is also a major predator, but haddock (Melanogrammus aegefinus (L)) predation is more local (Ritchie, 1932; Brown and Cheng, 1946; Jones, 1954). The heaviest inshore predation by gadoids off the Isle of Man was by whiting, pollack (Pollachius pollachius (L)), coalfish (P. virens (L)) and poor-cod (Trisopterus minutes (L) in April-June and by cod in October-December (Nagabhushanam, 1965). Predation by plaice (Pleuronectes platessa (L)) may be important locally (Todd, 1914) and for small halibut (Hippoglossus hippoglossus (L)) sandeels are a major food both off Iceland and the Faeroes (McIntyre, 1952). Roessingh (1957) has recorded them in the diet of soles (Solea vulgaris) in the North Sea, and B.B. Rae (pers. comm.) has noted their importance to turbot (Scophthalmus maximus (L)). Spurdogs (Squalus acanthias (L)) feed heavily on sandeels in certain areas (Holden, 1966), and those species of ray (Raia species) inhabiting sandy areas in relatively shallow water also eat sandeels. A. tobianus is a favourite bait for bass (Dicentrarchus labrax (L)) in inshore waters, and sandeels are often present in their stomachs.

The above records, additional observations and also more general works on a wide variety of species (eg. Sim, 1884) suggest that most piscivorous marine vertebrate readily eat sandeels, - often in considerable quantity. Individual sandeels have no physical means of defence and in fact, their size and shape (an adaptation to burrowing) render them ideal food items for most predators. It is maintained that sandeels burrow into the sand to escape predators, but this is certainly not an inevitable reaction to the presence of prescence of predators, and there is no information to suggest how often it happens and how effective the behaviour is: certainly, even when in the sand they are probably still susceptible to predation by such fish as Raia species.

3.35 Parasites, diseases, injuries and abnormalities

Polyanski (1955) reported seven species of parasite from A. marinus in the Barents Sea;

Sinuolinea murmanika Basikalova. (Protozoa)
Brachyphallus crenatus (Rudolphi). (Digenea)
Derogenes varicus (Müller). (Digenea)
Scolex polymorphus Rudolphi. (Cestoda)
Contracaecum aduncum (Rudolphi). (Nematoda)
C. aduncum larvae
Anisakis sp. larvae. (Nematoda)
Echinorhynchus gadi Zöega. (Acanthocephala)

The highest incidence of infection (7 out of 21 fish) involved C. aduncum larvae, although no more than three individuals were present in any one fish; only the presence of S. murmanika resulted in a high intensity of infection.

There are no records of effects of infestation upon mortality.

3.4 Nutrition and Growth

3.41 Feeding

Roessingh (1957) found that most of the stomachs of A. marinus in the North Sea that were examined in the early morning were empty, whereas they were well-filled in the afternoon and evening; Richards (1963) inferred that A. americanus in Long Island Sound began to feed soon after dawn. Underwater observations on A. tobianus in the Baltic Sea (Kühlmann and Karst, 1967) showed that the main feeding period was in the morning, with a secondary peak towards evening. Popp Madsen (1963) related the feeding activity of A. marinus in the North Sea to current strength and has suggested that the fish are most active when a strong tidal current replenishes food supplies over the banks. Macer (1966) considered that A. marinus in the North Sea feed near the bottom because they are commonly caught with their stomachs full in bottom trawls; diet composition, however, indicates that feeding takes place in the water mass and not in the substrate. Richards (1963) inferred from the presence of sand in the stomachs of A. americanus, that at least some feeding takes place close to the bottom. Kühlmann and Karst (1967), from underwater observations in the western Baltic, have described the feeding behaviour of A. tobianus. The normal swimming schools become more or less stationary as feeding begins, and spread out both vertically and radially - thus often reaching from the sand to the water surface; each individual, with the body at an angle of 15^{o} to the horizontal, searches for food independently of the others, seldom snapping for longer than 20 - 30 seconds in one place.

There is little information on seasonal variation in feeding. Richards (1963) recorded intensive feeding by A. americanus in winter in Long Island sand, followed by a decrease in early spring. Along the Murman Coast, Bogarov et al. (1939) found that the intensity of feeding in Ammodytes sp. increased from the beginning of June to August and decreased towards October. In the North Sea, Kühl and Lühmann (1965) recorded feeding in April, May and June. At Portsmouth, South England, the present author has encountered full stomachs in A. tobianus from late March to early November; in the winter months, however, fish dug from the intertidal sand usually have empty stomachs. The capacity of sandeels to ensure starvation has been indicated by Inoue et al. (1967) who observed that A. personatus was able to survive 24 weeks in aquaria without food.

3.42 Food

In a study of the diet of 290 individuals of A. americanus (74 - 132 mm in length) from Long Island Sound, Richards (1963) noted that the food was similar to that described by Covill (1959) for the post-larvae in the same area. Ten species of pelagic crustaceans comprised most of the diet and it was found that 80% of the fish were feeding on Centropages species, 55% on Arcartia species, 42% on Temora longicornis, 79% on Balanus balanoides cyprid larvae and 60% on the nauplii. Fifty per cent had fish eggs in their stomachs, and algae (dinoflagellates and diatoms), the mysid Neomysis americana, and Ammodytes americanus larvae, each occurred in at least 10% of the stomachs.

In the N.E. Atlantic, Bogarov et al. (1939) recorded a wide variety of food species from Ammodytes sp. along the Murman coast, including such fresh-water organisms as insect larvae from Sedlovatyj Island; copepods were however the most important food group. Roessingh (1957) found mainly copepods and cladocerans in the stomachs of A. marinus from the North Sea, and in addition identified the eggs of anchovy. Copepods also dominated the diet of A. marinus in mid-summer in the eastern North Sea, according to Kühl and Luhmann (1965), but in contrast they found that the stomachs of 17 out of 22 fish caught in the Elbe estuary in April, were full of the diatom Coscinodiscus; Popp Madsen (1963) has recorded a similar phenomenon. Macer (1966) found copepods in all individuals of A. marinus (North Sea) that were feeding, the most important genera being, in order, Temora, Calanus and Pseudocalanus: in addition, invertebrate and fish eggs, crustacean larvae, newly metamorphosed polychaetes and amphipods were important food items. Macer found that the diet of A. tobianus was broadly similar to that of A. marinus although the absence of crustacean larvae and the greater frequency of amphipods, mysids and cladocera in the former species, were attributed to its more inshore habitat (Table VIII).

Roessingh (1957) found food items up to 1.5 mm long in A. marinus; Richards (1963) recorded copepods 1.0 - 1.8 mm long in A. americanus but mysids also occurred in the diet and these were from 4.4 - 13.7 mm long. Insufficient data is available for the assessment of geographical variation in diet within a species, but Richards (1963) has drawn attention to the seasonal variation in the copepod composition of the diet of A. americanus between January and April, and Macer's (1966) data has shown how diet varies with the size of the fish. (Table VIII).

TABLE VIII

The occurrence of food items in the diet of A. marinus and A. tobianus from the Southern North Sea, as weighted mean %. (from Macer, 1966)

Species	A. marinus			A. tobianus	
Length (cm)	< 10	10-20	> 20	< 10	10-15
No. of stomachs	59	207	30	20	21
Number empty	7	40	17	0	3
Mean fullness	69	50	17	91	49
Sand grains	15.3	9.6	8.0	30.0	27.5
Fish scales	0	0	0	0	50.0
Fish larvae	1.9	3.1	8.0	0	0
Fish ova	9.6	14.8	15.0	0	0
Invertebrate ova	36.3	30.2	8.0	35.0	0
Copepods	96.6	84.7	54.0	100.0	50.0
Calanus	30.9	22.8	30.0	5.0	0
Temora	69.4	64.1	23.0	60.0	33.0
Centropages	5.9	5.6	0	15.0	0
Pseudocalanus	17.5	27.4	15.0	15.0	5.8
Acartia	0	0.5	0	50.0	0
Caligus	0	0	0	15.0	0
Crustacean larvae	23.2	43.9	15.0	0	0
Cyprid	23.2	30.8	0	0	0
Zoea and Megalopa	2.0	23.8	15.0	0	0
Amphipods	11.6	2.3	23.0	35.0	5.8
Mysids	1.9	0	0	15.0	5.8
Euphausids	1.9	3.0	0	0	0
Isopods	2.0	0	0	0	0
Cumacea	1.9	0	8.0	0	0
Cladocera	0	2.6	0	10.0	0
Chaetognatha	9.7	5.5	15.0	0	0
Larvacea	3.9	11.8	15.0	0	0
Molluscs	3.8	0.5	0	0	0
Annelids	27.1	45.7	70.0	30.0	44.2
Echinoderms	0	0.6	0	0	0
Coscinodiscus	11.8	4.7	0	0	0
Miscellaneous	0	1.1	8.0	15.0	5.8

3.43 Growth rate

Published growth studies on sandeels have mainly involved the presentation of mean lengths of successive age-groups, and very little attention has been paid to growth in weight, intra-seasonal growth, and the analysis of growth parameters. Age has been determined by otolith reading, as initiated by Bahr (1935) and Kändler (1941). Data on mean length of successive age groups is summarised in Table IX; it is apparent that most growth takes place in the first two growth periods and that there is considerable intraspecific variation. Differences in length between populations of the same year-class on different banks in the southern North Sea are given in Table XVI; in addition, the growth of the 1959 year-class on the Haddock and Indefatigable Banks was so slight compared with the two subsequent year-classes and with that of the same year-class on the Southernmost Rough, that in 1961 and 1962, the 1959 and 1960 year-classes were of a similar length, (Macer, 1966). Macer has attributed such intraspecific differences in growth rate to the presence of different current regimes supplying variable densities of food to the different populations.

TABLE IX

Mean lengths (mm.) of age-groups; A. tobianus, A. marinus, A. dubius

AGE-GROUPS	0	I	II	III	IV	V	VI	Locality	Month of samples	Author
A. tobianus (Spring-spawning)	82 (355)	121 (82)	170 (17)					W. Baltic	Sept.Jul-Aug. (respectively)	Kändler (1941)
	49 (90)	130 (30)	170 (4)	195 (1)				Isle of Man (Irish Sea)	Jul.Jul.Jun.Jun. (respectively)	Cameron (1958)
	87 1.93 (225)	129 7.75 (89)	144 10.84 (31)	153 12.32 (11)	157 13.27 (3)	mean weight in grams		Portsmouth (S.England)	Oct. (all samples)	Original data
		112 4.91 (97)	136 8.88 (36)	149 11.76 (9)		mean weight in grams		Portsmouth (S.England)	Jun. (all samples)	Original data
A. tobianus (autumn-spawning)		89 (579	136 (144)	166 (30)				W.Baltic	Jul-Aug. (all samples)	Kändler (1941)
	44 (248)	102 (238)	157 (52)	177 (3)	200 (1)			Isle of Man (Irish Sea)	Nov.Jul.Jun. Jun.Jun. (respectively)	Cameron (1958)
		121 (49)	137 (58)	145 (69)	160 (13)	173 (2)		W.Irish Sea	May-Jul. (all samples)	Molloy (1967)
		106 (63)	152 (155)	173 (20)	188 (5)	192 (4)		Fowey (S.W. England)	Jul-Aug. (all samples)	Original data
A. marinus	70	123 (372)	168 (131)					W.Baltic	Jun-Jul. (all samples)	Kändler (1941)
	58 (202)	98 (81)	113 (117)					Isle of Man (Irish Sea)	Jul.Apr.May (respectively)	Cameron (1958)
		79 (57)	96 (344)	111 (376)	126 (119)	133 (34)	136 (4)	W.Irish Sea	May-Jul (all samples)	Molloy (1967)
	89 (72)	166 (31)	195 (176)	213 (19)	218 (173)			Dogger Bank (S.North Sea)	May-Jun. (all samples)	Macer (1966)
		141 (109)	146 (237)	173 (6)	169 (5)			Haddock Bank (S. North Sea)	Jul-Aug. (all samples)	Macer (1966)
		90 (12)	142 (30)	156 (37)	156 (9)	172 (16)	185 (4)	N.E. Scotland	-	N.P. Langham (pers.comm.)
	95	116	135	159	166			Murman coast	-	Kirillov (1936)
	64	75	81	94	104			Novaya Zemblya	-	Kirillov (1936)
A. dubius		140	205	240	275	310		Nova Scotia Banks	Aug. (all samples) mean lengths read from growth curve	Scott (1968)

* Boundary between age-groups
Dec. 31st/Jan. 1st

Macer (pers. comm.) has calculated Von Bertalanffy growth parameters for A. marinus in the North Sea as L_∞ (max. length) = 21.8 cm, K (rate at which L_∞ is approached) = 0.89. The small number of age-groups which are usually present however, render the calculation of such parameters difficult in most sandeel.

In the Irish Sea (Isle of Man), Cameron (1958) recorded little or no growth in A. tobianus and A. marinus between October and March, and rapid growth between March and July; this pattern of growth also applies to A. tobianus from English Channel localities (Fig. 4) and to A. marinus in the southern North Sea, (Macer, 1966). In Ammodytes species the spawning periods generally fall outside the growth period.

Condition (ponderal index) has been calculated for A. tobianus by the present author, and the seasonal changes in condition are indicated in Table X. The fish are generally unavailable when condition is likely to be lowest, but the total individual range found, (where condition = $W/L^{3.2} \times 10^5$) varied from 86 to 169. In A. marinus, seasonal changes in fat content are apparent from the work of Lühmann (1957) (Table XI).

TABLE X

CONDITION INDEX ($W/(L^{3.2} \times 10^5)$) in Spring-spawning A. tobianus; Portsmouth, England (original data)

AGE-GROUP	JAN.	FEB.	MAR.	APR.	MAY.	JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.
O-group 1969	-	-	-	-	-	-	151.6 (37)	147.9 (53)	127.1 (127)	119.9 (107)	129.3 (128)	123.0 (5)
I-group 1970	-	97.3 (3)	108.8 (60)	122.4 (278)	134.4 (279)	139.2 (206)	-	-	-	-	-	-
I-group 1969	101.7 (29)	-	118.3 (24)	127.1 (48)	143.0 (47)	132.3 (50)	145.8 (16)	153.7 (9)	130.0 (15)	136.6 (56)	-	138.7 (3)
II-group 1970	-	-	-	118.3 (4)	-	135.7 (21)	-	-	-	-	-	-

Sample numbers in brackets

TABLE XI

Percentage fat content in A. marinus (from Luhmann, 1957)

	Range of sample means	No. of samples
March	1.1 - 1.2	2
April	3.3 - 5.6	4
May	2.6 -12.4	9
June	6.0 -12.3	12
July	6.0 - 7.5	10
August	-	-
September	7.0	1
October	-	-
November	5.0	1
December	3.7	1

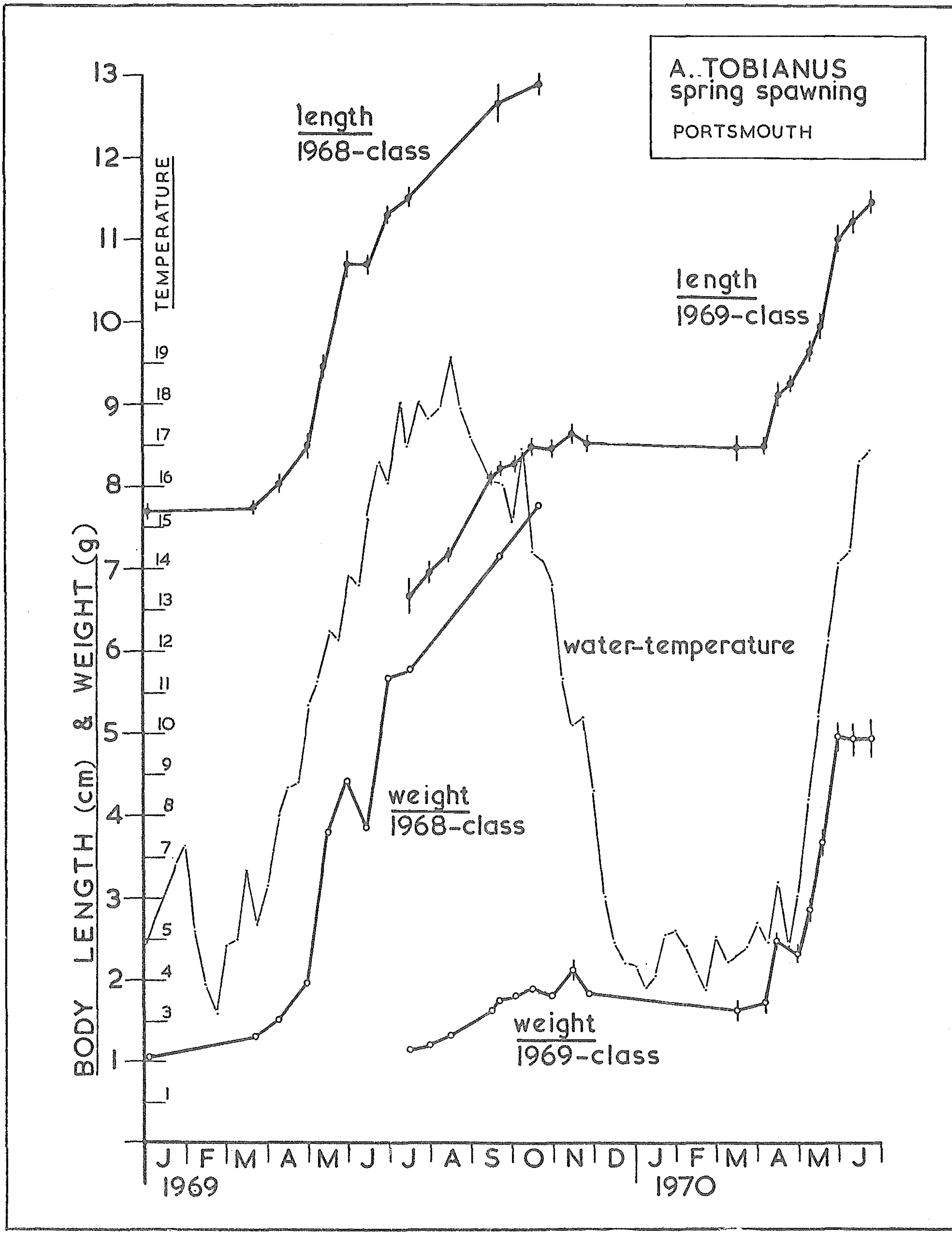

Fig. 4. Seasonal growth of A. tobianus, Portsmouth, S. England. (mean length and weight with 95% confidence limits). Original data.

3.5 Behaviour

3.51 Migrations and Local Movements

Kändler (1941), Andriashev (1954), Pearson (1969), and others have recorded influxes of sandeels towards the surface coastal waters in summer, and Kändler has also stated that sandeels move to deeper waters offshore in winter. Both Cameron (1958), in inshore waters around the Isle of Man, (Irish Sea), and Macer (1966), offshore in the southern North Sea, were able to catch sandeels in all months of the year, but in general very few free-swimming sandeels could be caught in the winter months and such catches were mainly composed of immature fish. Cameron in fact found adult A. tobianus (and all A. marinus) in Port Erin Bay only between May and August.

From the fact that large catches of A. dubius were made in both July and November at the same places over the Nova Scotia Banks, Scott (1968) suggested that there was little, if any, seasonal movement of the stocks, but that occasional reports of temporary local concentrations may have resulted from such movements or from undetermined hydrographical factors. Popp Madsen (1963) concluded, on the basis of tagging 858 A. marinus in the southern North Sea in the summer of 1958 (13% recovered), that sandeels are very stationary and undertake no feeding migration; his experiments however, did not extend throughout the year and the results, though of value, cannot be used to determine the extent to which sandeels move to favourable winter areas. In addition to such movement it appears that sandeels remain within the substrate during winter, and Cameron (1958) has produced evidence to this effect; she found that although sandeels could not be trawled on an offshore bank in winter, they could be caught in a modified scallop dredge. Apart from the instance recorded by Hansen (1949) of shoals of cod feeding on sandeels which were apparently moving northwards along the West Greenland coast in August, there are no published accounts of a definite migration in sandeels, and while there is some evidence for an inshore (summer) - offshore (winter) movement, particularly in northern latitudes, this may be obscured by movement into the substrate during unfavourable seasons. Macer (pers. comm.) has suggested that at least for certain North Sea stocks, the necessity of some sort of migration is indicated for their geographic maintenance; this would most likely be by juveniles at recruitment, and the decreases in mean length of A. marinus on the Indefatigable and Haddock Banks in the North Sea in 1961 (Macer, 1966) could possibly have been the result of prolonged recruitment bringing about influxes of smaller fish. Other changes in population structure and abundance, incompatible with the results of individual growth and mortality may also be indicative of some degree of movement in sandeel populations not associated with either recruitment or movement to wintering areas.

3.52 Schooling

The formation of schools in sandeel species is apparent from surface observations (for example, Cameron 1958), echogrammes (Roessingh, 1957; Drever and Ellis, 1968), and underwater observations (Kühlmann and Karst, 1967). The following account is taken from Kühlmann and Karst, (1967) and refers to underwater observations (mainly on A. tobianus) in the western Baltic. Although H. lanceolatus, A. tobianus and occasionally young herring occurred together in the same school, the fish were generally segregated into those containing individuals of approximately the same size. Close inshore, the number of individuals in a school was of the order of 10^2 fish, but, in deeper water, schools containing 10^3 fish were often encountered. School-shape was described as horizontally flattened, and blunt-linear in surface view, but close inshore this pattern was often disrupted, and other shapes developed. In a normal swimming school the lateral distance between individuals was found to be about two-thirds of the body length, and the front/rear distance about one-third of the body length, when escaping, however the schools tightened up and when feeding the distances between individuals became greater. It was estimated that the fish usually swam at a speed of 30-40 cm/sec; small groups swam faster than larger ones and in short escape bursts, speeds of 300-500 cm/sec were reached. Avoidance of a pursuer was mostly achieved by accelerating to one side and avoidance of weeds, rocks and large fish in the path of the school, by splitting and reformation. Schools of fish of a similar size were observed to amalgamate freely, and there were both accidental and apparently spontaneous instances of disassociation. In general, it has been found that at night, sandeels cannot be caught in either beach-seine (Cameron, 1958), mid-water trawls, (Macer, 1966) or bottom trawls, (Popp Madsen, 1963; Macer, 1966). Bertelsen and Popp Madsen (1958) found that it was much easier to catch sandeels in bottom grabs at night than in the daytime, and concluded that they generally spent the hours of darkness buried in the sand. However, both Anon (1958) and Drever and Ellis (1968) observed, by sonar, the movement of sandeel schools towards the surface at night in N.W. Atlantic areas. Macer (1966) has reported records of nocturnal observations of sandeels at the surface of the North Sea in March, and Bertelsen and Popp Madsen (1958) have referred to catches of sandeels at night in ring-trawls. These isolated records of nocturnal activity may have resulted from the effects of ship's lights (Macer, 1966), or moonlight, and it is thus of interest to find that Kühlmann and Karst (1967) were able to attract A. tobianus from the sand at night with an underwater torch, and that Inoue et al. (1967) have reported the successful attraction of A. personatus to a lamp at night for fishing purposes.

In inshore waters of the Baltic, Kühlmann and Karst (1967) have made underwater observations on the diurnal behaviour of A. tobianus. They found that the fish emerged from the sand-bank in small groups at sunrise, and that these groups gradually came together to form large schools of more than 1,000 individuals which then swam across an area of sea-grass to the feeding grounds about 1,000 metres from the vicinity of the inshore sand-bank. Around mid-day the fish returned from the feeding grounds and throughout the afternoon the schools swam about close inshore only occasionally stopping to feed. With increasing darkness the schools congregated over the sand-bank and small groups separated off and rapidly dived into the sand. Popp Madsen (1963) has suggested that activity in the daylight hours is associated with the state of the tide, since he found some correlation between peak catches on the North Sea fishing grounds and the strength and direction of the tide; most fish were caught when the tide running from the N.W. in the central North Sea, but two peaks, at both stages of maximum tidal flow, were identified in eastern areas such as Hornsreef. Macer (1969), however, found that in the southern North Sea maximum catches could occur at all states of the tide, and although there was some slight suggestion of relatively low catches at high water and on the ebb tide, he found no clear correlation between peak catches and either the state of the tide or the time of day. The implication of observations associated with seasonal and diurnal activity cycles is that in general terms, sandeels burrow into the substrate at night and during unfavourable seasons. From the observations reported by Kühlmann and Karst (1967), entry into the sand is very rapid, and simply appears to involve a continuation of the normal sinuous swimming movement. Usually the fish lie completely buried in the sand, but on being disturbed may protrude their heads in the direction of the disturbance: this may then be followed by either a rapid sideways movement out of the sand and rapid swimming away from the disturbance, or retreat into the sand and re-appearance some distance away.

3.53 Responses to stimuli

The importance of light in relation to the diurnal activity cycle has been implied in Section 3.52. Experimental work on the activity of A. marinus in relation to light intensity, food and current strength is currently in progress at Lowestoft.

4. POPULATION

4.1 Structure

4.11 Sex-ratio

Overall sex-ratios are shown in Table XII and in most cases indicate proximity to a 1.1 ratio. Some individual samples recorded by Bahr (1935), Kändler (1941) and Macer (1966) show significant deviations both during and outside the spawning seasons (see Section 3.16), and could indicate the presence of behavioural differences between the sexes. There is no evidence for sex-ratio changing with age and influenced by differential mortality.

4.12 Age composition

The oldest A. tobianus recorded are VII group, and the oldest A. marinus and A. dubius, IX group; since juveniles recruit to the demersal population and to the fishery as 0 - group fish, 7 - 9 year classes may therefore be present. The most recent 1 - 3 year classes invariably dominate however, and their importance can be seen from the age group compositions in Tables XIII and XIV. The pattern of recruitment of the most recent year class is mainly responsible for the seasonal variation in age composition, but there is some evidence, in A. tobianus, that the oldest fish only come close inshore in the summer months. Macer (1966) has noted the effect of variable year class strength in A. marinus on the age composition of North Sea populations. Sandeels are first captured as 0 and I group fish, reach maturity as I - II group fish, and reach a maximum age as VII - IX fish.

4.13 Size composition

The length composition of selected samples of A. tobianus, A. marinus and A. dubius is given in Table XV. The large size of A. dubius compared with the N.E. Atlantic species

TABLE XII
Overall Sex-ratios in populations of A. tobianus and A. marinus (Monthly samples combined)

	N	%	%	Locality	Author
A. tobianus					
	828	45.9	54.1	Western Baltic	Bahr (1935)
	1396	50.7	49.3	Western Baltic	Kändler (1941)
	1444	51.8	48.2	North Sea	Kändler (1941)
	401	52.2	47.8	South Coast, England	Original data
A. marinus					
	397	30.8	69.2	Southern Baltic	Kändler (1941)
	2252	45.0	55.0	North Sea	Macer (1966)

TABLE XIII
Analysis of research cruise catch data from the Southern North Sea 1960 - 1962 to indicate the importance of different age-groups in A. marinus (from Macer's (1966) data)

Age group	0	I	II	III	IV	V	VI	VII	VIII	IX		Total number of cruises = 23
a)	17	100	95	95	87	70	74	48	13	4	a) =	% of total cruises when age group present
b)	-	48	30	17	4	-	-	-	-	-	b) =	% of total cruises when age group dominant
c)	5	99	80	90	55	10	5	5	<5	<5	c) =	Maximum % of the age group in the total catch of the species from any one cruise

TABLE XIV

Percentage composition of age-groups in samples of A. tobianus

AGE GROUP *	0	I	II	III	IV	V	VI	VII	N	MONTHS	LOCALITY	AUTHOR
A. tobianus (spring spawning)	-	99.2	0.8	-	-	-	-	-	252	March-April	Isle of Man	Cameron
	68.9	28.9	1.8	0.4	-	-	-	-	284	June-July	(Irish Sea)	(1958)
	89.3	10.0	0.7	-	-	-	-	-	364	Sept-October		
	8.4	73.8	11.4	3.0	3.0	1.0	0.5	-	202	July	Portsmouth	Original
	93.8	4.4	1.1	0.4	0.1	-	0.1	0.1	612	October	(S.England)	data
	100.0	-	-	-	-	-	-	-	116	November		
A. tobianus (autumn spawning)	-	76.9	19.2	3.9	-	-	-	-	753	July-August	Western Baltic	Kändler (1941)
	-	86.3	13.7	-	-	-	-	-	1021	March-April		
	-	92.6	7.0	0.3	-	-	-	-	841	June-July	Isle of Man	Cameron
	91.3	8.2	0.5	-	-	-	-	-	537	October-November	(Irish Sea)	(1958)
		15.3	69.7	9.4	4.0	1.3	0.1	0.2	681	May-Dec.	Fowey River (S.England)	Original data

* Boundary between age groups is 31st December/1st January.

is conspicuous; further, A. marinus appears to be slightly larger than A. tobianus but the samples are not directly comparable because of the differences in gear used. Macer's (1966) research cruise data on A. marinus in the Southern North Sea are similar to those based on the commercial catches, although the total range in length (5-25 cm) and the range in modes (9-20 cm) are greater. Samples of sandeels are generally characterised by 1 - 2 modal peaks indicating the dominant year classes, and marked seasonal changes in these are determined by the rapid growth in the younger fish, and the pattern of recruitment. Conspicuous geographical differences in the length of the same year-class have been indicated by Macer (1966) for A. marinus in the Southern North Sea (Table XVI); Scott (pers. comm.) has found similar size variations over the Nova Scotia Banks for A. dubius. Mean lengths for age are given more fully in Section 3.43. Standard deviations for the lengths of 0 and I group individual year-classes of A. tobianus have been found to range from 4-7 mm by the present author. Size at first capture is considered in Section 5.42, and size at first maturity in Section 3.12. Although precise information is lacking, it is clear that with the gear commonly in use, fish begin to be caught before maturity. Concerning the maximum sizes reached, A. dubius is clearly distinct, with individuals as long as 37 cm. In the other species, the maximum recorded lengths are:- A. tobianus, 28 cm (present author); A. marinus 25 cm (Macer, 1966; Fives, 1967) and A. americanus, 22 cm (Leim and Scott, 1966). There is undoubtedly intraspecific variation, and in the case of A. tobianus, exhaustive work by Cameron (1958) around the Isle of Man, and by the present author at Portsmouth, has failed to reveal individuals greater than 20 cm and 17 cm respectively; the larger individuals were from the Fowey River, S. England. Length-weight relationships are summarised in Table XVII.

TABLE XV

Length composition of samples of A. tobianus, A. marinus and A. dubius

A. tobianus - % frequency in cm. groups (lengths given are the lower limits of the cm. groups)

3	4	5	6	7	8	9	10	11	12	13	cm. 14	15	16	17	18	19	20	21	22	23 24 25	No.	Months	Locality	Gear	Author
				1.9	7.7	8.4	1.5	0.2	0.4	2.5	10.3	9.5	3.7	0.7	0.8					Spring-spawning	461	May-June	W. Baltic (German coast)	Mixed	Kändler (1941)
	4.5	6.7	2.4			0.2	8.4	9.3	7.2	5.9	3.0	0.8	2.3	0.7	0.2					Autumn-spawning					
		0.3	5.9	14.7	17.3	10.1	2.0	0.3	2.0	6.8	10.3	7.0	2.3	0.9	0.4					Spring-spawning	698	Sept-Oct.	W. Baltic (German coast)	Mixed	Kändler (1941)
						0.6	2.8	4.9	5.1	2.0	0.9	1.6	0.6	0.4						Autumn-spawning					
							0.2	6.4	21.3	13.9	6.2	7.7	12.5	19.3	10.6	1.8	0.2			Autumn-spawning	455	April-June	Heligoland (North Sea)	Mixed	Kändler (1941)
	0.7	1.7	0.5	-	-	-	0.7	1.1	1.8	1.0	0.2	-	0.5	0.5	-	0.2	-			Spring-spawning	403	June 1955-57	Isle of Man (Irish Sea)	Beach-seine	Cameron (1958)
	-	-	-	1.2	29.5	45.7	2.7	-	-	-	1.2	8.2	3.4	0.4	0.2	-	0.2			Autumn-spawning					
				0.1	2.0	11.8	11.1	2.1	0.6	0.1		0.4	0.1							Spring-spawning	711	Nov. 1955-57	Isle of Man (Irish Sea)	Beach-seine	Cameron (1958)
1.6	61.3	5.4							0.1		1.0									Autumn-spawning					
		0.6	3.0	1.2	0.3	0.6	7.8	25.5	11.4	4.2	3.9	1.5	0.6							Spring-spawning	333	July 1969	Portsmouth (S.England)	Beach-seine	Original data
				1.5	12.9	21.9	2.4													Autumn-spawning					
				6.0	47.6	19.6	0.4	0.6	7.6	7.8	3.6	2.0	0.2							Spring-spawning	491	Oct. 1969	Portsmouth (S.England)	Beach-seine	Original data
							0.2	0.6	0.4	0.8	0.6	0.2								Autumn-spawning					
				6.0	63.8	29.3	0.8													Spring-spawning	216	Nov. 1969	Portsmouth (S.England)	Beach-seine	Original data
					0.8	3.7	15.7	6.0	0.8	2.8	20.2	28.4	12.1	3.6	4.4	0.4	0.4			Autumn-spawning	246	July-Aug. 1969	Fowey River (S.England)	Beach-seine	Original data

A. marinus - % frequency in cm. groups

									0.1	1.6	7.8	23.8	20.1	21.8	19.8	5.0	0.1						4066	May-July 1959	S.North Sea	Commercial trawl	Meyer-Waarden (1961)
						0.2	6.3	21.9	20.0	13.9	8.3	2.1	1.4	4.7	13.3	6.4	1.3	0.4					1986	May-July 1960	S.North Sea	Commercial trawl	Meyer-Waarden (1962)
								0.2	0.7	5.3	18.2	19.6	11.9	11.1	15.0	8.9	5.1	2.8	1.0	0.2			5840	May-July 1961	S.North Sea	Commercial trawl	Meyer-Waarden (1963
							2.1	11.5	23.8	28.4	16.6	8.0	4.7	2.5	1.6	0.7	0.1						4179	May-July 1962	S.North Sea	Commercial trawl	Meyer-Waarden (1964)
							0.2	1.8	9.2	16.0	35.9	27.1	5.6	1.7	1.3	1.0	0.2						7573	May-July 1963	S.North Sea	Commercial trawl	Meyer-Waarden (1965)
									0.1	3.3	26.7	42.3	19.1	4.7	2.0	1.2	0.5	0.1					5963	May-July 1964	S.North Sea	Commercial trawl	Meyer-Waarden (1966)
								0.3	2.0	7.4	8.8	23.6	34.7	17.3	3.8	1.0		0.1					2529	May-July 1965	S.North Sea	Commercial trawl	Meyer-Waarden (1967)
								1.1	6.7	23.0	27.8	17.1	11.4	7.6	3.7	1.4	0.1		0.1				2494	May-July 1966	S.North Sea	Commercial trawl	Tiews (1968)
					0.1		0.8	6.0	7.5	13.0	25.3	22.3	11.0	7.1	3.0	2.3	1.0	0.6	0.1				933	July 1967	Moray Firth (E.Scotland)	Research trawl	M.P. Langham (unpublished data)

A. dubius - % frequency in cm. groups

13	14	15	16	17	18	19	20	21	22	23	cm. 24	25	26	27	28	29	30	31	32	33	34	35	36	37	No.	Months	Locality	Gear	Author
-	1.3	2.6	5.3	5.3	10.7	4.0	7.9	7.3	8.6	10.5	13.4	10.0	10.0	14.7	15.8	10.0	5.3	6.0	2.6	3.9	-	-	-	0.6	149	July-Aug. 1967	Nova Scotia Banks	Research trawl	Scott (1968)

TABLE XVI

Lengths of 1959 and 1960 year classes of A. marinus in the North Sea, July/August, 1961 (from Macer, 1966)

Ground	N	1959 class Mean length (cm)	N	1960 class Mean length (cm)
Southernmost Region	19	21.0	212	18.5
Indefatigable Bank	86	16.0	204	14.2
Haddock Bank	29	13.7	160	12.5

TABLE XVII

Length-weight relationships for A. tobianus, A. marinus A. dubius of the form $W = aL^b$

Species	a	b	N	Season	Locality	Author
A. marinus	2.5×10^{-4}	3.068		-	S. North Sea	Macer (1966)
A. dubius	6.3×10^{-7}	2.778	589	Jan - Mar	Western Bank (Nova Scotia)	Kohler et al. (1970)
	7.8×10^{-6}	2.381	356	Jul - Sept		
	2.9×10^{-7}	2.976	207	Oct - Dec		
	9.9×10^{-8}	3.153	890	All Seasons		
A. tobianus (spring spawning)	1.5×10^{-7}	3.169 (95% C.L. = ± 0.106)	80	September	Portsmouth (England)	Original data

4.2 Abundance and Density

4.21 Average Abundance

Bertelsen and Popp Madsen (1958) calculated that in June, 1958 there were 1,800 million A. marinus on an area of the Southernmost Rough (approx. 140 km^2) in the North Sea; there is no other quantitative information on abundance.

4.22 Changes in Abundance

In any single area, sandeel abundance (catch per effort) varies from year to year; no evidence is available to suggest that the major cause of such variation in abundance is anything other than variable year class strength. Within a season, fishing mortality may be of significance in causing a decline in abundance (see Section 5.4).

4.23 Average density

See Section 4.21: the density quoted by Bertelsen and Popp Madsen would be 13 per square metre. The densities found in bottom grabs by these authors ranged from 2.5 - 3.8 per square metre.

4.24 Changes in density

See also Section 5.41 for catch per unit effort data. Although there is a tendency for some sandeels to move inshore in summer and offshore in winter (see Section 3.51), most populations are probably present throughout the year over the same grounds. However, the fish are typically more active in the summer months, and thus are more available for capture during this period.

4.3 Natality and Recruitment

4.33 Recruitment

For the Japanese sandeel, A. personatus, Hamada (1966) has correlated landings of 0-group fish with the number of days on which the seasonal, west wind blew within twenty days after the peak of spawning ($r = +0.74$), and also found larger catches of 0-group fish after spawning seasons when water temperature had been lower than average; a negative correlation ($r = -0.868$) was found to exist between the percentage of I-group fish in the total parent fish catch, and the catch of 0-group progeny. Covill (1959) drew attention to annual variations in the abundance of A. americanus larvae in Long Island Sound; in years of low abundance, plankton food was not scarce, but catches of the larvae showed an abnormally high proportion of empty stomachs.

For A. marinus and spring-spawning A. tobianus adolescents recruit to the demersal populations between May and August about four to six months after the spawning periods; in autumn spawning A. tobianus some recruitment takes place in November after an early spawning period, but others appear to over winter as larvae and do not appear with the demersal populations until the following April. (Kändler, 1941; Cameron, 1958; Macer, 1966; present author).

4.4 Mortality and Morbidity

4.41 Mortality rates

Macer (1966) calculated the total mortality (as mean annual percentage) of A. marinus in the North Sea as 71% (instantaneous coefficient = 1.24), from the logarithmic plot of age group frequency over three years; with additional data, he has modified (pers. comm.) this to 65.8%. A similar mean annual mortality for A. marinus (75%) was obtained by Macer (1966) by comparing the abundance (as catch per unit effort) of individual year classes in successive years over the Dogger Bank. Data on other species and populations is not yet available, but examination of age class composition suggests a similar rate for both fished and unfished populations.

4.42 Factors causing or affecting mortality

Predation on sandeels is considered in Section 3.34, and it is likely that this mortality factor is of paramount importance; unfortunately no quantitative data is available. Occasionally reports of quantities of dead sandeels have been noted in the literature. These include the mortalities from near the Isle of May, Scotland, in July and August, 1964 (Anon, 1964), and from Rhode Island, North America in May, 1954 (Graham, 1956); in both of these instances, there was no obvious cause of death, although Graham found a significantly greater head length (relative to standard length) in live fish than in dead fish ($p < 0.01$) and suggested that fish with large heads were being favoured by natural selection.

Mass mortalities with known causes involve those associated with the oil and detergent pollution resulting from the wreck of the 'Torrey Canyon' in Cornwall in March, 1966 (Smith, 1968) and with the bloom of the dinoflagellate Gonyaulax tamarensis Lebour off the north-east coast of England in May, 1968 (Adams et al, 1968). In the latter incident, the first sandeel deaths were recorded a week after the dinoflagellate peak, the suggested causes of death being the release of toxins and lowered oxygen values resulting from the death and decay of the bloom.

4.6 The Population in the Community and the Ecosystem

As a family, sandeels are a group of fish living within and above sandy substrates in relatively shallow water. Although classified as demersal fish in fishery statistics, and certainly dependent upon a suitable bottom substrate for burrowing into, they lead a pelagic existence, generally feeding on plankton and moving throughout the water mass, when active. Typically the sands used by sandeels are clean and course with relatively little organic matter: thus, the permanent infauna is usually scarce, and Nagabhushanam (1965) referred to the substrate of Warts Bank (Isle of Man), and important sandeel ground, as unique in the area because of its poor benthic biomass. In such areas sandeels are often abundant and their biomass dominates that of other fish species; these fall into one of three categories: 1) pelagic species which are feeding on the plankton, e.g. clupeoids. 2) species feeding on what is usually a sparse invertebrate bottom fauna, e.g. pleuronectoids, 3) species feeding on the sandeels themselves, e.g. gadoids.

As shown in Sections 3.22 and 3.34, sandeels have many predators and are an important source of food throughout their range; in many places they are the dominant item in the diet of many species of fish and seabirds. The extent to which sandeels determine the abundance and distribution of their predators is, however, difficult to evaluate, but Ritchie (1932) has stated that the abundance and distribution of both post-laval and adolescent sandeels played an eminent role in shoal movements of haddock to the north and west of Scotland. Richards (1963) emphasised the importance of A. americanus as a consumer of zooplankton in Long Island Sound, N.Y., compared with most other fish species, and although as yet not quantified, sandeels, in general, must play a very significant role in the trophic network.

5. EXPLOITATION

5.1 Fishing Equipment

5.11 Gears

The gear used in the North Sea industrial fishery has been described by Macer and Burd (1970) as a wing-type, single-boat, bottom trawl with a high headline and a light foot-rope; the latter is lightly weighted with pieces of lead so that it trips along the bottom without digging in. The bridles are 60-80 metres long, and the mesh size of the net decreases to 5 mm in the cod-end from 100 mm in the wings.

The gear most commonly used in the inshore bait/food fisheries is a beach-seine, and nets up to 100 metres long are currently in use along the south coast of England; in addition, a variety of rakes, sickles, forks and even a horse-drawn harrow have been used to extract sandeels buried in intertidal sands. When the sandeels are used as bait, a small floating keep (courge) is sometimes employed to keep them alive.

According to Bertelsen and Popp Madsen (1958) and Macer (1966) sandeels are inconspicuous on echogrammes, but Roessingh (1957), Anon (1958), Drever and Ellis (1968) and Macer and Burd (1970) have recorded traces, and echosounders are important in the North Sea fishery. The sandeel fisheries are diurnal and no use is made of artificial light to attract the fish at night as Inoue et al. (1967) has recorded for the Japanese fishery.

5.12 Boats

Macer (1966) has described the typical North Sea industrial vessels as wooden seiner/cutters 20 - 25 metres long with 100 - 250 h.p. engines. Smaller vessels may however fish in pairs (Kühl and Luhmann, 1965) and the Norwegians have used a factory ship in conjunction with their small fleet (Anon. 1957)

5.2 Fishing Areas

5.21 General Geographic Distribution

Industrial sandeel fisheries are at present restricted to the N.E. Atlantic, and take place mainly in the Central North Sea (ICES region IVb), and Southern North Sea (IVc) and the Kattegat and Skaggerak (IIIa). Smaller quantities have also been landed from the Northern North Sea (IVa), the Norwegian Sea (IIa), the Baltic (IIId) and the Irish Sea (VIIa). Annual landings from the different areas are shown in Table XVIII. Only very small landings have been recorded from the N.W. Atlantic (Greenland in 1964, and occasionally in Canadian and U.S. statistics) but the sandeels in this area may receive more attention in the future (Scott, 1968).

Inshore bait/food fisheries are more widespread than the industrial fisheries, but are of lesser importance. Bigelow and Schroeder (1953) and Jerome et al.)1965) have referred to such fisheries along the New England coast of North America, and others noted in the literature include the Murman coast (Andriashev, 1954), Norwegian coasts (Soleim, 1945), the Baltic (Smitt, 1895; Bahr,1935) and Scotland (McIntosh and Masterman, 1897). At the present time sandeels are still taken in quantity for bait and food along French coasts; along the south coast of England they are of importance as bait for sport fishermen.

TABLE XVIII

Percentage of Annual Catch 1961-67 taken in different Regions of ICES Statistical Area (N.E. Atlantic)

ICES Regions	IIa Norwegian Sea	IIIa Kattegat/ Skaggerak	IIId Baltic	IVa Northern North Sea	IVb Central North Sea	IVc Southern North	VIIa Irish Sea
1961	-	5.2	-	-	93.1	1.7	-
1962	-	21.5	-	+	78.5	-	-
1963	-	12.0	-	+	88.0	-	-
1964	-	2.5	+	+	95.8	1.5	0.2
1965	-	7.2	-	3.5	89.1	0.2	-
1966	0.6	10.2	-	10.1	79.6	0.1	-
1967	0.2	9.9	-	0.5	89.5	-	-

NB. Danish landings from the south-western North Sea are probably all included in Region IVb, although the Norfolk Banks from where a considerable part of the catch arises, are strictly in IVc. (Macer, pers. comm.)

5.22 Geographic ranges

The industrial fisheries involve the exploitation of grounds which are up to 200 km from the nearest coastline and up to 600 km from port. Most grounds are within 100 km of the coast however, and in the North Sea involve Danish, German and Dutch coastal areas south to the Zeeland Islands, the south-western edge of the Dogger Bank (Southernmost Rough, South-West Spit and the Outer Well Bank), and on and around the Norfolk Banks (Meyer-Waarden 1959-67, Popp Madsen 1963). The former coastal areas, which include the Horns Reef, the Terschellinger Bank and the Borkum Rough, were the only areas fished before the rich sandeel grounds in the south-western part of the North Sea were discovered in the late 1950's, (Macer, 1966).

5.23 Depth ranges

The industrial fisheries in the North Sea take place on grounds less than 40 metres in depth (Macer, 1966).

5.24 Conditions of the grounds

All the grounds have a clean sand/fine gravel bottom, and in the south-western North Sea fishing takes place along the edges of the large banks and over the tops of the smaller flatter ones. According to Macer and Burd (1970) the towing course is particularly critical on the Hills and Outer Dowsing areas where the crests of the banks are sharply ridged; to avoid net damage, the trawl is towed parallel to the ridge, on one side of the crest or the other.

Popp Madsen (1963) has suggested that the most important catches are made in areas where the maximum current speed exceeds 0.5 knots.

5.3 Fishing Seasons

5.31 General pattern of seasons

All sandeel fisheries appear to take place in the summer months, and there are very few landings between October and April in either industrial or bait fisheries. The general pattern of seasonal landings for the North Sea is given in Table XIX.

5.32 Dates of beginning, peak and end of seasons

Table XIX shows that the North Sea fishery begins in April, reaches a peak in June and may finish any time between August and November. 88.6% of the landings between 1961-66 were taken in May, June and July and all the Norwegian and German landings have apparently been taken in these three months. The 1966 season has been the longest so far (March to December) but the pattern of monthly landings remained unchanged.

TABLE XIX

Monthly landings of sandeels from the North Sea 1961-66 in metric tons x 10^3

Data from ICES Bulletin Statistique

Year	TOTAL	March	April	May	June	July	August	September	October	November	December
1961	83.7	-	12.5	15.2	46.0	9.2	0.6	0.1	0.1	-	-
1962	110.0	-	2.6	30.4	40.1	35.0	1.7	0.2	-	-	-
1963	151.3	-	9.1	46.7	50.5	38.3	6.7	-	-	-	-
1964	128.3	-	8.8	34.8	60.7	15.3	7.1	1.5	0.1	-	-
1965	125.8	-	10.1	40.0	43.9	27.0	3.0	1.8	-	-	-
1966	138.5	< 0.1	6.8	41.7	58.7	19.6	5.6	2.5	3.3	0.3	<0.1
TOTALS	737.6	< 0.1	49.9	208.8	299.9	144.4	24.7	6.1	3.5	0.3	<0.1
%		< 0.1%	6.8%	28.4%	40.6%	19.6%	3.4%	0.8%	0.5%	<0.1%	<0.1%

5.33 Variation in date or duration of season

Although sandeels appear to reach a peak of abundance or availability in mid-summer (Bertelsen and Popp Madsen, 1958; Kühl and Luhmann 1965 and others), the dates and duration of the season are also influenced by the demand imposed by the fish meal factories with respect to other sources of raw material - particularly the oil-herring - and the international price of fish meal (Meyer-Waarden, 1965). The fishery is, in addition, to some extent dependent upon the prevailing weather conditions (Kühl and Luhmann, 1965).

5.4 Fishing Operations and Results

5.41 Effort and intensity

Catch per unit effort data are not generally available for the Danish fishery, but on the Southernmost Rough (North Sea) in the summer of 1958, Bertelsen and Popp Madsen (1958) encountered average peak catches in late May and early June at about 2,500 kg per hour; they ascribed the decline in c.p.u.e. after the June peak to the effects on the populations of intensive fishing. The 75 vessels present on the ground at the time represented a fishing intensity of about 10 metric tons/day/km^2. Catch per unit effort (as tons per trip), in addition to total catch also reached a June peak in the German fishery from 1957-60 (Lundbeck, 1958-61, Macer, 1966). Macer and Burd (1970) have referred to catch-rates as high as 15,000 kg per hour, at the height of the season, and Scott (pers. comm.) has encountered similar catch-rates (experimental) over the Nova Scotia Banks.

Annual c.p.u.e. data (as tons per trip) have been provided by Lundbeck (1958 et seq.) for the now discontinued German fishery. Average catch per trip has ranged from 25 tons in 1959 to 48 tons in 1961, and although a slight decline in c.p.u.e. in later years accommpanied a marked decline in effort, an increase was apparent after 1959 coinciding with the initial exploitation of the Dogger and Norfolk Bank areas (Meyer-Waarden, 1962).

It is of interest to note that there are no instances of a decline in c.p.u.e. with increasing effort in the intense sandeel fisheries around Japanese coasts, where more data on catch and effort is available.

5.42 Selectivity

The North Sea industrial fishery is based on A. marinus and inshore bait fisheries in the N.E. Atlantic on A. tobianus. Macer (1966) considered that the selection length of A. marinus in the North Sea, using commercial 6 mm bar meshing was slightly less than 8-9 cm: thus the fish begin to be caught when about 5-6 months old as 0-group fish. There are no other selective factors.

When small-meshed nets are used, undersized individuals of otherwise protected species are liable to be caught as part of the by-catch, and thus this problem of interspecific selection is an important one when dealing with sandeels, for not more than 10% by weight of the total landing is allowed to consist of undersized protected species. (Section 6.1). In fact, however, all available data (Anon. 1960; Bertelsen and Popp Madsen, 1958; Kuhl and Luhmann, 1965; Macer, 1966; Meyer-Waarden, 1959 et seq; Molloy, 1967, and Roessingh, 1957) show that the 10% level is only very rarely reached, and when it is, there remains the possibility that undersized fish have been deliberately sought because of the scarcity of sandeels (Macer, 1966).

On seven out of ten research cruises in the North Sea, Macer (1966) found that sandeels predominated (78.8-99.3% by number, 60.0-91.4% by weight of total catch). The other three cruises were either out of the sandeel season or were dominated by clupeoids. The quantity of undersized protected fish ranged from 0.1-5.9% by number, 0.1-3.5% by weight, and mainly involved whiting (Odontogadus merlangus (L) and dab (Limanda limanda (L)).

Analysis of commercial landings by Meyer-Waarden between 1957 and 1965 revealed that sandeels formed 86.1-95.7% by weight of the landings, with the incidence of undersized protected species ranging from 0.8-3.1%.

5.43 Catches

Total industrial landings from the ICES Statistical Area are given in Table XX and Fig. 5. The first landings were made in 1952 by Germany (Meyer-Waarden, 1959), but Danish landings began in 1953, increased very rapidly, and have always formed by far the most significant part of the total catch. Sandeels form up to 20% of the total annual Danish landings of all species, and although the quantity varies from year to year, it shows no sign of declining. Only Norway and Denmark now fish for sandeels in the North Sea, although a U.K. fishery has now started following successful experimental trips in 1969 (Macer and Burd, 1970) and the introduction in 1968 of the legislation permitting the landing of up to 10% undersized protected species. A small fishery for sandeels from Ireland in 1964 has been described by Molloy (1967), but more interest in Irish stocks is likely to arise from the recent development of several fish-meal factories. Statistics are not generally available for the bait fisheries, but it is estimated that over 7,000 kg were caught in the Merrimack River Estuary, Mass. U.S.A. in 1964, (Jerome et al. 1964) and about 4,000 kg at Portsmouth, U.K. in 1968.

TABLE XX

Industrial landings of sandeels from ICES Area (N.E. Atlantic) in metric tons 1953–67
(Data from ICES Bulletin Statistique unless otherwise stated)

	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
Denmark		4,500[a]	10,600[b]	41,800[b]	87,700[b]	75,300[b]	74,600[b]	77,500[b]	105,106	78,181	127,050	155,773	107,962	133,835	156,755	208,099	200,608
Germany	+	+	+	+	5,297[c]	25,524[c]	22,000[c]	21,248[c]	9,481	4,675	1,454	16,898	13,398	2,228	4,388	343	
Norway					1,435[d]	3,220[d]	4,817	7,979	13,687	5,400	11,601	11,563	10,402	4,926	19,492	1,448	613
Netherlands						3,700[e]	1,522	5,062	3	64							613
U.K. England													5				
Ireland													271				
	+	4,500	10,600	41,800	94,432	107,744	102,939	111,789	128,277	88,320	140,105	184,234	132,038	140,989	180,635	209,890	201,221

a) Popp Madsen (1957)
b) FAO Yearbook of Fishery Statistics
c) Lundbeck (1957-1960)
d) Statisk Arbok for Norge
e) Anon. (1960)

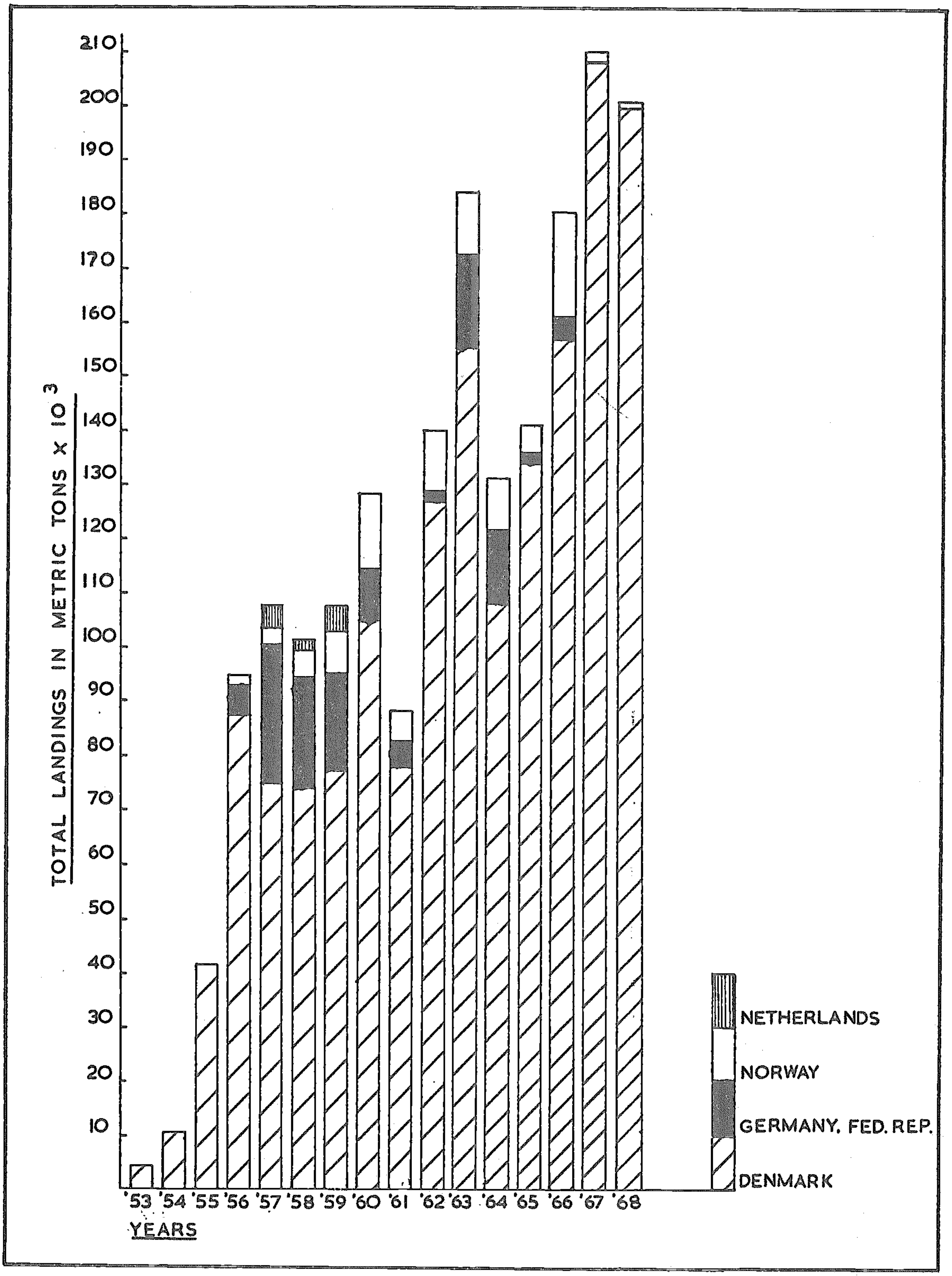

Fig. 5. Total industrial sandeel landings, North Sea, 1953-68. (from the data in Table XX)

6. PROTECTION AND MANAGEMENT

6.1 Regulatory (Legislative) Measures

As one of the 'Article 6' species of the International Fisheries Convention of 1946 (repeated in N.E. Atlantic Fisheries Commission of 1959), sandeels may be fished for with small meshed nets provided that not more than 10% by weight of landings are composed of undersized protected species (for data on by-catch, see Section 5.42).

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SYNOPSIS OF FISHERIES BIOLOGICAL DATA

This is one of a series of documents issued by FAO, CSIRO and USFWS concerning species and stocks of aquatic organisms of present or potential economic interest. The primary purpose of the series is to make existing information readily available to fishery scientists according to a standard pattern, and by so doing also to draw attention to gaps in knowledge. It is hoped that synopses in the series will be useful to other scientists initiating investigations of the species concerned or of related ones, as a means of exchange of knowledge among those already working on the species, and as the basis for comparative study of fisheries resources. They will be brought up to date from time to time as further information becomes available either as revisions of the entire document or their specific chapters.

The relevant series of documents are:

FAO	**Fisheries Synopsis No.** replacing, as from 1.1.63 FAO Fisheries	FR/S
	Biology Synopsis No.	FB/S
CSIRO	**Fisheries Synopsis No.**	DFO/S
	and	
USFWS FAO	**Fisheries Synopsis No.**	BCF/S

Synopses in these series are compiled according to a standard outline described in FIb/S1 Rev. 1 (1965). FAO, CSIRO and USFWS are working to secure the cooperation of other organizations and of individual scientists in drafting synopses on species about which they have knowledge, and welcome offers of help in this task. Additions and corrections to synopses already issued will also be most welcome. Comments including suggestions for the expansion of the outline and requests for information should be addressed to the coordinators and editors of the issuing organizations.

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Marine Biology and Environment Branch
Food and Agriculture Organization
of the United Nations
Via delle Terme di Caracalla
00100 Rome, Italy

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Office of Scientific Publications
Bldg. 67, U.S. Naval Air Station,
Seattle, Washington 98115, U.S.A.

CSIRO:
Scientific Editor
CSIRO Division of Fisheries and Oceanography
Box 21
Cronulla, N.S.W.
2230 Australia

Consolidated lists of species or groups covered by synopses issued to date or in preparation will be issued from time to time. Requests for copies of synopses should be addressed to the issuing organization.

The following synopses in this series have been issued since January 1969:

BCF/S40	Synopsis of biological data on the Pacific mackerel *Scomber japonicus* Houttuyn (Northeast Pacific)	February 1969
FRi/S30 Rev. 1	Synopsis of biological data on the pike *Esox lucius* (Linnaeus) 1758	May 1969
DFO/S3	Synopsis of biological data on the tiger prawn *Penaeus esculentus* Haswell, 1879	July 1969
FRm/S43	Synopsis of biological data on the anchoveta *Cetengraulis mysticetus* Günther, 1866	October 1969
FRh/S35 Rev. 1	Synopsis of biological data on West African croakers *Pseudotolithus typus, P. senegalensis* and *P. elongatus*	November 1969
BCF/S42	Synopsis of biological data on the Atlantic menhaden, *Brevoortia tyrannus*	November 1969
FRm/S78	Synopsis of biological data on smelt *Osmerus eperlanus* (Linnaeus) 1758	December 1969
FIRI/S80	Synopsis of biological data on the eel *Anguilla anguilla* (Linnaeus) 1758 (Provisional version)	April 1970
DFO/S4	Synopsis of biological data on the rainbow prawn, *Parapenaeopsis sculptilis* (Heller, 1862)	1970
BCF/S4	Synopsis of biological data on chum salmon *Oncorhynchus keta*	July 1970
DFO/S5	Synopsis of biological data on the school prawn *Metapenaeus macleayi* (Haswell, 1879)	1970
FIRI/S80	Synopsis of biological data on the eel *Anguilla anguilla* (Linnaeus) 1758	October 1970
FIRM/S82	Synopsis of biological data on North Atlantic sand eels of the genus *Ammodytes (A. tobianus, A. dubius, A. americanus* and *A. marinus)*	October 1970