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ON SUBSPECIES AND RACES OF THE LESSER SAND EEL (*AMMODYTES LANCEA* S. LAT.)

A CONTRIBUTION TO THE DISCUSSION OF THE SPECIES PROBLEM IN FISHES

BY

AD. S. JENSEN

KØBENHAVN
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Nomenclature.

As regards the designation of the two species of the genus *Ammodytes* (*lanceolatus* and *lancea*) which are common in north-European waters there prevailed and still prevails to-day a difference of opinion which has led to complete confusion. Before I proceed to the actual subject of the present paper I wish to set forth some guiding remarks.

By international agreement the 10th edition of LINNÉ's Systema Naturae forms the basis of zoological nomenclature. In this edition LINNÉ gives only one species of *Ammodytes* which he calls *A. Tobianus*[1]. In the 12th edition LINNÉ came to the conclusion that two species of *Ammodytes* are found on the Swedish coasts, writing: "Species mihi videntur in Svecia duæ esse distinctæ"; but he used only one species name for both, viz. *Tobianus*[2]. It cannot be seen from the text of any of these two editions which of the two species LINNÉ had before him.

LESAUVAGE is the first to separate the two species under the names *A. lanceolatus* and *A. tobianus*[3]; he thus retains the latter name giving it to the species which was later established by CUVIER under the name *A. lancea*, while

[1] CAROLI LINNÆI Systema Naturæ, Tomus I, Ed. Decima, p. 247, 1758.

[2] CAROLI A LINNÉ: Systema Naturæ, Tomus I, Ed. Duodecima, p. 430, 1766.

[3] Bull. des Sciences, par le Société Philomatique, 1824, p. 140—141. To this paper I have had no accession.

Cuvier is of the opinion that it is Lesauvage's *A. lanceolatus* which ought to retain the name *A. tobianus*[1].

In the following years the species name *tobianus* is used now for the one and now for the other of the two species.

In a paper on specimens contained in Linné's collections Lönnberg too mentions "*Ammodytes Tobianus*", writing that it is *A. lanceolatus* Lesauvage. At the same time it appears from Lönnberg's account that the specimen originated from Alströmer's collections, which were known and seen by Linné, and that some of these animals were Linné's types, but this is not said to be the case with *A. tobianus*[2]. As it is stated in the literature that according to Lönnberg, Linné's type specimen of *Ammodytes Tobianus*, which still exists, is *A. lanceolatus*—which would cause the latter name, being the younger, to be replaced by *tobianus*—I asked Prof. Lönnberg for his opinion on this point. Prof. Lönnberg writes in a letter of 16th May 1941 that the specimen of *A. Tobianus* which is mentioned in connection with Jonas Alströmer's collections, and which is of the form that was later described by Lesauvage under the name *A. lanceolatus*, is of no importance to nomenclature; for Linné did not consider it a type specimen, but only a specimen of "*A. Tobianus*". If Linné in any way had chosen it for a type specimen, things would have been different; but this did not happen: the Alströmer specimen cannot be made the type of the name *tobianus*. According to the evidence we have there is no ground for retaining the species name *Tobianus* for *lanceolatus*.

[1] Cuvier: Le Règne animal, Tome II, 1829, p. 360.

[2] Einar Lönnberg: Linnean Type-Specimens of Birds, Reptiles, Batrachians and Fishes in the Zoological Museum of the R. University in Upsala. Bihang till K. Svenska Vet.-Akad. Handlingar, Bd. 22, Afd. IV, No. 1, 1896, pp. 3, 5 & 41.

In elucidation of the relation between *A. Tobianus* and *A. lancea* the following is noted. In his 10th edition of Systema Naturæ LINNÉ refers under *A. Tobianus*, among other works, first to ARTEDI's description of *Ammodytes*, which at that time had not been given any species name[1].

That ARTEDI had *Ammodytes lancea* before him is clear from the following paragraph in his detailed description: "Dentes nulli in maxillis observari possunt. Palatum quoque totem glabrum". One of the most characteristic features in *A. lancea* is just that teeth are absent on the vomer, whereas the vomer in *A. lanceolatus* is provided with two fairly large pointed teeth. Since LINNÉ refers to ARTEDI it may be presumed that he also did not find teeth on the vomer in his *A. tobianus;* hereby the idea that the Linnean species is identical with *A. lanceolatus* Lesauvage is further invalidated.

Now it happened, however, that RAITT in 1934 separated an essential part of the north European population of *A. lancea* as a new species, *A. marinus*—which segregation will be discussed later—among other things characterized by a higher number of fin rays. This will appear from the following table which is based on several hundred specimens.

	Dorsal fin	Anal fin	Pectoral fin
A. lancea	51—57	26—31	11—13
A. marinus	55—63	28—34	12—15

That ARTEDI had *A. lancea* before him appears from the fact that he gives the following number of fin rays which all fall within the limits in *A. lancea*, while the number of rays in the dorsal fin excludes *A. marinus*:

D. 53—54 A. 27—28 P. 12.

[1] PETRI ARTEDI Descriptiones Specierum Piscium, 1738, p. 55—57.

In his 10th edition of Systema Linné refers, besides to Artedi, to some works by himself in which the number of fin rays is as follows:

D. 54	A. 28	P. 13
- 50	- 26	- 12
- 60	- 32	- 15
- 60	- 30	- 14

The figures in the two first lines thus refer to *A. lancea*, in the two last to *A. marinus* (see p. 9, note 1).

In other words: Linné's *A. Tobianus* is a mixture of the two forms which were later established as *A. lancea* Cuvier and *A. marinus* Raitt.

Cuvier's description of *A. lancea* is short, and only meant to distinguish it from *A. lanceolatus*, the differences he notes are, among other things, the different extent of the dorsal fin in relation to the pectorals. Cuvier does not mention the number of fin rays, but this is given shortly afterward by Yarrell in his description of *A. lancea*: D. 51, A. 25, P. 13[1].

On the basis of the information above and in order to clarify the matter I prefer to leave out the name *Tobianus*. If this name has been used in one or other sense by authors quoted in the following it has therefore been replaced by a specific name which cannot be misunderstood, but it is, at the same time, given in brackets and in quotation marks.

In the following we shall discuss *A. lancea* Cuvier, paying also regard to *A. marinus* Raitt and *A. dubius* Reinhardt.

Ammodytes lancea Cuv. and *A. marinus* Raitt.

In 1934 Raitt, of the Fishery Board for Scotland, Aberdeen, gave the surprising information that in the North

[1] W. Yarrell: A History of British Fishes, 1. Ed., II, 1836, p. 322.

Sea and N. E. Atlantic, both inshore and offshore from the Faroes to St. Kilda, and from the Shetland to the Firth of Forth, a species, hitherto entirely overlooked, of the genus *Ammodytes* occurs in large numbers, and he gave it the name *A. marinus*[1]. It is distinguished from *A. lanceolatus*, among other things by the absence of teeth on the vomer and by the upper jaw being protrusible. In these and other respects the new species agrees with *A. lancea* ("*A. tobianus*") but *A. marinus* differs outstandingly from this in fin ray and vertebral numbers. The mean numbers of vertebrae and fin rays found in samples of the two species specially examined for the purpose were:

	Vertebrae	Dorsal fin rays	Anal fin rays	Pectoral fin rays
A. lancea	63.37	53.40	27.96	12.05
A. marinus	69.21	59.07	30.61	13.72

A. marinus is far more common in Scottish waters than *A. lancea* which has so far been found only at inshore positions. In the course of six years 3357 adult specimens were collected of *A. marinus* against 364 adult specimens of *A. lancea* (and 812 of *A. lanceolatus*).

Biologically, the two species differ from each other according to Raitt in that *A. marinus* spawns in early spring, while *A. lancea* ("*tobianus*") ripens in summer.

A. marinus occurs in the larval stage in the northwestern North Sea in countless millions in the month of March year after year and provides important nourishment to many food fishes: "This vital yearly influx of fish food,

[1] D. S. Raitt: A preliminary account of the Sandeels of Scottish Waters. Journal du Conseil, Vol. IX, No. 3, 1934, p. 365. — Idem: The occurrence of four species of Sand Eels, of economic importance, in Scottish waters, one of which is new to science. The Scottish Naturalist, 1935, p. 62.

which has formerly been taken to belong to the species *A. lancea* (*"tobianus"*), is now seen to be the new form *A. marinus"*.

Urged by Raitt's find of the new species of *Ammodytes* Duncker and Mohr made a revision of the collection in the Hamburg Museum in view of the possibility of finding new localities for *A. marinus*[1]. As the material of the museum had to be spared, a determination of the number of vertebrae could not be made; instead of this the oblique cutaneous folds (*plicae*), corresponding to the transversal scale rows, were counted, the numbers of these *plicae* must to some extent be in a fixed relation to the myomere numbers and thus also to the numbers of vertebrae (in the present case about twice the number of the vertebrae). The rays in dorsal, anal, and pectoral fins were also counted. It appeared that the Hamburg Museum possesses specimens of *A. marinus* from the North Sea (56°28′ N, 5°57′ E and the Helgoland Bay) and from Norway (Bergen) and the Murman coast (Port Wladimir).

In 1936 and 1937 Kändler, of the Deutsche wissenschaftliche Kommission für Meeresforschung, found that *A. marinus* is also very common in the Baltic, especially off the coast of Pomerania[2]. The number of vertebrae varies from 66 to 72, the mean value being 68.5, while the species *lancea* (*"tobianus"*) has 61 to 65 and mean value 63.1. Also the number of rays in the different fins agrees with

[1] Georg Duncker und Erna Mohr: Die nordeuropäischen Ammodytes-Arten des Hamburger zoologischen Museums. Zool. Anz., Bd. 110, p. 216, 1935.

[2] R. Kändler, Report: *Ammodytes*. Rapp. et Proc.-Verb. des Réun. Cons. Perm. Internat. pour l'Explor. de la Mer, Vol. C 2. P., 1936, p. 75. — Idem: Beobachtungen über die Laichzeiten der *Ammodytes*-Arten in Nord- und Osteee. Zool. Anz., Bd. 118, 1937, p. 1.

that given by RAITT for his Scottish material. Near the coast *A. marinus* is caught only singly, but if one fishes away from the coast in deeper water (about 15—20 metres) it is often caught in numbers. The spawning period falls in November to February. The spawning places are not near the coasts; thus in March 1935 a large quantity of larvae and young fishes were caught in the Bornholm basin[1].

At Helgoland the mean value of vertebrae was, according to KÄNDLER, in *A. marinus* 69.9, in *A. lancea* (*"tobianus"*) 64.0.

For *A. lancea* (*"tobianus"*) KÄNDLER found the peculiar feature that in the Helgoland Bay it has two spawning periods, viz. near Cuxhaven at the mouth of the Elbe in spring (March to May) and out at the island of Helgoland in summer (August to September), and that there are two varieties which cannot, it is true, be distinguished in outward appearance, but which show considerable differences in the number of vertebrae and fin rays as will appear from the following table:

	Mean value of vertebral number	Mean value of rays in dorsal fin	anal fin	pectoral fin
Spring spawners (Cuxhaven).....	63.1	53.4	28.1	12.0
Summer spawners (Helgoland).....	64.1	54.2	27.7	12.5

[1] I can add that *A. marinus* also occurs in the Baltic off southeastern Sweden. This can be interpreted from a note by LINNÉ in his Fauna Svecica (1761, p. 109): he writes under A. TOBIANUS, which should be referred to the *A. lancea* group (cf. p. 5), as follows: "Obs. Numeravimus plures radios in pinnis, quam ichthyologus, sc. Dors. 60, pector. 15, ani 32, Caudæ 14". These figures show that the *Ammodytes* whose number of rays LINNÉ here states must be *A. marinus* (cf. p. 6). As to its native place LINNÉ states in the same place as follows: "Habitat in mari Baltico, ad australem Oelandiæ angulum copiose, & in Scania ad urbem Cimbrishamn". (It is found in the Baltic at the southern corner of Öland

Kändler also examined a sample (30 individuals) from Iceland; they proved all to belong to *A. marinus*, but the mean value showed a high number of vertebrae, viz. 71.1, which is no less than 2.6 vertebrae more than found in the same form in the inner part of the Baltic.

Bruun recently examined samples of *Ammodytes* from the Faroes and Iceland[1]. He found that the number of vertebrae falls distinctly into two groups, one with 60—66 vertebrae and another with 68—73; the average numbers are 64.5 (22 Faroese specimens) and 62.6 (52 Icelandic specimens) for the lower group and 69.7 (129 Faroese specimens) and 71.5 (97 Icelandic specimens) for the higher group (cf. his tables 2—3). The number of dorsal fin rays falls in two distinct groups, while the anal fin rays show a very slight, and the pectoral fin rays a somewhat larger overlapping. The group with the lower number of vertebrae is identified with *A. lancea*, and the group with the higher number of vertebrae with *A. marinus*. But Bruun finds, like Kändler, that the Icelandic population of *A. marinus* has a considerably higher number of vertebrae than any known elsewhere, while on the other hand the Icelandic population of *A. lancea* has a somewhat lower number of vertebrae than any hitherto examined. The Icelandic specimens therefore seem to form two races somewhat different from the European races of *lancea* and *marinus*, as Bruun writes.

On the basis of Bruun's statements in his tables 2—9

in large numbers, and in Skåne near the town Cimbrishamn). By "ichthyologus" Linné presumably means Peter Artedi who found a smaller number of fin rays in his *Ammodytes* (cf. p. 5).

[1] Anton Fr. Bruun: Observations on North Atlantic Fishes. 2. The Ammodytes lancea group. Vidensk. Medd. fra Dansk naturhist. Foren., Bd. 104, 1941, p. 329.

Table 1. *A. lancea* and *A. marinus* from the Faroes.

Number of vertebrae incl. urostyle	Percentages of specimens examined		Number of Dorsal Fin Rays	Percentages of specimens examined		Number of Anal Fin Rays	Percentages of specimens examined		Number of Pectoral Fin Rays	Percentages of specimens examined	
	A. lancea	*A. marinus*		*A. lancea*	*A. marinus*		*A. lancea*	*A. marinus*		*A. lancea*	*A. marinus*
72	..	0,8	61	..	7,1	32	..	66,7	15	..	21,4
71	..	20,2	60	..	50,0	31	..	25,9	14	..	71,4
70	..	36,4	59	..	21,4	30	5	7,4	13	22,7	7,1
69	..	31,0	58	..	21,4	29	40	..	12	72,7	..
68	..	11,6	57	4,5	..	28	45	..	11	4,5	..
67	..	..	56	18,2	..	27	10	..	..	..	..
66	13,6	..	55	31,8	..	..	..	..	..	..	..
65	36,4	..	54	31,8	..	..	..	..	..	..	..
64	31,8	..	53	13,6	..	..	..	..	..	..	..
63	18,3	..	..	..	..	..	..	..	..	..	..
Number of specimens	22	129	..	22	28	..	20	27	..	22	28
Mean ..	64,5	69,7	..	54,7	59,4	..	28,4	31,6	..	12,2	14,2

Table 2. *A. lancea* and *A. marinus* from Iceland.

Number of vertebrae incl. urostyle	Percentages of specimens examined		Number of Dorsal Fin Rays	Percentages of specimens examined		Number of Anal Fin Rays	Percentages of specimens examined		Number of Pectoral Fin Rays	Percentages of specimens examined	
	A. lancea	*A. marinus*		*A. lancea*	*A. marinus*		*A. lancea*	*A. marinus*		*A. lancea*	*A. marinus*
73	..	18,6	63	..	6,5	34	..	3,2	15	..	3,7
72	..	37,1	62	..	35,5	33	..	19,4	14	..	44,4
71	..	28,9	61	..	25,8	32	..	38,7	13	30	51,9
70	..	11,3	60	..	19,4	31	..	38,7	12	60	..
69	..	2,1	59	..	12,9	30	..	..	11	10	..
68	..	2,1	58	..	..	29	..	..	..	..	..
67	..	..	57	..	..	28	35	..	..	..	..
66	..	..	56	..	..	27	40	..	..	..	..
65	1,9	..	55	..	..	26	25	..	..	..	..
64	13,5	..	54	35	..	..	..	..	..	..	..
63	36,5	..	53	30	..	..	..	..	..	..	..
62	36,5	..	52	25	..	..	..	..	..	..	..
61	9,6	..	51	10	..	..	..	..	..	..	..
60	1,9	..	..	..	..	..	..	..	..	..	..
Number of specimens	52	97	..	20	31	..	20	31	..	20	27
Mean...	62,6	71,5	..	52,9	61,0	..	27,1	31,9	..	12,2	13,5

the surveys p. 11 and p. 12 have been prepared showing the number of vertebrae and fin rays and their percentage distribution in *A. lancea* and *A. marinus* from the Faroes (table 1) and Iceland (table 2).

At Iceland *A. lancea* seems to spawn in spring, *A. marinus* in winter, which would be in good agreement with the experience of RAITT and KÄNDLER from European waters.

Ammodytes lancea and *A. marinus* from Danish waters.

After this survey of how our knowledge of the relation between *A. lancea* and *A. marinus* has developed I give an account of an investigation which I made on 83 specimens which belong partly to the Zoological Museum of

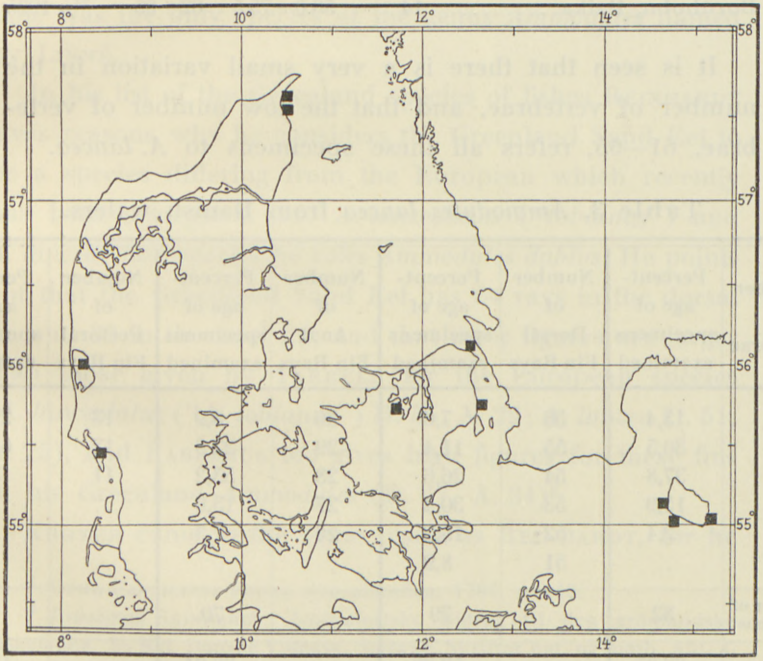

Fig. 1. ■ *A. lancea* taken in Danish waters.

Copenhagen, partly to the Danish Biological Station and lent to me by its director Dr. H. Blegvad. The specimens were taken in Danish waters from fiords and coasts in shallow water. The localities are seen in fig. 1.

The localities are as follows:

Locality	Number of specimens	Length in millimetres	Number of vertebrae	Date
Between Esbjerg and Fanø	6	112—189	62—65	$^{2-7}/_{9}$ 1935
Off Halby, Ringkøbing Fjord, 1—2 metres	1	142	63	$^{21}/_{7}$ 1920
Aalbæk beach.....	2	167.5—169	63—64	$^{8}/_{10}$ 1904
Aalbæk Bay, 1—3 metres.	4	135.5—156	63—65	$^{7}/_{11}$ 1905
Hellebæk	21	32.0—81.5	62—65	1898
Hellerup yacht harbour ..	18	57.0—81	61—65	$^{3}/_{9}$ 1940
Holbæk Fjord.....	10	53.5—61.5	62—65	
Bornholm, Hvide Odde ..	1	95	63	$^{28}/_{7}$ 1938
Bornholm, Arnager.....	6	92—107.5	62—64	$^{28}/_{7}$ 1938
Bornholm, Balka.....	14	58.0—75.5	62—65	$^{24}/_{6}$ 1935

It is seen that there is a very small variation in the number of vertebrae, and that the low number of vertebrae, 61—65, refers all these specimens to *A. lancea*.

Table 3. *Ammodytes lancea* from Danish waters.

Number of Vertebrae	Percentage of specimens examined	Number of Dorsal Fin Rays	Percentage of specimens examined	Number of Anal Fin Rays	Percentage of specimens examined	Number of Pectoral Fin Rays	Percentage of specimens examined
65	13,4	56	7,6	30	8,9	13	27,8
64	30,5	55	11,4	29	22,8	12	68,4
63	37,8	54	26,6	28	53,2	11	3,8
62	15,9	53	30,4	27	13,9	..	..
61	2,4	52	15,2	26	1,3	..	..
..	..	51	8,9	..	..	..	..
Number of specimens	82	..	79	..	79	..	79
Mean...	63,37	..	53,39	..	28,24	..	12,24

Table 3 further shows the percentage distribution of vertebrae within the range of variation and the number of fin rays and their percentage distribution.

The only aberration in the collection examined by me from Danish waters is due to a specimen collected on 8th May 1926 in the Little Belt south of Halk Hoved; it has the following figures:
Vert. 69, D. 59, A. 32, P. 14 and thus proves to be *A. marinus*.

On the Greenland *Ammodytes*.

Otto Fabricius, in his famous work on the fauna of Greenland, has already mentioned that the Sand Eel is found in Greenland waters; he calls it *A. Tobianus*[1] which at that time was the only species of the genus *Ammodytes* named by Linné.

In his list of the Greenland species of fishes Reinhardt gives reasons why he considers the Greenland Sand Eel to be a species differing from the European which recently has been segregated into *A. lanceolatus* ("*tobianus*") and *A. lancea;* this species he calls *Ammodytes dubius*. He points out that the Greenland Sand Eel has 64 rays in the dorsal fin and 33 in the anal fin, and that these figures are larger than those given by Yarrell for the European species (*A. lanceolatus* ("*A. tobianus*") D. 55, A. 29; *A. lancea* D. 51, A. 25), and Fabricius too gives high figures for these fins in his Greenland *Ammodytes* (D. 67, A. 34)[2].

Krøyer came to the same result as Reinhardt, for he

[1] Otho Fabricius: Fauna Groenlandica, 1780, p. 140.

[2] Johannes Reinhardt: Ichtyologiske Bidrag til den grönlandske Fiskefauna. D. Kgl. Danske Vidensk. Selskab, Skrifter nat. og math. Afd. 4. VII, 1838, p. 131, No. 54.

wrote[1]: "The species common in Greenland I consider absolutely distinct from both our species" (*A. lanceolatus* ("*A. tobianus*") and *A. lancea*).

Vanhöffen also[2] records the Greenland Sand Eel as a distinct species: *Ammodytes dubius* Reinhardt, since he found 66 rays in the dorsal and 35 rays in the anal fin in a specimen which he got near Umanak, while the *A. lancea* ("*A. tobianus*") occurring on the German coasts has 51—59 rays in D. and 27—30 in A.

Lilljeborg, too, has taken up the problem[3]. After having compared a Greenland specimen given him by Krøyer with one equally large from northern Norway Lilljeborg decides that *A. dubius* specifically agrees with *A. lancea*. He mentions a number of characters in which they agree adding, that the Greenland specimen has no more rays in the dorsal and anal fins, viz. 59 in the former and 31 in the latter, as the Norwegian specimen has 61 in the former and 32 in the latter. As will be seen later (p. 21) these figures for the rays in the dorsal and anal fins show that neither this Greenland specimen nor the Norwegian specimen belong to *lancea*, nor to *dubius* either.

In the paper of 1935 mentioned above, Duncker and Mohr (p. 218—19, No. 621) state that the Hamburg Museum possesses a specimen from Greenland, which was presented by Jap. Steenstrup in 1856 as *A. dubius* Reinh.; but they point out that since D. is 62 and A. 32 it differs from the description of *A. dubius* which has a larger number of rays in these fins (D. 64—67, A. 33—36). Duncker and Mohr, therefore, refer this specimen to *A. marinus*.

[1] Henrik Krøyer: Danmarks Fiske, III, 1846—53, p. 590. Note *.

[2] Drygalski: Grönland-Expedition der Gesellschaft für Erdkunde zu Berlin 1891—93, 2. Bd., I. Teil, 1897. E. Vanhöffen: Die Fische, p. 113.

[3] W. Lilljeborg: Sveriges och Norges Fiskar, II, 1891, p. 222, note.

More recently still DUNCKER and MOHR have, by means of material not only of the Hamburg Museum but also from the museums of Berlin and London, extended their studies on *Ammodytes* to comprise all the described genera and species belonging to the family *Ammodytidae*[1]. As regards the species which are of interest in this connection, these authors unite *A. marinus* with *A. dubius* into one species (p. 17), which, with certain alterations of the specific characters, is now called *Ammodytes dubius* Reinhardt and thus gets a wide-spread geographical distribution.

In the paper of 1941 mentioned above BRUUN examined some Greenland *Ammodytes* (p. 335—36). He finds that they can be divided into two well limited groups according to their vertebral numbers, one with an average number 69.9 vertebrae (12 specimens, variation 68—71 vertebrae) and another with 75.2 vertebrae (21 specimens, variation 73—78 vertebrae). The group with the low number of vertebrae he identifies with *A. marinus*, that with the higher vertebral number may be *A. dubius*, as he cannot agree with DUNCKER and MOHR who consider *A. marinus* as synonymous with *A. dubius*.

After this survey I shall give the result of an investigation made by me on the Greenland collection of the genus *Ammodytes*. There are from West Greenland more than two hundred specimens from 19 different localities distributed between $60^1/_2°$ and $72^1/_2°$ N[2]. Most of them are from fiords or near the coast; some from banks in Davis Strait (Fyllas Banke, Store Hellefiskebanke). A number of the specimens were extracted from cod stomachs.

[1] GEORG DUNCKER und ERNA MOHR: Revision der Ammodytidae. Mitteil. aus dem Zoolog. Museum in Berlin, 24. Bd., 1939, p. 8—31.

[2] *Ammodytes* is not known from the east coast of Greenland.

In the first place it can be laid down that in all the Greenland specimens teeth are absent from the vomer, and the upper jaw, or more correctly the intermaxillary, can be pushed a very considerable way forwards and downwards when the gape is widely opened. All the specimens agree in these fundamental characters with *A. lancea* and *A. marinus*. *A. lanceolatus* (subgen.: *Hyperoplus* Günther) does not occur in Greenland waters.

The vertebrae were then counted in 217 specimens. The specimens fall in two distinct groups which in my opinion correspond to Raitt's *A. marinus* and Reinhardt's *A. dubius*. In the group *A. marinus*, which comprises 38 individuals, the vertebral number lies between 67 and 72, in the group *A. dubius* which contains 179 specimens between 73 and 78. The percentage distribution appears from table 4. The mean figure in *A. marinus* is 69.39, in *A. dubius* 75.10.

Also as regards the number of fin rays the specimens fall into two groups although not so well defined. In *A. marinus* (39 specimens) the number of rays in the dorsal fin amounts to 55—62, in *A. dubius* (83 specimens) to 60—68, in the anal fin in *A. marinus* (37 specimens) 28—32, in *A. dubius* (99 specimens) 30—36, in the pectoral fin in *A. marinus* (37 specimens) 13—15, in *A. dubius* (98 specimens) 13—16. The mean figures are rather different, specially for the dorsal and anal fins:

	D.	A.	P.
A. marinus	59,05	30,27	13,84
A. dubius	64,71	33,16	14.24

If the values for vertebrae and fin rays in the Greenland *A. marinus* are compared with the figures which Raitt

Table 4. *A. marinus* and *A. dubius* from Greenland.

Number of vertebrae incl. urostyle	Percentages of specimens examined		Number of Dorsal Fin Rays	Percentages of specimens examined		Number of Anal Fin Rays	Percentages of specimens examined		Number of Pectoral Fin Rays	Percentages of specimens examined	
	A. marinus	*A. dubius*		*A. marinus*	*A. dubius*		*A. marinus*	*A. dubius*		*A. marinus*	*A. dubius*
78	..	1,1	68	..	2,4	36	..	1,0	16	..	3,1
77	..	8,4	67	..	6,0	35	..	9,1	15	13,5	27,6
76	..	27,4	66	..	20,5	34	..	28,3	14	56,8	60,2
75	..	32,4	65	..	25,3	33	..	37,4	13	29,7	9,2
74	..	24,0	64	..	31,3	32	13,5	16,2	..	..	..
73	..	6,7	63	..	9,6	31	35,1	7,1	..	..	..
72	2,6	..	62	2,6	2,4	30	27,0	1,0	..	..	..
71	18,4	..	61	10,3	1,2	29	13,5	..	..	..	..
70	21,1	..	60	30,8	1,2	28	10,8	..	..	..	..
69	39,5	..	59	23,1	..	..	..	..	..	..	..
68	10,5	..	58	20,5	..	..	..	..	..	..	..
67	7,9	..	57	7,7	..	..	..	..	..	..	..
..	..	..	56	2,6	..	..	..	..	..	..	..
..	..	..	55	2,6	..	..	..	..	..	..	..
Number of specimens	38	179	..	39	83	..	37	99	..	37	98
Mean...	69,39	75,10	..	59,05	64,71	..	30,27	33,0	..	13,84	14,24

found for the North-European *A. marinus*, it is seen that they agree closely:

Ammodytes marinus	Number of Vertebrae	Mean Number of Vertebrae	Number of Dorsal Fin Rays	Mean Number of Dorsal Fin Rays	Number of Anal Fin Rays	Mean Number of Anal Fin Rays	Number of Pectoral Fin Rays	Mean Number of Pectoral Fin Rays
Northern Europe.	67—72	69,21	56—62	59,07	28—33	30,61	12—15	13,72
Greenland	67—72	69,38	55—62	58,92	28—32	30,2	13—15	13,8

That the form which I have so far called *A. dubius* is actually identical with Reinhardt's *A. dubius* I conclude from the following:

Reinhardt points out that the Greenland Sand Eel has more rays in the dorsal and anal fins than the European species, the specimen more closely examined by him having 64 and 33 respectively; these figures fall within the values which I found above for the specimens which I called *A. dubius*, and are larger than those found in the Greenland *A. marinus*. The number of rays in D. is even so high that it is not reached by any European *Ammodytes*. Besides I think that I have found the specimen in which Reinhardt counted the fin rays; in the Zoological Museum is kept a specimen from Greenland (Catal. No. 82) from Reinhardt's time which has just the number of rays in D. and A. mentioned by Reinhardt; it is also of the same length as that stated by Reinhardt for his specimen, viz. 8 inches and 1 line Danish measurement (= 211 mm) and no other specimen kept in the Museum from Reinhardt's time reaches this length. I think I am right in regarding this specimen as identical with that mentioned by Reinhardt so that it should be considered to be his original

specimen. A Roentgen photo of this specimen, which has kindly been taken for me in the laboratory of Prof. C. M. STEENBERG, shows that it has 73 vertebrae which number falls within the limits of the specimens from Greenland here considered to be *A. dubius*. Also the Greenland specimens mentioned by FABRICIUS and VANHÖFFEN belong, on account of the high number of rays in D. (67 and 66) and in A. (34 and 35), to *A. dubius*, whereas the Greenland specimen recorded by LILLJEBORG (l. c.) is *A. marinus* (and also his specimen from northernmost Norway).

On p. 22 I give a list of the specimens of *Ammodytes* examined from Greenland with statement of locality (arranged from south to north), number of specimens, their total length, vertebral number, year of capture and date of capture, if such data exist.

As regards the distribution it will be seen from this list that *A. marinus* occurs from 7 localities, of which Lichtenau in the southern district of Julianehaab is the most southern (about 60°30′ N.) and Prøven in the district of Upernavik the most northern (about 72°20′ N.)—Sand Eels are not known farther north. *A. dubius*, on the other hand, occurs from 13 localities, and thus is the most common; its southern limit known is also in the southern district of Julianehaab at Sydprøven (about 60°25′ N.) which, like Lichtenau lies in Agdluitsokfjord; it is not known farther north than Umanak district (about 70°40′ N.). It can further be noted, as seen from the lists, that while *A. marinus* hitherto has been taken in fiords and near the coasts only, *A. dubius*, besides on the coast, was found several times in Davis Strait. However, it must be stated that the present collection is not sufficient to determine the distribution in detail.

Ammodytes marinus Raitt

Locality	Number of specimens	Length in mm	Number of vertebrae	Year and date of capture
Lichtenau Fjord	1	140	72	1906
Tunugdliarfik Fjord at Itivdlerssuak	13	72—92	69—71	1932 (8/6)
Kapisigdlit Fjord, 3—0 m	1	114	70	1925 (15/6)
Kapisigdlit Fjord, eel seine	1	114	70	1926 (28/6)
Sukkertoppen	2	117—164	69	1905
Sukkertoppen	3	94—106	70—71	1906
Godhavn	8	107—146	67—71	1902
Godhavn	3	108—134	67—69	1908 (July and August)
Godhavn	1	160	69	1911
Jakobshavn	1	165	69	1892
Jakobshavn	2	135—153	68—69	1899
Harbour of Prøven	3	94—135	69—71	1936 (17/7)

Ammodytes dubius Reinhardt.

Locality	Number of specimens	Length in mm	Number of vertebrae	Year and date of capture
Sydprøven	2	67—72	73—75	1916
Fiskenæsset, from stomach of cod	1	221	74	1915 (3/6)
Fyllas Banke, from stomach of cod	2	173—205	73—75	1924 (24/6)
Fyllas Banke, from stomach of cod	2	199—237	74—75	1925 (21/7)
Sukkertoppen	1	124	76	1885
Sukkertoppen	1	235	76	1905
Sukkertoppen	1	212	74	1909
Sukkertoppen	17	94—115	73—78	1924 (12/8)
Sukkertoppen, from stomach of cod	9	62—239	74—76	1924 (25–30/8)
Kangamiut, from stomach of cod	5	63—71	73—76	1934 (24/9)
Holsteinsborg	1	226	76	1899
Store Hellefiskebanke, 21 ftms	1	93	76	1912 (10/7)
Store Hellefiskebanke, 85—100 m W	3	62—70	75—76	1925 (23/6)
Store Hellefiskebanke, 100 m W	2	89—91	73—76	1925 (25/6)
68°05′ N., 54°37′ W. 80 m W	16	45—74	73—78	1924 (18/9)
Egedesminde	16	53—74	73—77	1895
Egedesminde, from stomach of cod	14	47—64	74—77	1936 (20/9)
Egedesminde, from stomach of cod	8	56—114	74—77	1936 (28/9)
Manitsok, from stomach of cod	19	55—102	74—76	1936 (29/9)
Manitsok, from stomach of cod	5	92—113	74—75	1936 (30/9)
Ikamiut	50	43—57	73—76	1905
Christianshaab	4	42—50	74—77	1901
Umanak	1	56	76	1879

It appears that *A. dubius* is most abundant, since 179 specimens have been available for counting the vertebrae, against only 38 specimens of *A. marinus*.

Finally, it can be noted, that *A. dubius* seems to attain a more considerable size than *A. marinus;* according to the lists there are among *A. dubius* from different localities specimens of 226, 237 and 239 mm against only 160, 164 and 165 mm among *A. marinus*.

For the reader's information a chart sketch is given of the distribution of *A. marinus* and *A. dubius* (fig. 2).

Among the characters by which *A. dubius* (*A. marinus* included) differs from *A. lancea*, DUNCKER and MOHR (l. c. 1939, p. 117) state that *A. dubius*, besides the two ventro-lateral cutaneous folds, has a lower ridge in the middle of the belly, while such a median fold is absent in *A. lancea*. I have examined a large number of specimens of *A. marinus* and *A. dubius* from Greenland to clear up this point and found the following: the belly between the two ventro-lateral folds is divided by two longitudinal grooves into a median part and two lateral portions. In the median part which runs from the isthmus to the anus a light (white or yellow) streak is seen along the midline. In several Greenland specimens this skin fold rises to a conspicuous ridge, and it must be such specimens which DUNCKER and MOHR had before them. But in other specimens which I have examined, it is only anteriorly and posteriorly, or only anteriorly or in the middle, but not on the rest of the stretch, that the median skin fold rises to a ridge; finally, there are many specimens on which the streak dwindles, becomes thin, thread-like or fine as a hair; in addition it is often sunk into a furrow in the median line of the belly and hardly visible or, at any rate, only by means of a

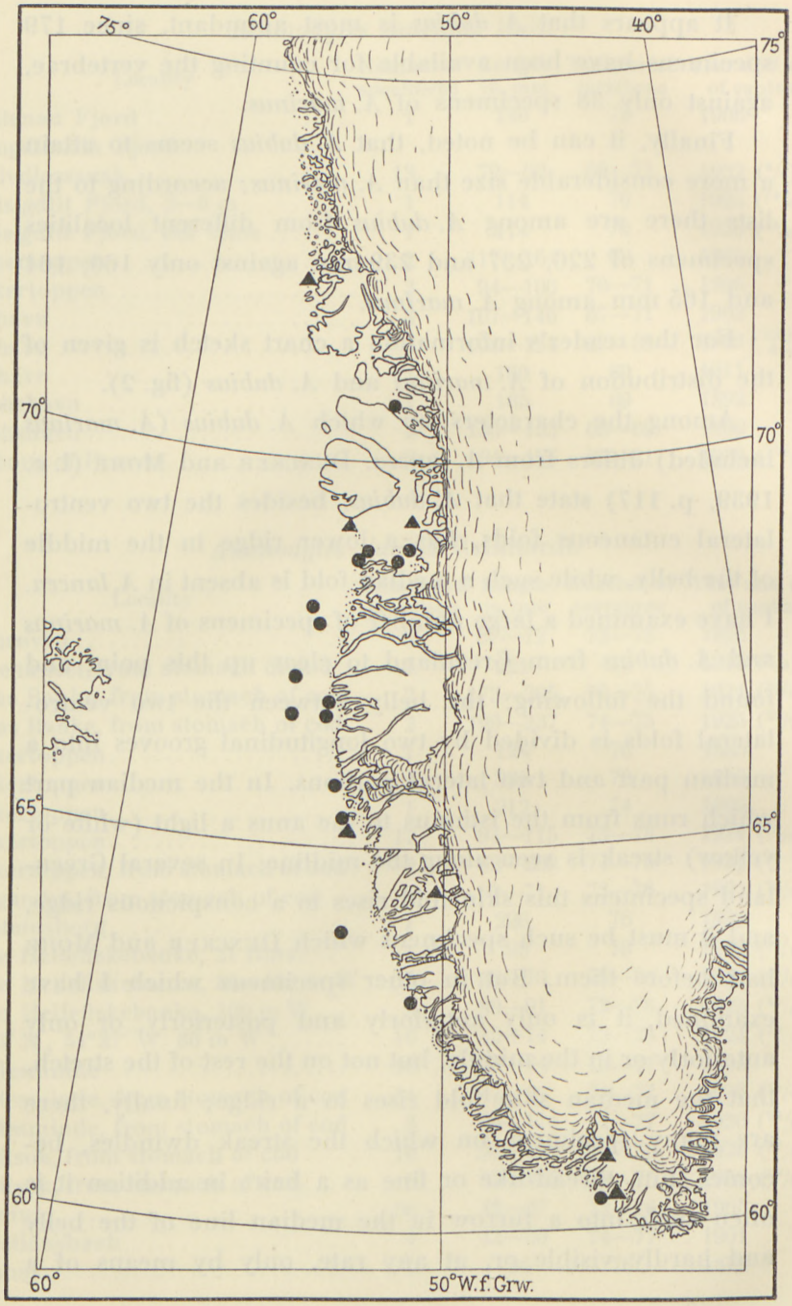

Fig. 2. Chart sketch of West Greenland showing localities where *A. marinus* (▲) and *A. dubius* (●) have been taken.

lens. I doubt therefore whether so variable a feature can be of any systematic value. As regards *Ammodytes lancea*, Danish specimens have, in the area between the two furrows, a corresponding, whitish or yellowish line; as a rule it is not very distinct, but may sometimes be slightly projecting. In *Ammodytes lanceolatus* a similar line is found.

Nor could BRUUN distinguish between *A. lancea* and *A. marinus* by aid of the character used by DUNCKER and MOHR, i. e. the absence or presence of a median fold; this fold was noticed in both species but at the same time specimens devoid of it were also found in both species.

As regards this feature I note that the middle area itself in which the ridge is found may be elevated, forming a longitudinal fold on either side of the median ridge, but in many cases the middle area is flat, sometimes even lowered.

Among the Greenland specimens of *Ammodytes* there is one measuring 144 mm sent down in 1911 by Mr. M. PORSILD, the leader of the Danish arctic station in Godhavn. It has a number of vertebrae and fin rays different from all other Greenland specimens, viz. vert. 65, D. 56, A. 29, P. 13, and thus is referable to *A. lancea*. It is hardly accidental that *A. lancea* occurs, though evidently rarely, just at Godhavn, since among the 13 specimens examined from this place there is no *A. dubius*, but only 12 *A. marinus* and the 13th specimen which is that mentioned above with still lower numbers of vertebrae and fin rays. All the 12 specimens have low figures for *A. marinus;* no other locality in Greenland shows such low figures for this species, having Vert. 67 (3 specimens) and D. 55 (1 specimen), 56 (1 specimen) and 57 (2 specimens).

Concluding remarks:

Do *Ammodytes lancea*, *A. marinus* and *A. dubius* represent seperate species, or are they only subspecies of one single species?

Hitherto I have examined the present collection on the assumption that it represents three species: *A. lancea*, *A. marinus* and *A. dubius*[1]. We will now enquire whether this supposition is justifiable.

In the first place we give in table 5 a survey of the

Table 5.

	Number of Verte-brae	Number of Dorsal Fin Rays	Number of Anal Fin Rays	Number of Pectoral Fin Rays
A. lancea				
Denmark (Jensen)	61—65	51—56	26—30	11—13
The Baltic (Kändler) ...	61—65	..	..	..
Scotland (Raitt).....	60—66	51—56	26—31	11—13
The Faroes (Bruun)	63—66	53—57	27—30	11—13
Iceland (Bruun)	60—65	51—54	26—28	11—13
Variation...	60—66	51—57	26—31	11—13
A. marinus				
The Baltic (Kändler)....	66—72	..	..	..
Scotland-Faroes (Raitt) .	67—72	56—62	28—33	12—15
The Faroes (Bruun)	68—72	58—61	30—32	13—15
Iceland (Bruun)	68—73	59—63	31—34	13—15
Greenland (Jensen)	67—72	55—62	28—32	13—15
Variation...	66—73	55—63	28—34	12—15
A. dubius				
Greenland (Jensen)	73—78	60—68	30—36	13—16
Variation...	73—78	60—68	30—36	13—16

[1] As mentioned, Duncker und Mohr however united *marinus* and *dubius* into one species.

different authors' statements of numbers of vertebrae and fin rays, found by analysis of hundreds of specimens.

If we regard the number of vertebrae and fin rays we find that there is no sharp limit between the three species,

Table 6.

	Mean Number of Vertebrae
A. lancea	
Denmark (Jensen)	63,37
The Baltic (Kändler)	63,1
Cuxhaven (Kändler)	63,1
Helgoland (Kändler)	64,1
Scotland (Raitt)	63,4
The Faroes (Bruun)	64,5
Iceland (Bruun)	62,6
	62,6—64,5
A. marinus	
The Baltic (Kändler)	68,5
Helgoland (Kändler)	69,9
Scotland-Faroes (Raitt)	69,2
The Faroes (Bruun)	69,7
Iceland (Kändler)	71,1
Iceland (Bruun)	71,5
Greenland (Jensen)	69,4
	68,5—71,5
A. dubius	
Greenland (Jensen)	75,1
	75,1

since the figures overlap, least for the vertebrae, more for the unpaired fins; intermediate individuals are found.

If, on the other hand, we regard the average figures for vertebrae (table 6) they are seen to be well separated. The mean figures for fin rays stated by the various authors

are also different from one species to the other as will be seen from table 7.

Thus it is evident that by calculating the mean figures for a large number of specimens, both as regards vertebrae and fin rays, limits can be fixed for the three species. And

Table 7.

	Mean Number of Dorsal Fin Rays	Mean Number of Anal Fin Rays	Mean Number of Pectoral Fin Rays
A. lancea			
Denmark (Jensen).....	53,39	28,24	12,24
Scotland (Raitt).....	53,40	27,96	12,05
The Faroes (Bruun)	54,7	28,4	12,2
Iceland (Bruun).....	52,9	27,1	12,2
	52,9—54,7	27,1—28,4	12,05—12,24
A. marinus			
Scotland-Faroes (Raitt)..	59,07	30,61	13,72
The Faroes (Bruun)	59,4	31,6	14,2
Iceland (Bruun).....	61,0	31,9	13,5
Greenland (Jensen).....	59,05	30,27	13,84
	59,05—61,0	30,27—31,9	13,5—14,2
A. dubius			
Greenland (Jensen).....	64,71	33,16	14,24
	64,71	33,16	14,24

it is on this basis that *A. marinus* was recently segregated from *A. lancea* (see p. 7).

In my opinion, however, too much stress has been put on the importance of the average figures, seen from a species point of view. If we regard e. g. the Greenland *A. marinus* (table 4) the most frequent variant for the number of vertebrae is 69, while that for *A. dubius* is 75, consequently, the average figures for the vertebrae of the two species must be widely separated, while the plus

deviators in *A. marinus* and minus deviators in *A. dubius* meet, being in one case 72 and in the other 73 vertebrae. Similar conditions are found in *A. lancea* and *A. marinus;* it is seen from RAITT's table p. 367 that the most frequent variant for the vertebral number is 64 and 69 respectively, while the plus and minus deviators lie so near each other as 66 and 67. But an establishment of species in a Linnean sense merely on differences in average numerical values of such organs as vertebrae and fin rays is in my opinion not well founded, and can only rarely be carried through in practice, the presumption being that a very large number of specimens is available to allow the count of vertebrae which is the most important criterion. Nor is it possible to show other distinguishing marks; the numerical characters are not accompanied by other differences in the other structures of the body, which show good agreement in all the specimens. In museums the designation *A. lancea* s. lat. might probably as a rule only be used.

On the other hand, the variation in the organs which have been considered cannot be regarded as accidental; there is generally a correlation between the various characters: to a low number of vertebrae in *A. lancea* corresponds a low number of fin rays, and with the increasing number of vertebrae in *A. marinus* and still more in *A. dubius* the number of fin rays is increased correspondingly. I am therefore of the opinion that the three divisions should be retained, not as species but only as subspecies of the species *Ammodytes lancea* Cuvier, and they should be called *A. lancea lancea* Cuvier, *A. lancea marinus* Raitt and *A. lancea dubius* Reinhardt.

If one asks what the reason or reasons may be why subspecies have arisen in *Ammodytes lancea*, an inves-

tigation of the external conditions under which the respective subspecies live seems to give some hints:

It is mentioned above that *Ammodytes lancea* has been taken in large numbers in Danish fiords and near the coasts in shallow water, while only a single specimen of *A. marinus* was taken off the coast (Little Belt). According to Kändler *A. lancea* is a coastal form in the western and intermediate Baltic, while *A. marinus* occurs at some distance from the coast in deeper water. According to the same author *A. marinus* is found in the North Sea at 20 to 40 metres depth, while *A. lancea* lives in the coastal waters. According to Raitt *A. lancea* near Scotland occurs in the coastal waters only, while *A. marinus* is also met with offshore, from Scotland to St. Kilda, Shetland and the Faroes. On the basis of Bruun's records (l. c. p. 330—31) I find that as well at the Faroes as at Iceland *A. lancea* occurs in shallow water, *A. marinus* mainly in deeper waters, as is seen from the list below:

	Depth metres	Specimens *A. lancea*	Specimens *A. marinus*
The Faroes	6—0	22	8
The Faroes	58—100	0	121
Iceland	0—5	52	2
Iceland	34—54	0	89

As regards the vertical distribution there is thus on the whole a distinct difference between *A. lancea* and *A. marinus*, the former being found in fiords and near the coasts in shallow water, while the latter occurs away from the coast in deeper water.

Moreover, these subspecies have a different spawning season: Raitt says that *A. marinus* spawns in early spring, while *A. lancea* ripens in summer. According to Kändler

the spawning period occurs in winter for *A. marinus*, for *A. lancea* in spring and summer. According to BRUUN *A. marinus* at Iceland seems to spawn in winter, *A. lancea* in spring.

Finally, *A. dubius* is a pronounced arctic subspecies, since it occurs at Greenland, being the predominant form there. Characteristic is the high number of vertebrae and fin rays, a feature which is not unique as among some other species of fishes there may be forms in which correlation has been found between a low temperature and high number of vertebrae and fin rays.

Within the subspecies there may be a tendency to a further segregation into systematic subdivisions, races. KÄNDLER found in *A. lancea* the following peculiar feature: At Cuxhaven, which is situated near the mouth of the Elbe, it spawns in spring, while 58 km northwest hereof, at Helgoland, it spawns in late summer, and these two populations differ from each other by a distinct difference in the number of vertebrae and fin rays (cf. p. 9). Moreover, according to BRUUN, *A. marinus* of Iceland has a higher number of vertebrae and fin rays than in Europe, a feature which he is no doubt justified in connecting with the colder conditions; it may presumably be said that the Icelandic *A. marinus* in some degree forms a transition to the Greenland *A. dubius*, though it is more closely related to *marinus* than to *dubius* (this is found by studying BRUUN's fig. 3 and my fig. 3 which was made on the same principle, with addition of the Danish population and a more numerous representation of the Greenland population).

The general impression is, in my opinion, that the different conditions under which the species *Ammodytes lancea* lives, e. g. depth, temperature and salinity of the

water, spawning time, contribute towards the formation of subspecies and races, which in this respect can be considered as ecologically conditioned.

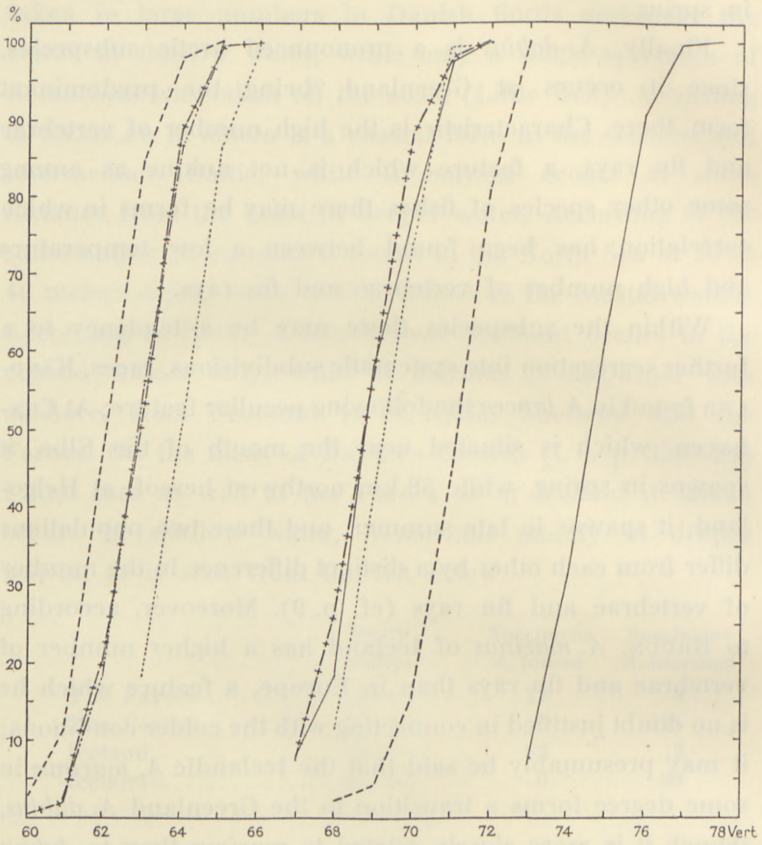

Fig 3.

Fig. 3 gives the number of vertebrae in *A. lancea* (to the left), *marinus* (in the middle), and *dubius* (to the right) for the different areas in summation curves: —·—·— Denmark, —+—+— Scotland and the Faroes, ····· the Faroes, ----- Iceland, —— Greenland. These curves show the difference between the individual groups better than

ordinary distribution curves. The calculation of the summation curve is made as follows: For *A. lancea* from Denmark we have e. g. the following distribution according to number of vertebrae:

	Number of vertebrae	61	62	63	64	65
Frequency	Percentage.....	2,4	15,9	37,8	30,5	13,4
	Summations	2,4	18,3	56,1	86,6	100

The summation curve is formed by adding to each percentage the preceding summation, as indicated in the example above; each figure thus indicates the percentage of individuals which has the particular number of vertebrae plus those below that figure. The highest figure thus will always be 100.

Mr. Paul Hansen, M. Sc. has assisted me in the calculations, and Miss Esther Hansen has counted the vertebrae and fin rays on alizarine stained specimens. I thank them both for their valuable assistance.

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