MUSEUM RERUM NATURALIUM REYKJAVÍKENSE
NÁTTÚRUGRIPASAFNIÐ Í REYKJAVÍK

The Post-larval Stages of Sand-eels (Ammodytidae) in Faroe, Iceland and W-Greenland Waters

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WITH
2 PLATES AND 54 FIGURES IN THE TEXT

ACTA NATURALIA ISLANDICA
VOL. I – NO. 7

REYKJAVÍK
1951

PRINTED IN ÍSAFOLDARPRENTSMIÐJA H.F. 1951

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INTRODUCTION

It has been known for a long time, that the species of sand-eels are of great importance as food for various economically valuable fishes, such as cod, haddock and plaice. Areas where these fishes are abundant are extremely fertile fishing grounds and owe their fertility in a high degree to the presence of shoals of these fishes. This has been emphasized by *Sæmundsson* (1926) with regard to Faxaflói on the south-west coast of Iceland.

Until quite recently our knowledge on the biology of sand-eels has been very scanty indeed and to this day the systematic position of the various species has received little attention. Although the present paper is mainly concerned with the larval stages of sand-eels it will be necessary to sum up the main results of the investigations on adults in later years, which have supplied most interesting information about these species of fishes.

A fresh impetus to the study of the species of *Ammodytidae* was given by a paper by *Raitt* (1934) on a new species of Lesser Sandeel in Scottish waters, which he called *Ammodytes marinus* Raitt. Previously only four species were recognized as occurring in Northern Atlantic waters, viz.: *A. lanceolatus* Lesauvage, *A. lancea* Cuvier,[1]) *A. dubius* Reinhardt and *Gymnammodytes semisquamatus* (Jourdain) (*A. cicerelus* Rafinesque partim).

The new species described by *Raitt* is closely related to *A. lancea* (s. *tobianus*) and *A. dubius* as it lacks teeth on the vomer and has

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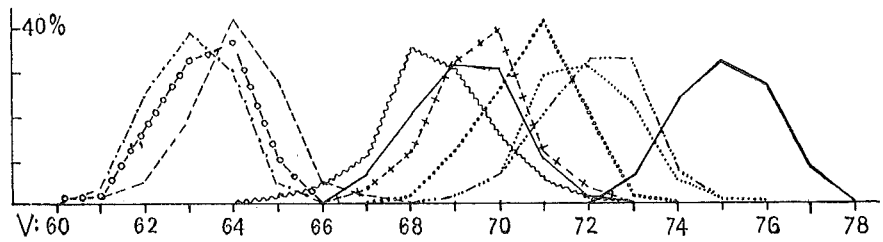
1) The name *A. tobianus* L. is commonly used for this form, but according to *Jensen* (1941), „*Linné's A. Tobianus* is a mixture of the two forms which were later established as *A. lancea* Cuvier and *A. marinus* Raitt". *Jensen's* practice of calling this form *A. lancea* Cuvier is followed in the present paper.

a protrusible mouth. In fact, it is indistinguishable from these species by other characters than the meristic ones, *A. marinus* holding an intermediate position, having higher number of vertebrae than *A. lancea,* but lower than *A. dubius.* On the other hand it differs most clearly from *A. lanceolatus,* which has teeth on the vomer and a mouth that is not protrusible.

Since *Raitt* published his results there has been a great deal of controversy as to the specific validity of *A. marinus. Duncker & Mohr* (1939) consider it as synonymous with *A. dubius* Reinhardt. *Bahr* (1935) is not satisfied that *A. marinus* constitutes a species of its own, but considers it a race in the „rassenkreis" of *A. lancea* (s. *tobianus*). *Bruun* (1941) leaves the question open „whether we ought to speak of three species or subspecies" (l. c., p. 336), while *Jensen* (1941) considers *A. lancea* divided into three subspecies, viz. *A. lancea lancea* Cuvier, *A. lancea marinus* Raitt and *A. lancea dubius* Reinhardt. *Kändler* (1941) is of the opinion that *A. marinus* is probably identical with *A. dubius* without discussing this problem further. Lastly *Soleim* (1945) found specimens, with vertebral and fin ray numbers intermediate between *A. marinus* and *A. dubius,* as seen from the graph reproduced here (fig. 1) which shows the frequency distribution of vertebral numbers in various areas where these forms of the *lancea*-group have been examined.

The present work started as an endeavour to elucidate the seasonal occurrence of sand-eel post-larvae off Iceland, based on the catches



Frequency distribution of vertebrae.

- *A. lancea,* spring spawner. North Sea. (According to KÄNDLER.)
- *A. lancea,* (According to RAITT.)
- *A. lancea,* autumn spawner. North Sea. (According to KÄNDLER.)
- *A. marinus.* Baltic. (According to KÄNDLER.)
- *A. marinus.* (According to RAITT.)
- Lesser Sandeels from Bergen harbour, Norway.
- Lesser Sandeels from Grense Jakobselv, Finnmark, Norway.
- Lesser Sandeels from Lavonjarg, Tana, Finnmark, Norway.
- Lesser Sandeels from Fosnavåg, Sunnmøre, Norway.
- *A. dubius.* Greenland. (According to JENSEN.)

Fig. 1. (From *Soleim* 1945).

made by the Danish research vessels in Icelandic waters by means of stramin net hauls. The preliminary treatment of these collections pretty soon showed various discrepancies in the accounts formerly published, wherefore I decided to widen the scope of the work by including collections from the Faroes as well as „Dana"s samples taken in W-Greenland waters in 1925. These collections were most cordially placed at my disposal by Mr. *Å. Vedel Tåning,* Dr. Phil., the keeper of the Dana-collections, who aided me in every possible way during the preliminary work which was carried out in the Marine Biological Laboratory in Copenhagen. It was my hope to be able to carry out some further investigations in Icelandic waters after having returned to Iceland, but so far various other duties have prevented this.

I should like to take the opportunity to thank Mr. *Páll Ragnarsson* who assisted me in various ways in Copenhagen and who has drawn the diagrams. To Mr. *Poul M. Winther* I am indebted for the drawings of the post-larval stages and the vomer. My thanks are also due to Mr. *Erik Bertelsen,* M. Sc., for preparing the vomer for drawing. To Mr. *G. H. Vevers,* B. A., I owe a debt of gratitude for correcting the manuscript.

PART I.

IDENTIFICATION OF POST-LARVAL STAGES OF AMMODYTIDAE

1. PREVIOUS RESULTS.

The larvae of sand-eels were first identified and described by *McIntosh* (*McIntosh* 1889, 1890, *McIntosh & Prince* 1890). They are characterized by the elongated form of the body, the anus lying just behind the middle of it. The pigmentation is also of good use for the identification. The larvae have both dorsally and ventrally behind the anus a row of black chromatophores and ventro-laterally, above or on the side of the intestinal canal, a row of black chromatophores is easily discernible.

Ehrenbaum (1904, 1909) and *Ehrenbaum & Strodtman* (1904) distinguished between larvae of two species of sand-eels, viz. *A. tobianus* L. and *A. lanceolatus* Lesauv. *Ehrenbaum* (1909 p. 299) points out that „Die Unterscheidung der Entwicklungsformen beider Arten bietet sehr grosse Schwierigkeiten, die bisher durchaus nicht gelöst sind, obwohl die Laichzeiten keineswegs zusammenfallen". According to this author the spawning of the former species occurs in the autums in about 20 m. depth, the eggs of both species being submersal, sticking to sand grains on the bottom. Some larvae emerge already in the autumn, but the great majority not till the beginning of the following year, in January—March. On the other hand, the spawning period of *A. lanceolatus* is during May—August.

The results arrived at by *Ehrenbaum* were reached both by means of rearing experiments and observations on larvae caught in plankton hauls.

In 1920 *Ford* published a paper on the post-larval stages of *Ammo-*

dytes captured in Plymouth waters. He found two types of larvae represented, viz. type A, characterized by small teeth in the upper jaw, the black dorsal chromatophores reaching to anus only at a length of 20—27 mm., and displaying two black chromatophores just in front of the tail. This type was identified as belonging to *A. lanceolatus*. Type B was characterized by stronger pigmentation the dorsal row stretching from tail to head at a length of 9—10 mm., and identified by him as *A. tobianus*.

Raitt's discovery of *A. marinus* stimulated the German biologist *R. Kändler* to re-examine the whole question of the reproduction of the *Ammodytes*-species in the North and the Baltic Seas and in 1941 he gave a comprehensive survey of his results, as mentioned above.

In this work he states that it is possible to distinguish the larval stages of *A. lancea* from those of *A. marinus* and in the identification of the larvae of *A. lanceolatus* he agrees with *Ford*. With this account at my disposal I thought it a very straightforward matter to identify the larvae in the Icelandic collections, as it had previously been shown by *Bruun* (1941) that it was precisely these species of *Ammodytes* which had been observed in Icelandic waters.

The larvae described by *Kändler* (1941, p. 63—66, fig. 3 a—d.) are characterized as follows:

1) *A. marinus*. Dorsal row of chromatophores only slightly developed, does not reach anus until about 23 mm. size. Already in earliest stages the ventro-lateral chromatophores are very conspicuous in a row on both sides of the intestine.

2) *A. lancea*. Dorsal pigment is much more strongly developed than in *A. marinus* stretching towards the head at a size of 10 mm. This larva has no ventro-lateral chromatophores but peritoneal pigment is distinguishable above the intestine.

3) *A. lanceolatus*. Differs most conspicuously from all other *Ammodytes* larvae by having tooth-like structures in the upper jaw. Upper jaw also longer than in the other species.

2. AMMODYTES-LARVAE IN THE NORTH ATLANTIC COASTAL AREA.

The curious fact emerged from my examination of the large „Dana" collections from Icelandic waters, that only two of the types described by *Kändler* were present.

The first type is shown on Pl. I, in various degrees of development.

Larva 4,5 mm. in length (Pl. I, fig. 1).

The earliest pelagic stage still has a yolk sac. The caudal fin shows the beginnings of the rays, but neither the dorsal nor the ventral fins show any signs of these. The larva is very slender. The form of the head is almost circular the snout being short and blunt. The eyes are especially large. The pectorals are fan-shaped without true rays.

The pigmentation is on the whole weak. The ventral side of the yolk sac has a single row of about 4 chromatophores. The ventro-lateral pigment, on both sides of the intestine, consists of *large stellate chromatophores*. The postanal pigment is well developed and *extends to the tip of the notochord*. Dorso-caudally only one chromatophore is usually developed.

Larva 6 mm. in length (Pl. I, fig. 2).

The yolk sac has disappeared. The head is more oblong in shape. The rays of the caudal fin are now distinct.

The pigment is similar to that of the younger stage, but dorso-caudally one to four chromatophores are present.

Larva 11 mm. in length (Pl. I, fig. 3).

The shape of the larva is similar to the preceding stages and the end of the notochord is still unbent. The antero-ventral pigment does not reach far behind the pectoral fins and dorso-caudally there is a varying number of chromatophores and these are *confined to the hindmost part*. Subdorsally there are now chromatophores along the notochord, sometimes reaching to the head (not shown in the drawing). The fins are embryonic in character.

Larva 16 mm. in length (Pl. I, fig. 4).

The larva is now somewhat different in shape. The head is longer and the mouth larger. The fins, with the exception of the pectoral fins, have developed true rays, but not throughout. The notochord is bent upwards.

The ventro-lateral pigment is very distinct on the sides of the intestine. Caudally there is *a distinct row of chromatophores at the base of the caudal fin*. The dorsal pigment has a varying number of chromatophores, but *it does not reach the anus and is on the whole weak*.

Larva 33 mm. in length (Pl. I, figs. 5 and 6).

The fin rays are now fully developed, but otherwise the larva is very similar to the preceding stage. The dorsal pigment reaches anteriorly to the anus or thereabout.

It will be seen that this type agrees with the larval form described by *Kändler* as *A. marinus*.

The second type is shown on Pl. II, about the same sizes being drawn.

Larva 6 mm. in length (Pl. II, fig. 1).

Compared with the type described above, the same size is further developed, i. e. has about the same degree of development as an 11 mm. long post-larva. The most distinct differences are:

1. The post-larva is comparatively shorter and higher. 2. The ventro-lateral pigment is confined to the upper side of the intestine (peritoneal pigment) and has not such large chromatophores. 3. The caudal pigment is totally absent. 4. The dorsal pigment is more conspicuous and consists of 4—6 chromatophores.

Larva 11 mm. in length (Pl. II, fig. 2).

This stage differs from the preceding as there is now strong dorsal pigment developed reaching beyond the anus. Otherwise it is similar.

Larva 16 mm. in length (Pl. II, fig. 3).

The dorsal pigment reaches forward to the head, while the subdorsal pigment is less developed than in the first type.

Larva 25 mm. in length (Pl. II, fig. 4 and 5).

The stage is similar to the preceding but a few inconspicuous chromatophores are now developed at the base of the caudal fin.

There can be no doubt that this is the same larva as *Ford* and *Kändler* describe as *A. tobianus (s. lancea)*.

After having examined the collections from the Faroes and W-Greenland is was evident that the first type is the only one which is found in Greenland waters, and constitutes the main bulk of the material from Iceland and the Faroes. The second type was found both off the Faroes and Iceland, but is far less frequent than the first one.

According to this explantion of the observations the post-larvae of *A. lanceolatus* do not occur in the coastal waters off the Faroes, Iceland and Greenland. This is extremly surprising, as we know that

TABLE I.

Number of vertebrae in post-larvae of Ammodytes in Faroe, Iceland and Greenland waters.

No of vertebrae	*lancea*-group			*lanceolatus*	
	Faroes	Iceland	Greenland	Faroes	Iceland
78			2		
77			9		
76			18		
75		1	17		
74		16	16		
73		40	4		
72		51			
71	21	42			
70	49	13		1	
69	59	4		7	4
68	29			9	27
67				2	18
66				2	2
65		1			
64		10			
63	1	30			
62		13			
61		2			
60		1			
A. lanceolatus No.				21	51
M				68,14	67,65
m				±0,204	±0,096
A. lancea dubius No.			66		
M			75,27		
m			±0,165		
A. lancea marinus No.	159	167			
M	69,35	71,97			
m	±0,075	±0,092			
A. lancea lancea No.	1	57			
M		63,03			
m		±0,116			

adults of this species have been frequently found in Faroese and Icelandic waters. The only other explanation of the facts related above, is that some mistake was made by *Ford,* when he identified the post-larva of *A. lanceolatus* and that *Kändler* did repeat this error. It seemed to me a possibility, in view of the close relationship between the adult forms of the *lancea-group* (*A. dubius, marinus* and *lancea*), that they might have the same, or very smilar larval types, and then the larvae of the present material identified as *A. lancea (s. tobianus*) would in reality belong to *A. lanceolatus.* This possibility was examined by counting the vertebrae in those larvae, where staining was possible. An experiment showed that larvae above 20 mm. in length could be stained, by means of the alizarine method.

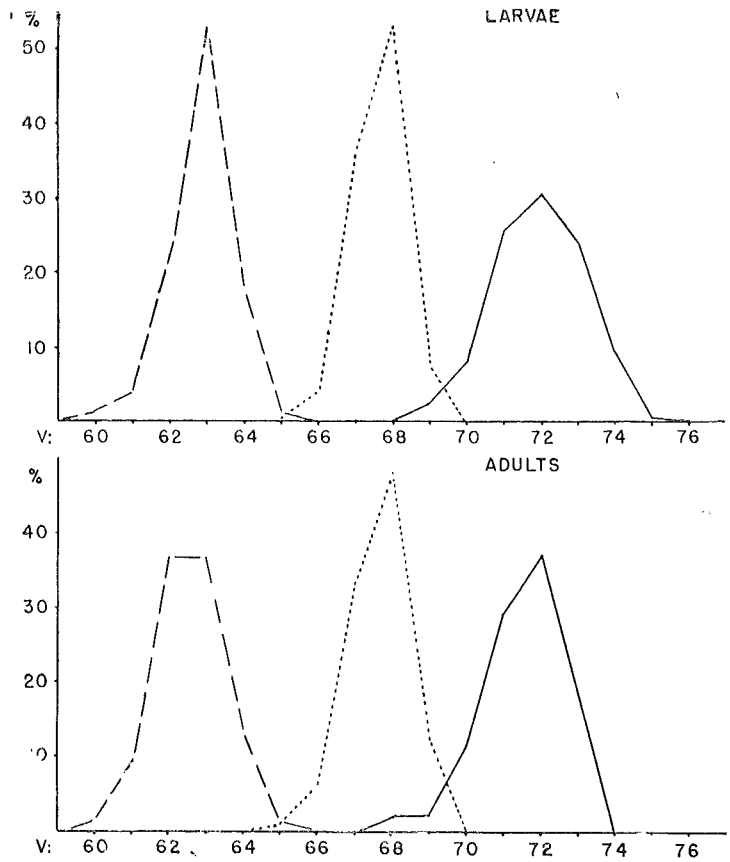


Fig. 2. Frequency distribution of vertebrae of *A. lanceolatus* (....), *A. lancea lancea* (- - -) and *A. lancea marinus* (—) in Icelandic waters.

3. VERIFICATION BY COUNTINGS OF VERTEBRAE.

The material was already divided into the two larval types just mentioned and the result of the countings is shown in table I and figs. 2—5.

As to the material from Icelandic waters, the first type (*lancea*-group, see table I) is clearly divided into two forms with vertebral numbers between 60 and 65 (M = 63,03) and 69 and 75 (M = 71,97) respectively. The second type (*lanceolatus* table 1) shows vertebrae numbers between 66 and 69 (M = 67,65). It is thus intermediate between the other two.

The frequency distribution of vertebral numbers in larvae and adults of *A. lancea, A. marinus* and *A. lanceolatus*[1]) is shown in fig. 2. Considering the rather limited number of specimens examined the agreement could not be expected to be closer. It seems evident that the second type, with vertebral numbers between 66 and 69, must belong to *A. lanceolatus,* while the first type comprises the two forms of the lancea-group, *A. lancea* and *A. marinus.* The mean vertebral number in post-larvae of *A. marinus* is, however, higher than that of the adults. Probably the explanation is that all the adult specimens were caught off the south and west coasts of Iceland where vertebral numbers tend to be lower than off the colder north and east coasts, where some of the post-larvae were caught.

The result of the countings on the Faroese specimens is also shown in table I. Most of the larvae are evidently larvae of *A. marinus,* while only one specimen had 63 vertebrae and is thus *A. lancea.*

1) As to number of vertebrae in adult specimens of *A. lancea* and *A. marinus,* I have used the figures given by *Bruun* (1941) and *Jensen* (1941). With regard to *A. lanceolatus* I have examined specimens from Iceland and the Faroes. The statistical analysis of the various characters gave the following result:

	Vertebrae								Anal fin rays					
	65	66	67	68	69	70	n	M	28	29	30	31	n	M
Heimaey (Iceland) ..	1	7	35	51	13		107	67,64	4	12	27	8	51	29,76
Hvalböur (Faroes) ..		1	6	22	20	1	50	68,28	1	10	24	15	50	30,06

	Dorsal fin rays									Pectoral fin rays				
	53	54	55	56	57	58	59	n	M	12	13	14	n	M
Heimaey (Iceland) ..	1	2	4	19	17	6	1	50	56,42	3	41	8	52	13,10
Hvalböur (Faroes) ..			3	7	19	14	5	48	57,22	4	42	4	50	13,00

As regards A. marinus the mean number of vertebrae is lower in Faroese than in Icelandic waters, viz 69,35 off the Faroes and 71,96 off Iceland. This is in accordance with the general rule that vertebral numbers are higher farther north. It is remarkable that the opposite is the case as regards A. lanceolatus. The mean vertebral number is higher in the Faroese (M = 68,14) than in the Icelandic (M = 67,65) specimens.

The graphs on fig. 3 show the frequency distribution of vertebral numbers in post-larvae and adults, which were caught in Faroese waters. If we compare these graphs with the Icelandic ones it will be seen how clearly the differences mentioned emerge. And at the same time it will be noticed that the variation polygons of post-

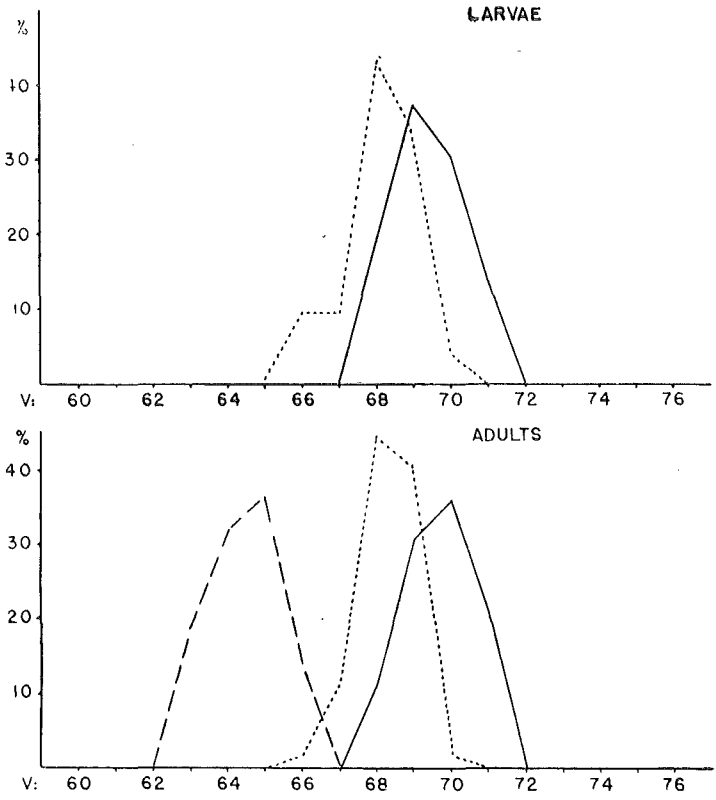


Fig. 3. Frequency distribution of vertebrae of *A. lanceolatus* (....) *A. lancea lancea* (----) and *A. lancea marinus* (—) in Faroese waters.

larvae and adults, show a close agreement. I consider this as a definite proof as to the identity of the larval types described above.

It has already been mentioned that in W-Greenland waters larvae of the *lancea*-group type only have been observed. From the investigation of *Jensen* (1941) we know that two closely related forms are found here, viz., *A. marinus* and *A. dubius,* with mean vertebral numbers of 69,39 and 75,10 respectively.

Unfortunately most of the material from W-Greenland waters was unsuitable for staining as the larvae were either too small or the vertebrae did not react to the staining process. A sample was, however, put at my disposal by Mr. *Paul M. Hansen,* Dr. phil., and the vertebrae of these specimens could be counted as shown in table I, which also includes the poor result of the 1925 catches of „Dana". All the larvae evidently belong to *A. dubius* as will be seen by the graph fig. 4, which shows the frequency distribution of vertebrae

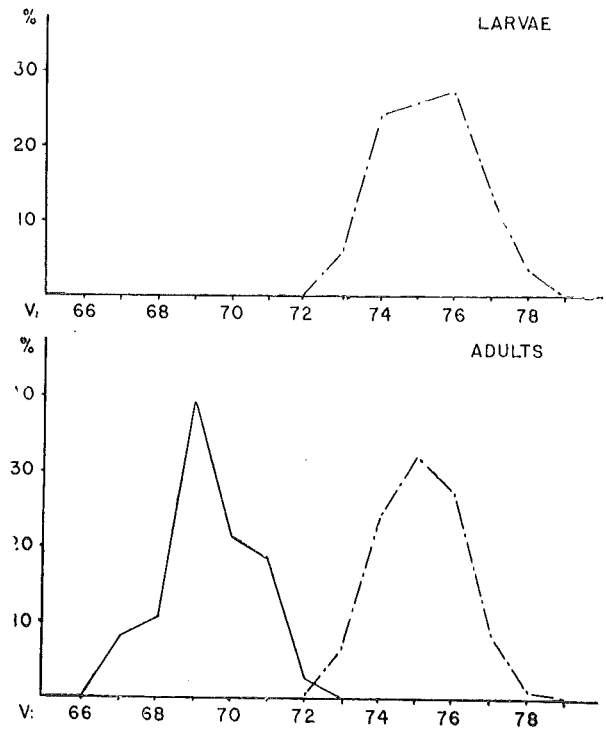


Fig. 4. Frequency distribution of vertebrae of *A. lancea marinus* (—) and *A. lancea dubius* (— · —).

in post-larvae and adults respectively. As to the adults I have made use of *Jensen's* (1941, p. 19, table 4) results. The graph shows a high degree of similarity between the frequency distribution in vertebral numbers of adults and post-larvae.

I have not been able to find any reliable characteristic, which distinguishes these post-larvae from the post-larvae of the lancea-group in Icelandic and Faroese waters. In the earliest stages the chromatophores in the tail region are perhaps a little more conspicuous, but as I have no specimens from Greenland waters, which with certainty can be referred to *A. marinus* I cannot say if this is of any use in distinguishing the larvae of the two forms. The conspicuousness of the chromatophores may also vary in different areas, as has been shown by *Schmidt* (1906, p. 4) with regard to *Gadus callarias* and *G. merlangus.*

Now it is of great interest to note that in *A. marinus* we observe a non-conformity to rule as to vertebral numbers in the Iceland and W-Greenland specimens, viz., *those of the Icelandic specimens are higher than those observed in the W-Greenland ones.* Curiously enough this is not pointed out by *Jensen (1941).* I made a note of this same phenomenon in connection with *A. lanceolatus* from the Faroes and Iceland. The data available do not give a satisfactory explanation of this phenomenon.

4. CRITICAL REMARKS AND CONCLUSIONS.

a. The species problem.

The observations related above justify some remarks on the species problem of *Ammodytes.* It seems significant that it has now been proved that *all the three forms of the lancea-group have the same larval type, or at least a very similar one. Schmidt* (1909) has convincingly shown how the arrangement of chromatophores in Gadoid larvae reveals the relationship of the species to each other. That *A. lancea, A. marinus* and *A. dubius* have the same larval type seems therefore to indicate that *we have here to deal with the same species divided into races or subspecies as maintained by Bahr* (1935), *Jensen* (1941) and *Soleim* (1945).

But even the validity of these subspecies can be questioned as has already been done by *Soleim* (1945). Off Finmark he found vertebral numbers intermediate between those of *marinus* and *dubius.*

In the Icelandic material many specimens fall within the variation range of the Greenland *dubius* as will be seen from the graph fig. 5., which shows the frequency distribution of vertebral numbers of Icelandic *A. marinus* larvae and Greenland *A. dubius* larvae. Further it will be seen by comparing fig. 1 and 5 that the Finmark and Icelandic specimens show very similar frequency distribution in vertebral numbers.

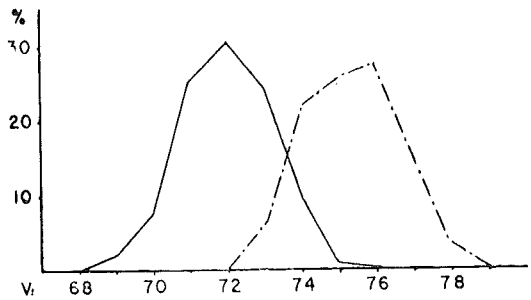


Fig. 5. Frequency distribution of vertebrae of *A. lancea marinus* (—) and *A. lancea dubius* (— · —) in Icelandic and W-Greenland waters respectively.

This seems too definite to ignore. *A. marinus* Raitt and *A. dubius* Reinhardt seem to be very vaguely defined varieties. But in order to understand fully their relationship, a closer analysis of the Greenland larvae seems desirable. On the other hand *A. lancea lancea* seems more distinct as we have so far no observations of intermediate vertebral numbers between this form and *A. lancea marinus*.

In accordance with *Jensen* (1941) we will therefore reckon three subspecies to the lancea-group, viz. *A. lancea lancea* Cuvier, *A. lancea marinus* Raitt and *A. lancea dubius* Reinhardt, but as stated, the two last-named are probably synonymous and should be called *A. lancea dubius* Reinhardt.

The variation in vertebral numbers inside the *lancea*-group is surprisingly great, i. e. between 60 and 78 vertebrae. Certainly this should be made an object of further study by those scientists who have an opportunity to do experimental work. Experiments are obviously needed in order to understand fully the importance of external factors which most probably influence the racial characteristics of the individual, and this unusual large variability should give excellent opportunity to study the effect of these factors in detail.

b. To which species does the larva, previously described as A. lanceolatus, belong?

If we examine the earlier descriptions of post-larval stages of *Ammodytes* in the light of our present knowledge it will be seen that *Ehrenbaum* (1904) was correct in his identification of the larvae of *A. lanceolatus*. His drawing showing a 12,5 mm. long larva of this species agrees well with the larva shown on Pl. II, fig. 3, which is of a similar size. *Ehrenbaum* (1909, p. 300), remarks that this larva has a row of black chromatophores from the head to the base of the caudal fin.

There is every reason to suppose that the peculiar larval type described by *Ford* as *A. lanceolatus* did not occur in *Ehrenbaum's* material at all, the characteristics being so peculiar that they would undoubtedly have been observed by this conscientious scientist.

Neither have any larvae of this type been observed in the collections from Faroe, Iceland and Greenland waters. The only specimens of this type, which I have seen, were from hauls in the Firth of Forth made by the research vessel „Thor", but these were very much damaged and had lost all the pigment.

If seems probable that these larvae belong to *Gymnammodytes semisquamatus* which appears to be a common species in Scottish waters (*Raitt* 1934, *A. cicerelus*) and this larval type is evidently almost as common as *A. lanceolatus* in the Channel, according to *F. S. Russell* (1930—1937).

c. Conclusions.

The present results are especially damaging to *Kändler's* (1941) work, which in other respects is of great value. He does not seem to have stained and counted vertebrae in any post-larvae except some of *A. marinus,* which would not show anything suspicious as these post-larvae are correctly identified. These countings are given in his table II, pp. 140—141. He does not mention any other countings on post-larvae.

It is not my intention to reconsider the data on the occurrence of post-larval stages of *Ammodytes* previously published. I must leave this task to scientists who have collections at disposal from the areas in question. Only some main conclusions will be drawn here for further consideration.

These conclusions of the present work are:

1. All previous data on post-larvae of *A. lancea marinus* must apply to *A. lancea lancea* as well.
2. The previous data on post-larvae of *A. lancea lancea* (s. *tobianus*) must be referred to *A. lanceolatus*.
3. The data on post-larvae of *A. lanceolatus* must be referred to another species of *Ammodytidae,* not definitely known as yet, but most probably *G. semisquamatus*.

APPENDIX TO PART I.

Since the above paper was written, a new contribution to our knowledge regarding the post-larval stages of sand-eels has appeared, viz., *P. G. Corbin's* and *Vidya Vati's* paper: The post-larval sandeels (*Ammodytidae*) of the Celtic Sea and Plymouth area, (1949). This contribution necessitates some additional remarks on the problems encountered in identifying the post-larval stages of *Ammodytidae*.

In the beginning of 1947 the present writer had the opportunity to compare notes with Mr. *Corbin* and Miss *Vati*, who were then engaged in studies on post-larval stages of *Ammodytidae* in Plymouth waters. Subsequently the present paper was sent to the Plymouth laboratory and in turn Mr. *Corbin* was kind enough to inform me of the different results they had arrived at, sending figures of the post-larval stages together with stained and unstained specimens of the post-larval type identified by *Ford* (1920) and *Kändler* (1941) and also by *Corbin & Vati* (1949) as *A. lanceolatus*.

The vomerine teeth of A. lanceolatus.

As previously mentioned (p. 9) the post-larvae in question have a very characteristic appearance, having tooth-like structures in the upper jaw. Now *Corbin & Vati* made the significant observation that these post-larvae have vomerine teeth and this fact led them to the conclusion that we have here an unmistakeable characteristic of *A. lanceolatus*. In their paper (l. c., p. 294) they state: „*A. lanceolatus* appears to be the only species in which the post-larvae can with certainty be linked with the adult", and further (l. c., p. 301):

„It is of some importance to draw attention to the vomerine teeth in the post-larva of *A. lanceolatus*. They are a primary specific character of the adult. But as far as is known, there is no reference in the literature to their presence in the post-larva which thus establishes a complete chain of specific characters in the development of *lanceolatus* from the late larva to the adult".

The specimens sent to the present writer by Mr. *Corbin* show the vomerine teeth very distinctly, and this seemed a very strong point in favour of the interpretation of the post-larval stages given by *Ford, Kändler* and *Corbin & Vati*. On the other hand, serious discrepancies appear between the mean vertebral numbers of post-larvae and adults, when this interpretation is applied. This will be further discussed below.

The vertebral numbers of the forms of the *lancea*-group have hitherto been the sole means of distinguishing these „species", and they cannot, in my opinion, be ignored. Besides, it was extremely difficult to imagine how the consistent figures, given in the preceding paper, could be explained, if this interpretation was applied to the post-larval stages examined by the present author.

As the mean vertebral numbers of the post-larvae of *A. lancea, marinus* and *dubius* were compared with figures given by *Bruun* (1941) and *Jensen* (1941), Miss *Esther Hansen,* who had done these countings, was asked to check some of our countings of the vertebral numbers in the post-larvae. This checking showed full agreement.

Unfortunately a series of different sizes of *lanceolatus* post-larvae, as identified by the present writer, was not available, the largest post-larvae being about 25 mm. in size. By closer examination of these post-larvae, small protuberances on the lateral parts of the vomer, could be seen, indicating what might be considered a beginning to vomerine teeth. But this could not be definitely established, as the further development of these protuberances could not be followed through intermediate sizes to the adult. However, this matter was considered of such importance, that it was resolved to postpone the publication of this paper until the observation mentioned could be verified.

During a short stay in Copenhagen in January 1950 the writer got the opportunity to examine intermediate sizes of *A. lanceolatus,* kindly put at his disposal by the Danish Biological Station. A con-

tinous series of post-larvae, assigned by the present writer to *A. lanceolatus,* together with intermediate sizes and adult specimens was now available. The vomer were cut from the stained specimens and the development of the vomerine teeth could now be easily followed from the small protuberances previously observed to the large pointed teeth of the adult. For comparison the vomer of a specimen sent by Mr. *Corbin* and identified by him as *A. lanceolatus,* was also examined and drawn, and further the vomer of *A. lancea* (*tobianus*) post-larvae and adults were also treated. The drawings figs. 6 and 7 show the result of this examination.

A. lanceolatus. **(Figs. 6 a—d, 7 a).**

The protuberances on the vomer that are seen to develop into the vomerine teeth are visible in post-larvae of about 20—25 mm. size. It will be seen that from this stage on there is a small median cleft into the frontal part of the vomer, and this cleft developes further with increasing size.

A. lancea lancea. **(Figs. 7 c—d).**

The difference in the structure of the vomer of *lancea* and *lanceolatus* are clearly seen in larvae of about 30 mm. size. The frontal part of the vomer is pointed in the *lancea* post-larvae, where the median cleft is situated in the *lanceolatus* larvae.

Ammodytes sp. **(A. lanceolatus of Ford, Kändler and Corbin & Vati). (Figs. 7 b).**

This larva has distinct teeth on the vomer as pointed out by *Corbin & Vati,* but the frontal part of the vomer is pointed, similarly as in the *lancea* post-larvae. It is difficult to imagine that this type of vomer can be linked with the subadult and adult *lanceolatus* having a median cleft in this place.

The question as to the identity of the characteristic post-larvae with teeth on the upper jaw and vomerine teeth, is still open. As far as is known, no species of *Ammodytidae,* other than *A. lanceolatus,* has teeth on the vomer. This seems contrary to the hypothesis that these post-larvae belong to *G. semisquamatus* as suggested in the preceding paper.

On the other hand these larvae probably belong to a species of *Ammodytidae,* judged by their outer appearance and pigmentation. Without being able to examine the further development of these

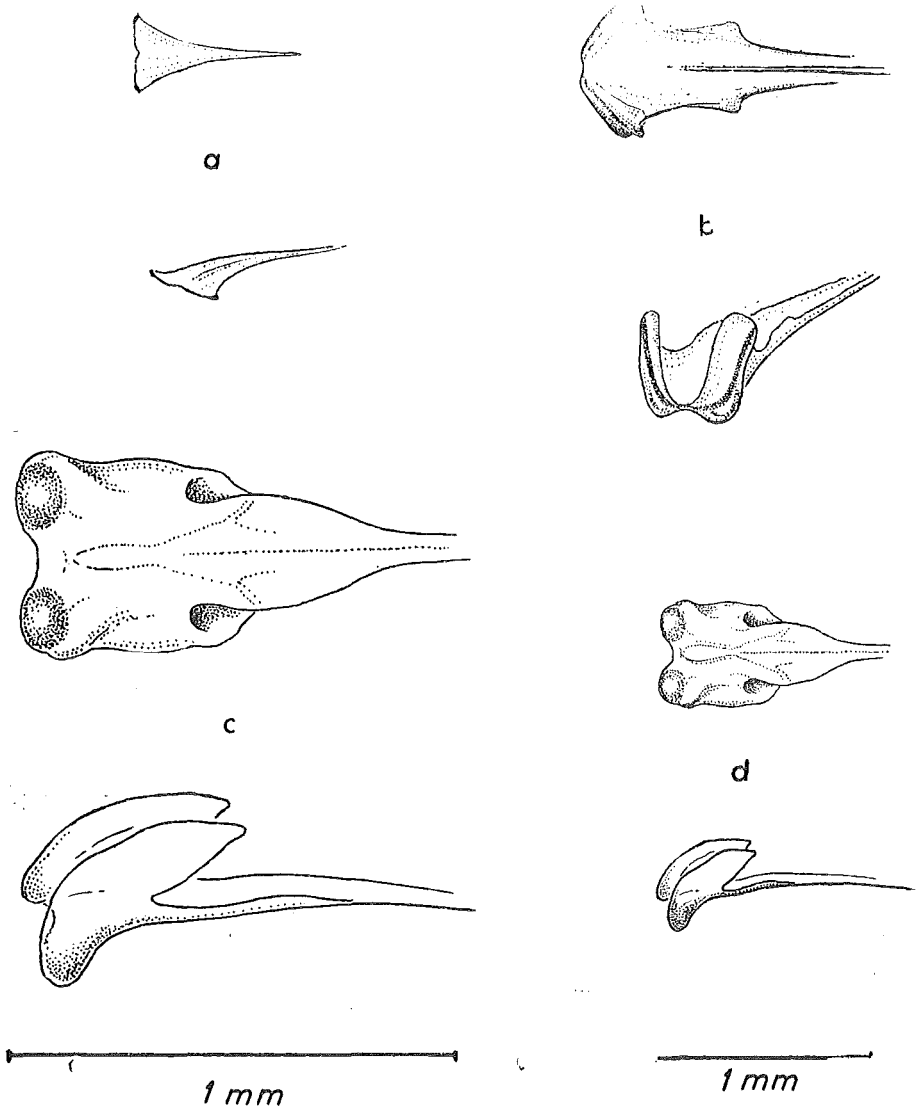


Fig. 6. The development of vomerine teeth in *A. lanceolatus*, above : ventral view, below : fronto-lateral view.

a. Vomer in postlarva 23 mm. Dana stat. 4246, 31/7 1931.
b. Vomer in postlarva 57 mm. Thor stat. 806, 10/4 1906.
c. Vomer in adolescent 72 mm. Thor stat. 806, 10/4 1906.
d. Same as c, but drawn at the same magnification as fig. 7 a.

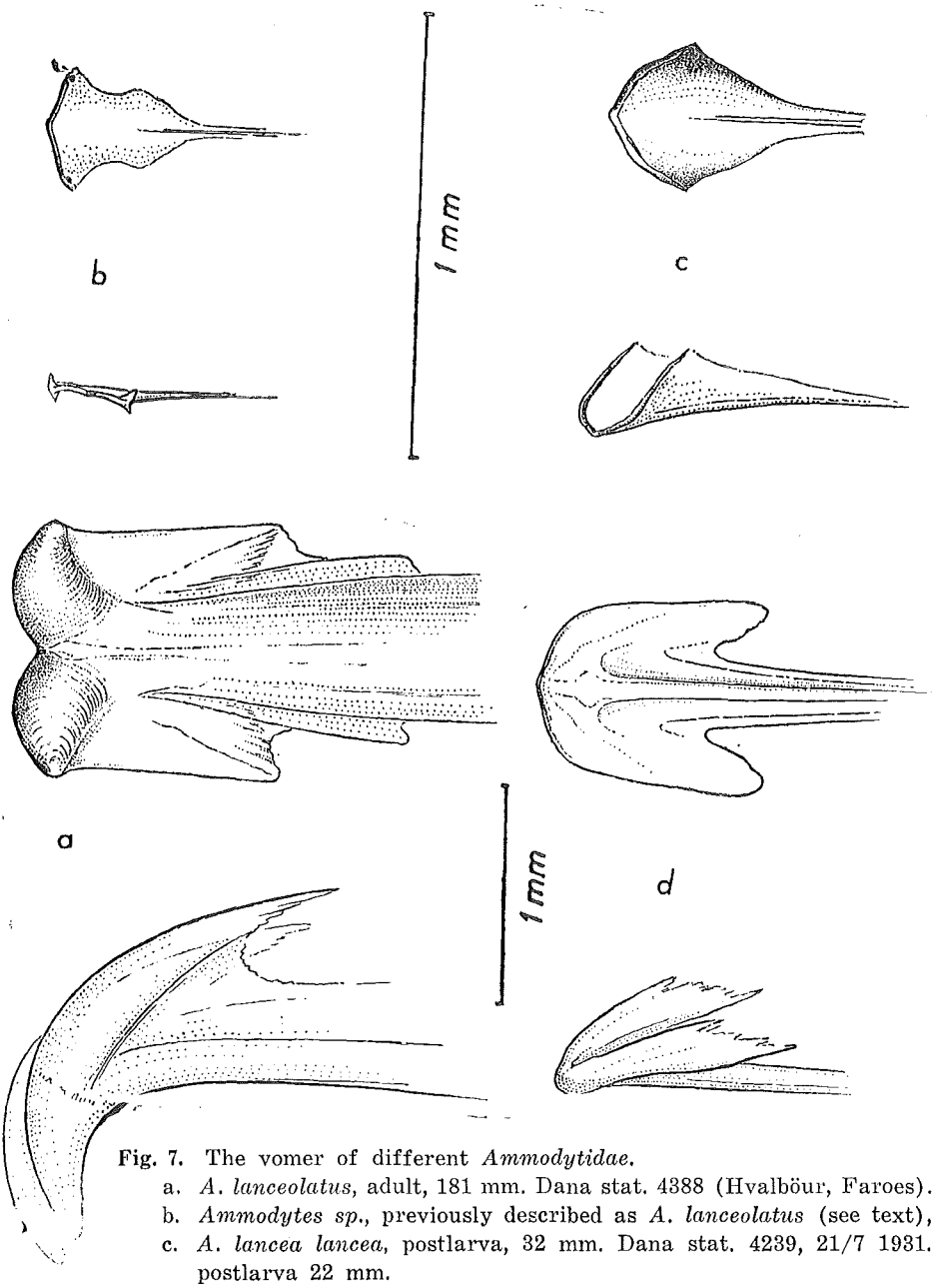


Fig. 7. The vomer of different *Ammodytidae*.
a. *A. lanceolatus*, adult, 181 mm. Dana stat. 4388 (Hvalböur, Faroes).
b. *Ammodytes sp.*, previously described as *A. lanceolatus* (see text),
c. *A. lancea lancea*, postlarva, 32 mm. Dana stat. 4239, 21/7 1931. postlarva 22 mm.
d. *A. lancea lancea*, adult, 121 mm. Dana stat. 5811.

teeth, the present writer would suggest that we have here to do with larval teeth that are not present in the adult. The vertebral counts support this suggestion as will be shown below.

Vertebral numbers.

The vomerine teeth observed in the post-larvae, which *Ford, Kändler* and *Corbin & Vati* identify as *A. lanceolatus* seemed so conclusive, as a specific characteristic of this species, that the latter authors based their identification of post-larvae on this character. Various observations recorded in their own paper, especially regarding differences in vertebral numbers between post-larvae and adults are either left unexplained or taken as signs of insufficient investigations. Some of the vertebral numbers are in fact so inconsistent as to cause grave doubts in the minds of the authors themselves, whether the identifications are correct.

With regard to the mean vertebral number of Plymouth post-larvae of *A. lancea* (or *tobianus*), which the present author identifies as the post-larvae of *A. lanceolatus, Corbin & Vati* state: „But the mean of the post-larvae suggest, despite the smallness of the sample, that what are here taken to be *tobianus* do not in fact belong to this species". (l. c., p. 303). Adults taken off Exmouth have the mean 64,15 $\pm$ 0,134 (n = 52), while the Plymouth post-larvae have the mean 66,33 $\pm$ 0,360 (n = 12). If we refer the post-larvae to *A. lanceolatus* this anomaly is explained. The vertebral numbers of *A. lanceolatus* are then as can be seen from table II. This table is rearranged from *Corbin & Vati's* table II (l. c., p. 302), according to the present authors views on the post-larval stages of *Ammodytidae,* with the addition of the records given in the present paper.

The mean values for southern and northern areas respectively, differ considerably, as could be expected, but they are consistent when collections from similar areas are compared.

It was suggested that the vomerine teeth in the larvae previously identified as *A. lanceolatus* might be larval teeth, not present in the adult. These larvae would then probably belong to *G. semisquamatus*, not previously recognized, although the species seems to be fairly common or perhaps abundant in English and Scottish waters. Otherwise the absence of the larvae of this species in these waters is another anomaly that needs an explanation. The vertebral numbers

are in accordance with this assumption, as seen by table II. Further investigations on the development of these larvae will undoubtedly give a clear answer to this problem.

As seen from table II the mean vertebral numbers for post-larvae of *A. lancea, marinus* and *dubius*, recorded in the present paper, tally excellently with the mean numbers known for the adults. In fact these figures give very strong support to the present writers' identification of the post-larval stages of *Ammodytidae.*

It is evident that if the conclusions which have been supported in the present paper, are correct, all recent data on the biology of the sand-eels must be reconsidered. Both *Kändler's* and *Corbin & Vati's* papers contain many contradictory observations, which the authors have difficulties in explaining. Insufficient investigations are most often made responsible for the discrepancies in the accounts. Thus it seems extremely difficult to account for the absence of post-larvae of *A. lanceolatus* and *G. semisquamatus* where adults of these species are very abundant. It was stated in the present paper that the larval form hitherto considered as that of *A. lanceolatus*, does not occur off the Faroes or Iceland, where adults of these species are frequently found. The frequency of adult sand-eels in the Baltic was according to *Kändler's* investigations as follows (l. c., Tabelle 22, p. 116) : *A. lanceolatus* 1298 specimens, *A. marinus* 1076 specimens and *A. tobianus* 3693 specimens. But in the catches of post-larval *Ammodytes* from this area he found only one post-larva of *A. lanceolatus*, 23 mm. in length. In view of the extensive collections of post-larvae from various months, which were at this authors' disposal, insufficient investigations do not explain this anomaly convincingly.

The results recorded in this paper also make *Kändler's* investigations on the seasonal races of *A. tobianus* very problematic. From the records of the post-larvae it would seem as if *A. lanceolatus* and not *A. tobianus* had seasonal races. But investigations which the present author has no chance of carrying out are needed to ascertain the possibility of this. It is to be hoped that such an investigation will be carried out by scientists who have collections at disposal for such studies. Further investigations along the lines given in the present paper may in fact greatly change our views regarding the biology of the sand-eels in the North Sea and the Baltic.

TABLE II.

The Number of Vertebrae in the North Atlantic Species of Ammodytidae.

(The data are rearranged from table II, *Corbin & Vati* 1949, p. 302, and *Corbin 1950*, p. 67, with addition of present records).
N.-no of specimens, M- mean no of vertebrae, m- standard error of mean, ad- adults, p-l- post-larvae.

Area	Author	Synonyms	No	M	m	Range
	A. lanceolatus					
Baltic (ad)	Kändler 1941	lanceolatus	126	66,73	± 0,076	65–69
North Sea (ad)	— —	lanceolatus	293	66,85	± 0,047	65–69
Plymouth (p-l)	Corbin & Vati 1949	tobianus	12	66,33	± 0,360	64–69
Iceland (ad)	Present records	lanceolatus	107	67,64	± 0,054	65–69
— (p-l)	Present records	lanceolatus	51	67,65	± 0,096	66–69
Faroes (ad)	Present records	lanceolatus	50	68,28	± 0,085	66–70
— (p-l)	Present records	lanceolatus	21	68,14	± 0,204	66–70
	A. lancea lancea					
Exmouth (ad)	Corbin & Vati 1949	tobianus	52	64,15	± 0,134	62–66
Denmark (ad)	Jensen 1941	lancea	82	63,37	± 0,108	61–65
Northern North Sea (ad)	Raitt 1934	tobianus	199	63,37	± 0,063	60–66
North Sea,						
spring spawners (ad)	Kändler 1941	tobianus	274	63,09	± 0,057	61–65
autumn spawners (ad)	— —	tobianus	566	64,08	± 0,043	61–68
Baltic						
spring spawners (ad)	— —	tobianus	961	63,17	± 0,033	60–67
autumn spawners (ad)	— —	tobianus	566	63,49	± 0,051	60–67
Faroes (ad)	Bruun 1941	lancea	22	64,45	± 0,200	63–66
Iceland (ad)	— —	lancea	52	62,56	± 0,125	60–65
— (p-l)	Present records	lancea	57	63,03	± 0,116	60–65
	A. lancea marinus					
Celtic Sea (p-l)	Corbin & Vati 1949	marinus	45	68,56	± 0,128	67–70
Central Baltic (ad)	Kändler 1941	marinus	114	68,90	± 0,107	66–72
East Baltic (ad)	— —	marinus	291	68,50	± 0,066	65–72
North Sea,						
German Bight (ad)	— —	marinus	67	69,75	± 0,124	67–72
Northern North Sea	Raitt 1934	marinus	205	69,21	± 0,079	67–72
Faroes (ad)	Bruun 1941	marinus	129	69,67	± 0,084	68–72
— (p-l)	Present records	marinus	159	69,35	± 0,075	68–71

Area	Author	Synonyms	No	M	m	Range
S-Norway, Bergen (ad)	Soleim 1945	marinus	200	69,53	± 0,076	67–72
N-Norway,						
Grense Jakobselv (ad)	— —	marinus	200	71,74	± 0,088	69–75
— — (ad)	— —	marinus	168	72,06	± 0,088	69–74
Tana (ad)	— —	marinus	89	71,88	± 0,119	69–74
Iceland (ad)	Kändler 1941	marinus	31	71,13	± 0,217	69–73
— (ad)	Bruun 1941	marinus	97	71,53	± 0,112	68–73
— (p-l)	Present records	marinus	167	71,97	± 0,092	69–75
Greenland (ad)	Jensen 1941	marinus	38	69,39	± 0,195	67–72
	A. lancea dubius					
W-Greenland (ad)	Jensen 1941	dubius	179	75,10	± 0,082	73–78
— (ad)	— 1944	dubius	53	75,07		?–80
— (p-l)	Present records	dubius	66	75,27	± 0,165	73–78
	G. semisquamatus					
W-Scotland and N-North Sea (ad)	Corbin & Vati 1949	semi-squamatus	51	68,16	± 0,144	65–70
Plymouth (ad)	Corbin 1950	semi-squamatus	108	68,44	± 0,098	66–72
Celtic Sea (p-l)?	Corbin & Vati 1949	lanceolatus	52	68,08	± 0,082	64–70
	A. species IV					
Celtic Sea (p-l)	Corbin & Vati 1949	A. species IV	28	72,00	± 0,175	70–74

PART II.

DISTRIBUTION OF POST-LARVAL STAGES OF AMMODYTES

In the following account data from the 2 m stramin net hauls will mainly be used for the sake of comparison. This net was used in the years 1924—1939. A considerable number of samples dates back to 1903—1908 when the Petersen young fish trawl was operated and these will be used as supplement if they show some striking differences or are derived from other parts of the year than the more recent ones. The „Dana" collections have previously been made an object of a thorough treatment as regards herring fry (*Tåning* 1936 a, 1936 b). I have followed rather closely his treatment of the numerical data, as this seems an advantage for the comparison. The records are in the following arranged according to time of capture.[1])

1) Because of limited funds it is not possible to print the detailed lists of capture, with position of localities, length measurements of post-larvae and particulars on the hauls. A transcript of these will be made available to those specially interested. A request should be adressed to Atvinnudeild Háskólans, Fiskideild, Reykjavík.

Fig. 8—15. Distribution of the postlarval stages of the Lesser Sandeel (the *lancea*-group. $\frac{120}{274}$: number of postlarvae caught with 15 and 65 mw. respectively. Greater wirelengths (mostly 100 mw.) indicated by bracketed numbers + post-larvae not present. Number per 15 min. haul.

Fig. 8. Cruise March 27th — April 7th 1935. Fig. 9. May 6th — 18th 1938. Fig. 10. May 19th — 22nd 1925. Fig. 11. April 24th — May 6th 1934. Fig. 12. May 24th — 31st 1924. Fig. 13. May 25th — 31st 1934. Fig. 14. May 22nd— June 9th 1926. Fig. 15. June 21st — 23rd 1932.

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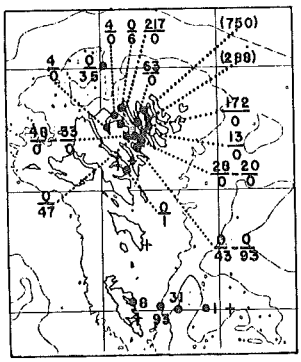

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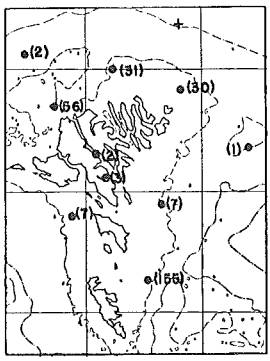

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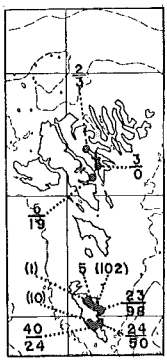

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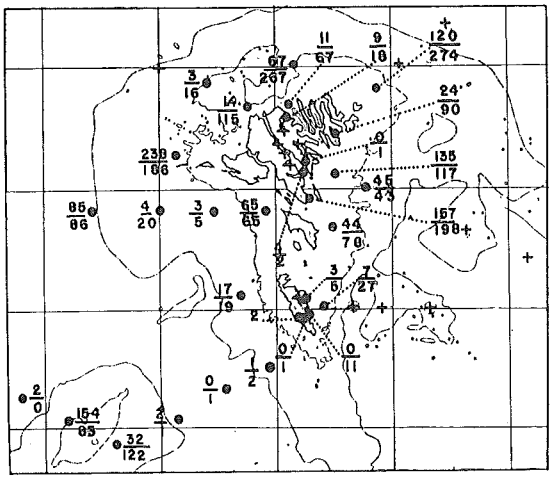

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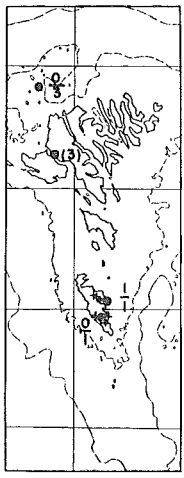

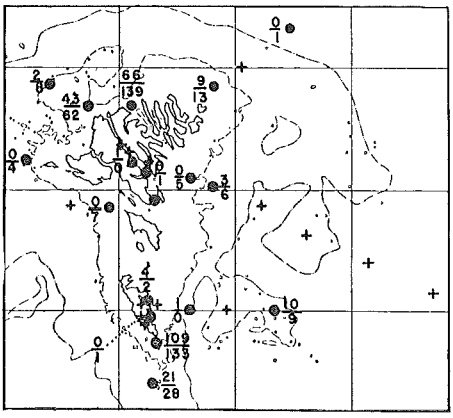

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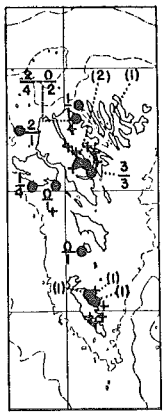

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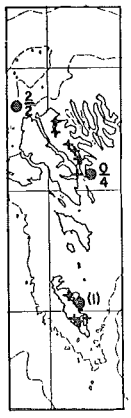


15

1. THE LANCEA-GROUP.

A. THE FAROES.

March—April.

The chart fig. 8 shows the stations investigated 27/3—7/4 1935 and the results of the hauls. The larvae were all recently hatched, the average size being 4,5—5,7 mm. Most of the stations lie inside the fjords and it will be seen that *an extensive hatching takes place here at this time of the year.*

The highest numbers were found on three stations between Kunoy and Borðoy 750, 282 and 172 specimens per 15 minutes haul.

May.

From the last part of April and the beginning of May 1934 (fig. 11), a fine series of samples is at disposal, both from the fjords and the outer areas, including the Faroe Bank. The average size of the larvae is about 10 mm, the range being from newly hatched larvae about 5 mm. long to about 16 mm. long larvae.

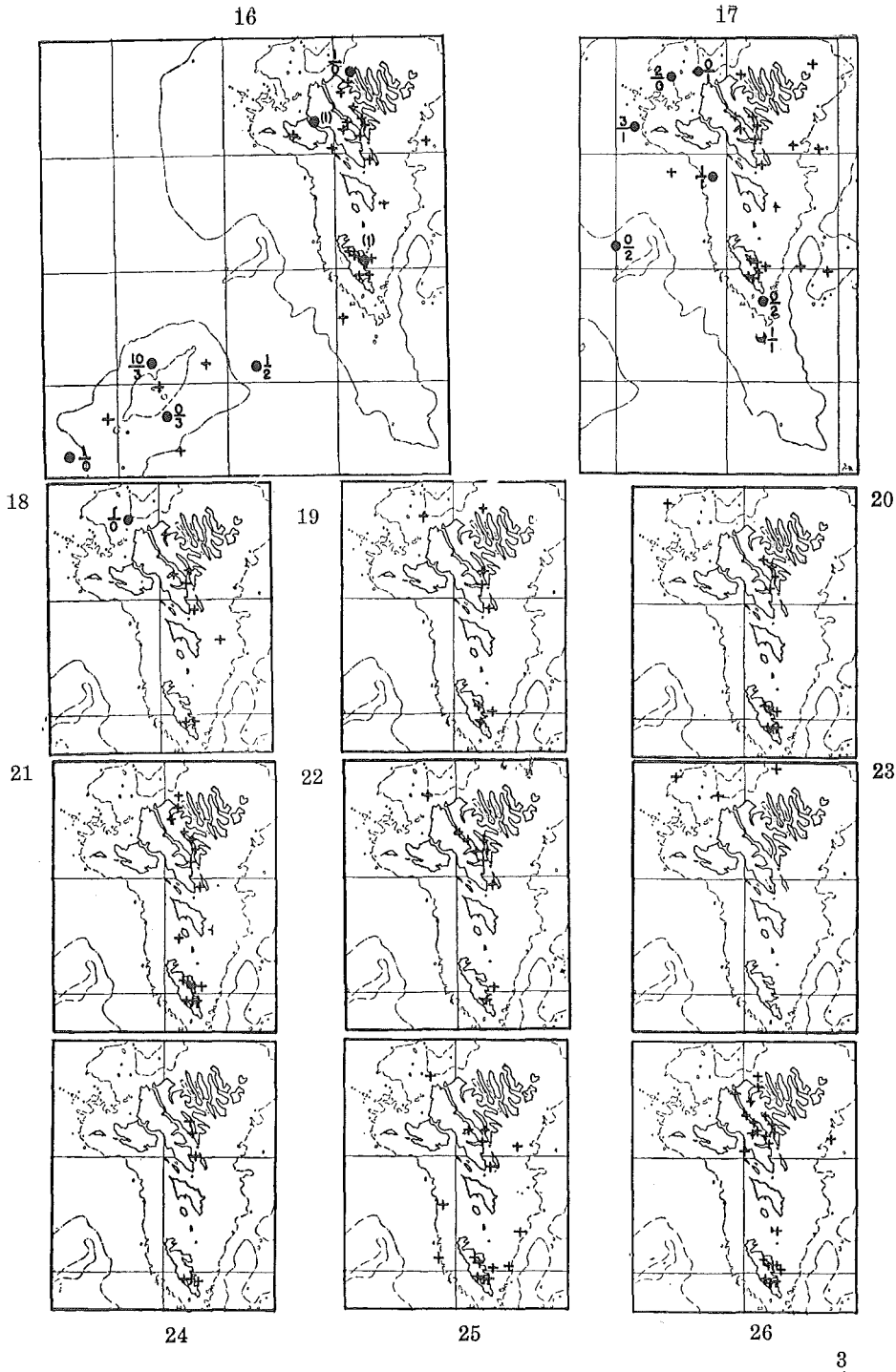
Thus *hatching is still going on in the beginning of May.* The larvae are so small that probably they have not drifted far from the spawning area. It will be seen from the chart fig. 9, that the larvae are *most numerous in the outer areas, especially in the neighbourhood of the 100 m. depth line.* This seems to be true all around the islands and on the Faroe Bank.

The next series of observations is from 6—18/5 1938 (fig. 9), when the hauls were mainly made in the outer areas, with 100 meters of wire out. The average size varies between 10,0 and 14,5 mm. May 6th 50% of the larvae are less than 10 mm. in length, but after that date much smaller numbers of tiny larvae are found.

Thus *hatching seems to fall rapidly off about 6th—10th of May in that year.* The larvae are still most numerous near the 100 m. depth contour.

Fig. 16—26. Distribution of postlarval stages of the Lesser Sandeel (the *lancea*-group) in Faroese water (cf. text fig. 8—15).

Fig. 16. Cruise June 20th — July 4th 1927. Fig. 17. July 4th — 12th 1934. Fig. 18. July 24th — 27th 1938. Fig. 19. July 31st — August 7th 1932. Fig. 20. August 1st — 12th 1924. Fig. 21. August 4th — 9th 1926. Fig. 22. August 6th — 9th 1931. Fig. 23. August 12th — 23rd 1939. Fig. 24. August 18th — 19th 1925. Fig. 25. August 28th — September 2nd 1933. Fig. 26. August 21st — September 4th 1927.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From the latter half of May observations are available from three different years, viz., 1924, 1925 and 1934.

The hauls from the two former years are mainly from the Suðuroy area (see fig. 10 and 12). The average size varies somewhat, average lengths between 7,0 and 13,0 mm. being noted 20—22/5 1925. A considerable number of larvae are still below 10 mm. in length, i. e. newly hatched. Thus *hatching may still go on in the latter half of May.*

The collections from 24—31/5 1934 (fig. 13) show very much the same result, but the average size is higher in samples taken near the end of the month, viz. about 15—19 mm., and the percentage of small larvae is very low.

This year hatching seems to have come to an end in the latest third of May. The larvae are most numerous in the outer area and a comparison between fig. 8 and fig. 11 suggests that the hatching begins earlier in the fjords and then spreads to deeper offshore waters, where it lasts longer.

June.

From the end of May and the beginning of June (22/5—9/6) samples are available from the year 1926 (see fig. 14). The numbers encountered are everywhere low and the size of the specimens varies greatly. In this series of samples only one newly hatched larva was found and this confirms the conclusion set forth above, that hatching has come to an end. The numbers seem to fall off very suddenly, perhaps mostly because of a high mortality in the larval stock in a critical stage, but also because the larvae are, to a greater extent, able to evade the net when they grow larger.

Very similar conditions are encountered in the latter half of June as will be seen from the charts figs. 15 and 16, which show stations operated during 1927 and 1932.

July.

From now on the majority of the hauls prove to be negative and the size of the larvae varies greatly. Stations operated in two different years, viz., 1934 and 1933 are shown on the charts figs. 17 and 18, from which this will be seen.

August—September.

A large number of localities has been investigated in August and the beginning of September as seen by the charts figs. 19—26. These observations cover 8 years (1924, 1925, 1926, 1927, 1931, 1932, 1933 and 1939). *Not a single Ammodytes larva of the lancea-group was found.*

Discussion.

1. ***Hatching period.***

From the foregoing it is evident that *the „races" of the lancea-group have only one spawning period in Faroese waters.* According to the present investigations *the hatching intensity is at its highest in late March and the beginning of April.* This will be seen from the following table, which shows the numbers of *Ammodytes* larvae of the *lancea*-group in each month 1924—1939.

TABLE 1.

Number of larvae of Ammodytes (lancea-group) in each month taken in Faroese waters 1924—1939.

	March	April	May	June	July	August	Sept.	Total
Total no. of larvae	168	4118	2615	49	25	0	0	6975
No. of pos. hauls	5	44	102	13	17			181
Av. no. per 1h pos. haul	134,4	374,4	90,7	9,5	5,2			147,0
Larvae < 10 mm.	168	3143	797	0	0			4108
— — % ..	100,0	76,3	30,5	0,0	0,0			58,9

The number per positive haul are highest in April and in May the percentages of small larvae fall very rapidly off (see the table below). As mentioned above the very small numbers in June and July must be explained by a high rate of mortality and the selectiveness of the net.

This rapid falling off in numbers as the larvae grow larger in size is best seen from the following table, which shows numbers of *Ammodytes* of the lancea-group in different size categories caught in 1924—1939.

TABLE 2.

Number of larvae of Ammodytes (lancea-group) in different size-categories taken in Faroese waters 1924—1939.

Size in mm.	< 10	10—14	15—19	20—24	> 25	Total
Number	4108	2063	537	204	58	6970[1])
%	59,0	29,6	7,7	2,9	0,8	100,0

The older stages, which could be identified as to „race", by means of vertebral countings, all belonged to the *Ammodytes lancea marinus* „race", except one which must be referred to *Ammodytes lancea lancea.* Therefore nothing can, for the present, be said about any difference between these „races" as to spawning time or localities of spawning. There is no evidence that *A. lancea lancea* has seasonal races in Faroese waters, as maintained by *Kändler* (1941) with regard to the North and Baltic Seas.

2. ***Vertical distribution of fry.***

Most of the hauls were made quite near the surface and as seen from table 3, which shows numbers of larvae found in different layers of water, there is no difference of importance between the

TABLE 3.

Number of post-larvae of Ammodytes (lancea-group) taken in Faroese waters, according to depth of haul.

Metres of wire out	10—30 m.	40—65 m.	100—300 m.
No. of pos. hauls	83	82	16
Total no. of larvae	3375	3263	337
Av. no. per 1[h] pos. haul	160,2	147,6	75,0
Larvae < 10 mm.	2424	1642	42
— — — %	71,8	50,3	12,5

hauls 10—30 mw and 40—65 mw. The deeper hauls (100—300 mw) are few in number and also made late in the season so as to give unreliable evidence on the frequency. However, the table shows that *the tiny fry, less than 10 mm. in length, is mainly found quite near the surface.*

1) + 5 of doubtful length.

3. ***Horizontal distribution of fry.***

a. Distribution of fry < 10 mm.

The distribution of small fry less than 10 mm. in length is shown on chart fig. 27, and this gives us information as to the position of the spawning grounds. The small larvae have been found in considerable number both inside the fjords and in the outer areas especially near the 100 m. depth line. Thus spawning seems to take place everywhere where suitable bottom conditions are encountered. As a sandy bottom predominates all round the isles, because of the strong currents, which sweep the muddy particles off the shallow grounds, this means that *spawning of this species takes place almost everywhere inside about 100 m. depth.*

b. Distribution of all fry.

Dividing Faroese waters into two areas, a southern and a northern one, it will be seen that most larvae were taken in the northern area, where larger number of hauls were made (see Appendix). On the other hand herring larvae were more numerous in the southern area (cf. *Tåning* 1936 a, table 7, p. 15).

Then this table shows also that the growth of the post-larvae is very similar in both areas, but reliable information on this is not to be had after the month of June, as the material is too scanty after that time.

c. Distribution of fry according to depth of locality.

Information on this issue has been compiled in table 4. It will be

TABLE 4.

Number of post-larvae of Ammodytes (lancea-group) taken in Faroese waters, according to depth of locality.

Depth in m.	No. of pos. hauls	Total no of larvae	No. per 1h pos. haul	Larvae < 10 mm.	% of small larvae
< 50 m.	25	332	35,3	53	16,0
50— 75 —	43	1380	114,0	667	48,3
75—150 —	76	3338	174,6	1717	51,4
150—250 —	13	265	81,5	121	45,7
> 250 —	10	14	3,7	3	30,0

seen that *larvae occur especially numerously from 50 to 150 m. depth,* increasing in number per 1h positive haul as the hauls are made in

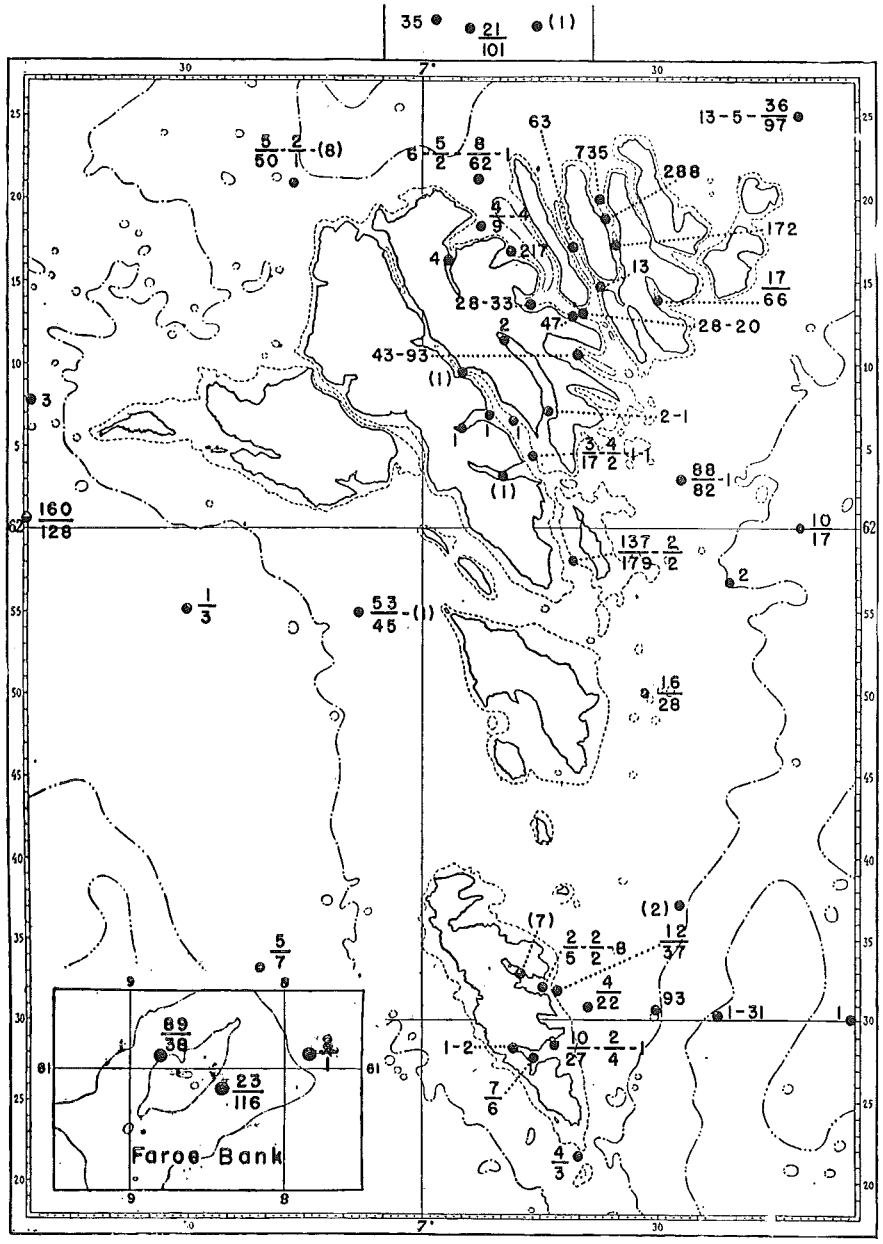


Fig. 27. Distributionn of post-larval stages of the Lesser Sandeel (the *lancea*-group) smaller than 10 mm. in Faroese waters.

deeper water, with a maximum number of 175 specimens in 75—150 m. depth. The percentage of small post-larvae shows that in these depths the main areas of spawning are situated.

B. ICELAND.

April.

The present collections include no specimens from Icelandic waters taken prior to April, and the April-samples date back to the year 1904. The hauls were all made at the surface or quite near it. The numbers per 1h hauls are shown on the chart fig. 28 and the sizes and numbers encountered at these stations were as follows.

TABLE 5.

Length and numbers of Ammodytes post-larvae caught 15/4—27/4 1904 in Icelandic waters.

Date	Length in mm.	5	6	7	8	9	10	11	12	Total no.	Average size	No. of pos. hauls	Tot. no. in. 1h pos. hauls.	No. per 1h pos. haul
15—27/4 1904		58	104	153	131	59	19	8	5	537	7.27	31	1743	56.2

This table shows that *hatching must have begun earlier, in late March or the beginning of April,* the average size now being 7,27 mm, but hatching is evidently still going on in the period recorded.

May.

From this month we have at disposal a series of samples from 8—22/5 1934. They were taken off the south-west, south and east coasts (fig. 29). *No Ammodytes larvae were found in these samples.*

This is a very curious result in view of the records just mentioned. What factors are responsible for this phenomenon is uncertain, but it seems evident that spawning or hatching was unsuccessful this year. The records of the „Dana"-journals from this cruise show

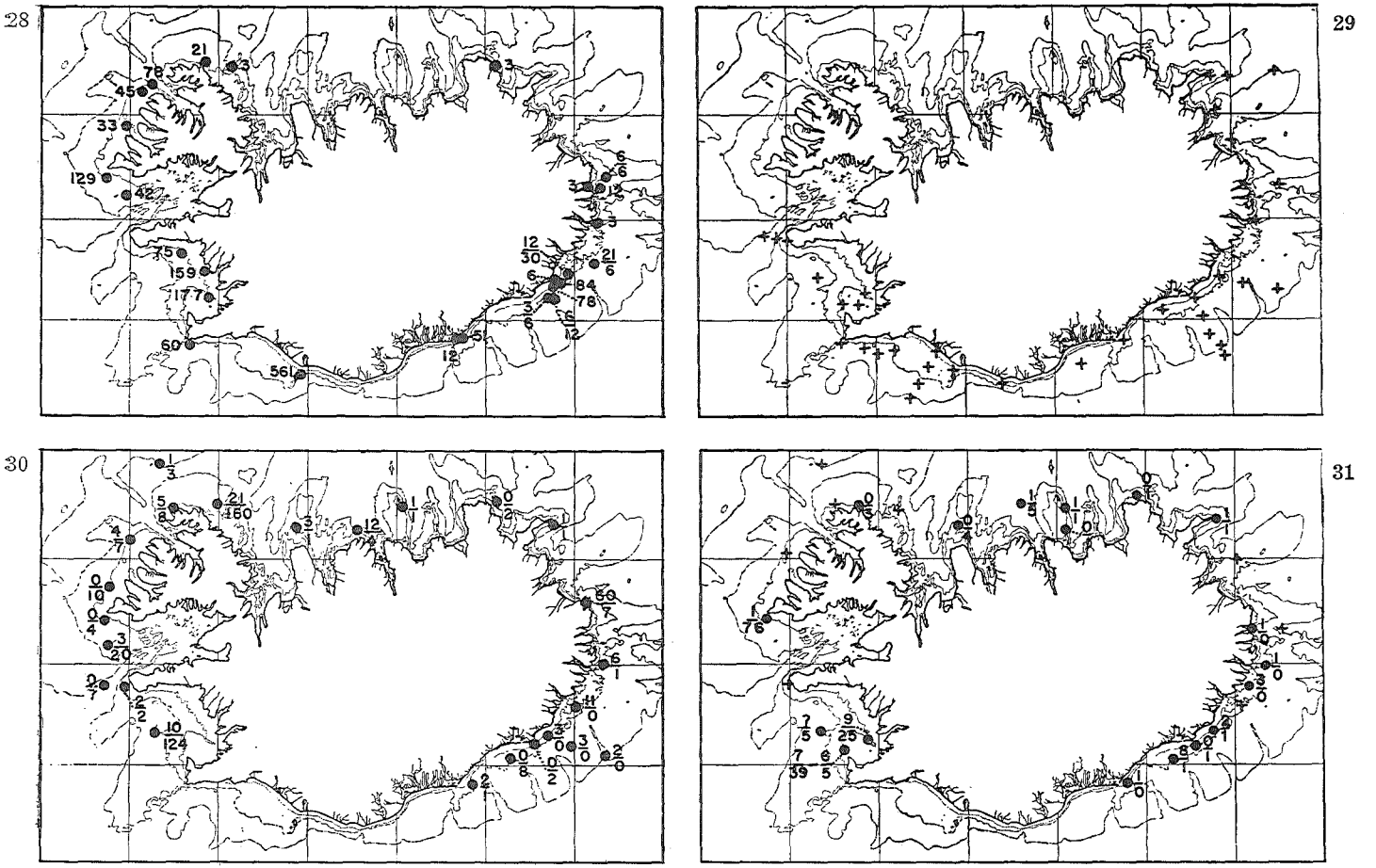


Fig. 28—31. Distribution of the post-larval stages of the Lesser Sandeel (the *lancea*-group) in Icelandic waters (cf. text fig 8—15).

Fig. 28. Cruise April 1904 (numbers per 1 hour haul, otherwise the numbers are per 15 min. haul.). Fig. 29. May 8th—22nd 1934. Fig. 30. June 1st—8th 1924. Fig. 31. June 11st—21st 1926.

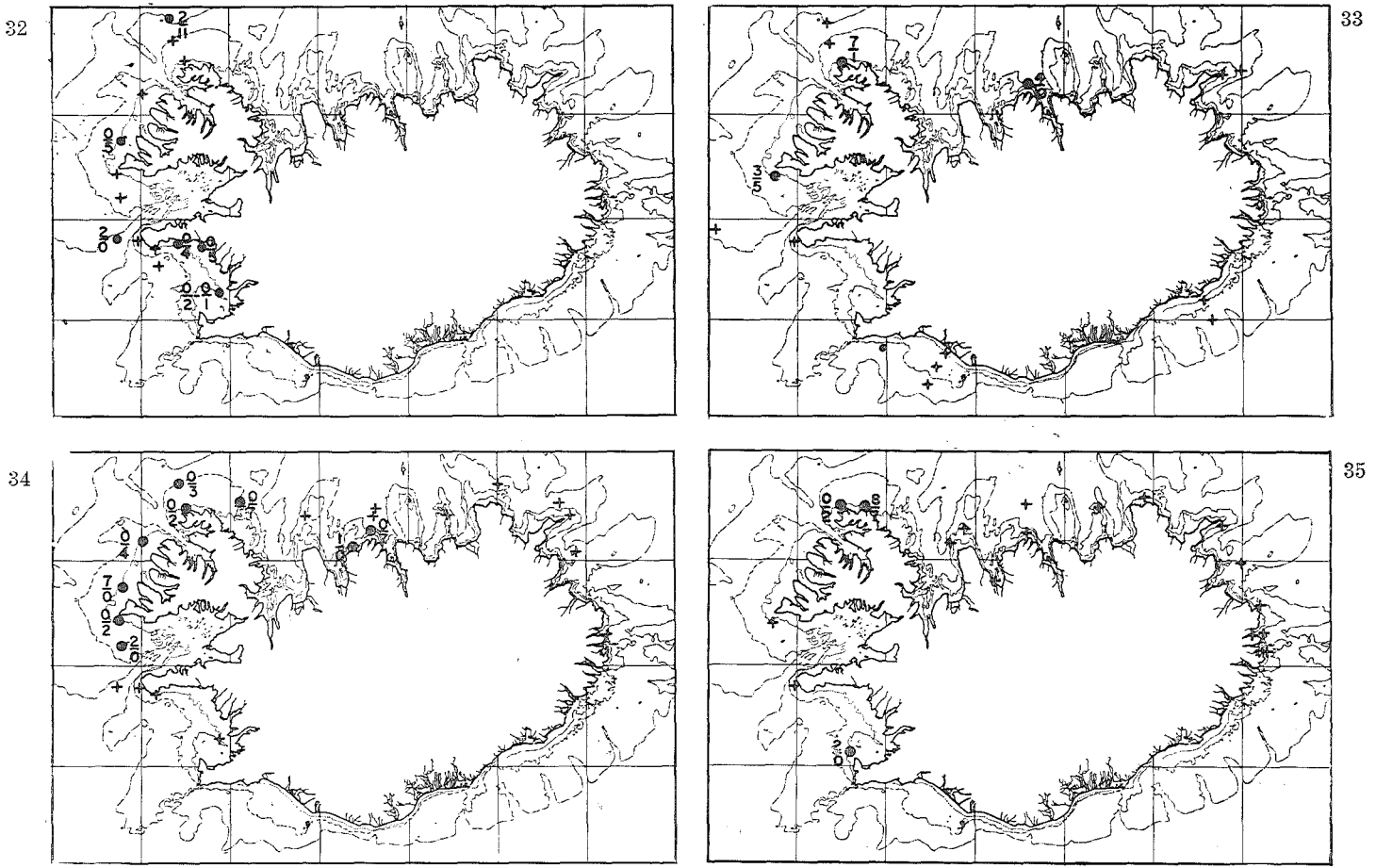


Fig. 32—35. Distribution of the post-larval stages of the Lesser Sandeel (the *lancea*-group) in Icelandic waters (cf. text fig. 8—15).

Fig. 32. Cruise June 19th—July 2nd 1924. Fig. 33. June 22nd—July 13th 1936. Fig. 34. July 6th—31st 1924. Fig. 35. July 1st—August 2nd 1926.

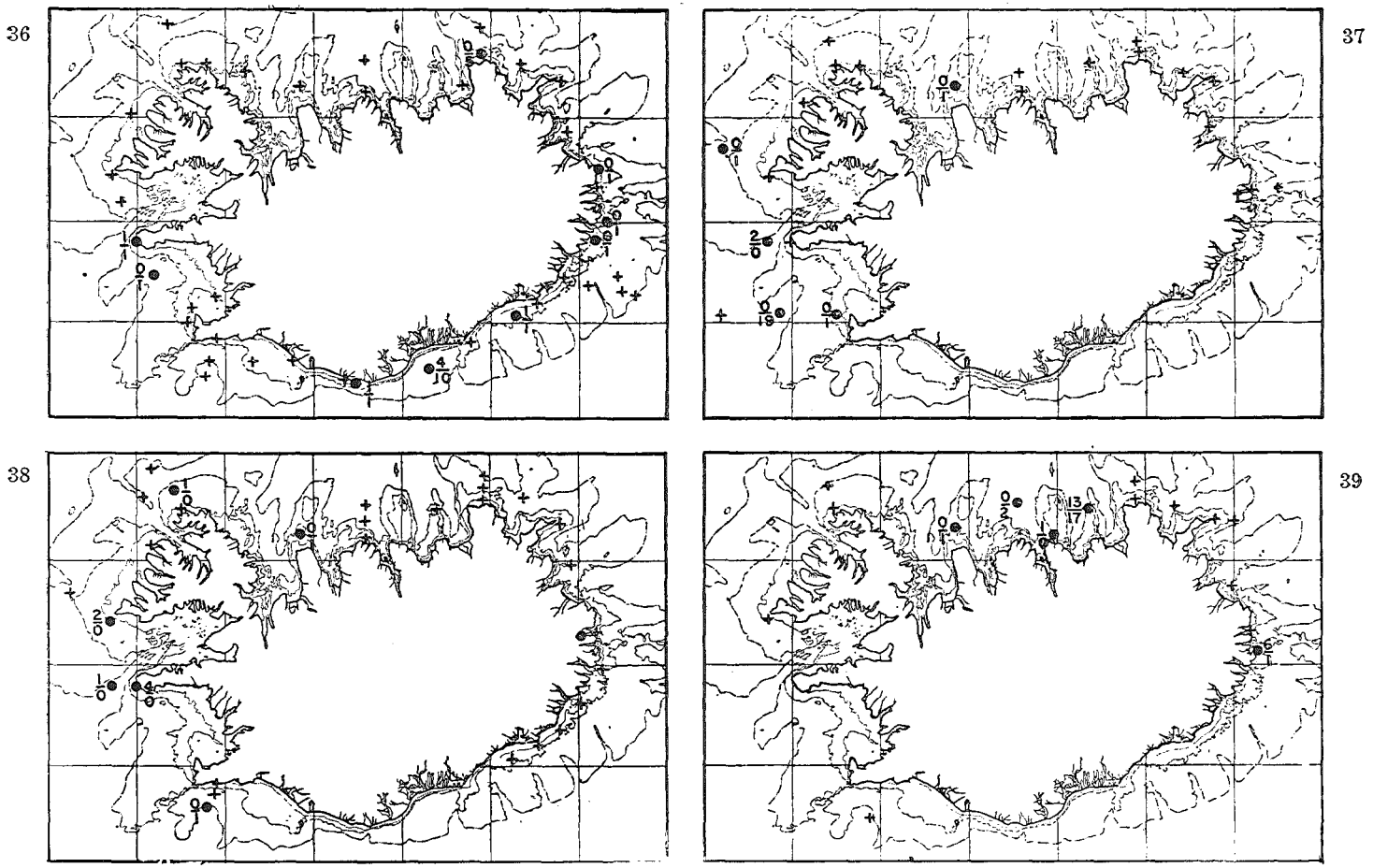


Fig. 36—39. Distribution of the post-larval stages of the Lesser Sandeel (the *lancea*-group) in Icelandic waters (cf. text fig. 8—15).

Fig. 36. Cruise July 5th—August 1st 1927. Fig. 37. July 14th—August 8th 1931. Fig. 38. June 28th—July 29th 1932. Fig. 39. July 5 th—23rd 1938.

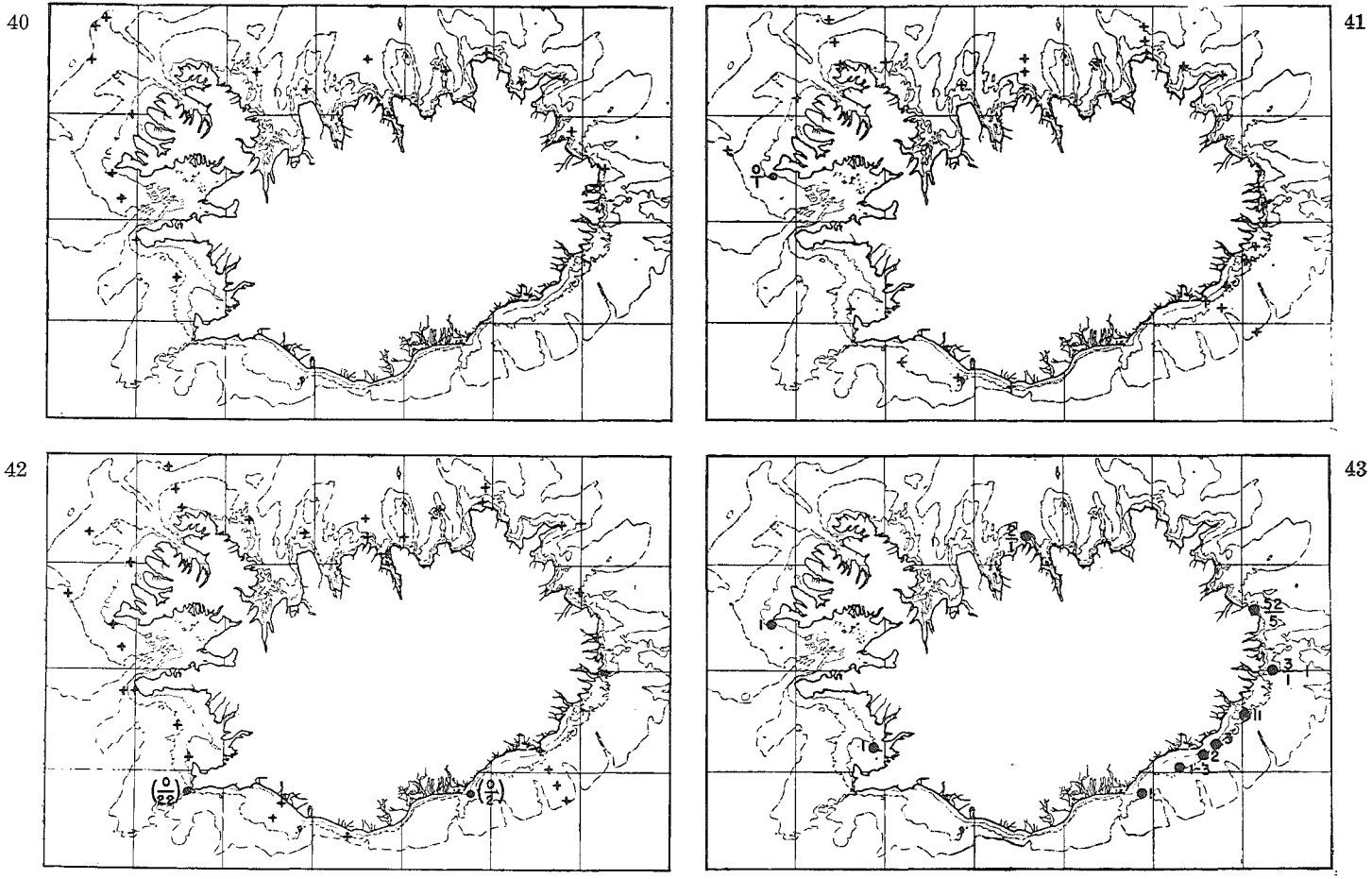


Fig. 40—43. Distribution of the post-larval stages of the Lesser Sandeel (the *lancea*-group) in Icelandic waters (cf. text fig 8—15).

Fig. 40. Cruise August 5th—19th 1927. Fig. 41. July 28th—August 26th 1933. Fig. 42. July 19th—August 10th 1939. Fig. 43. Distribution of Lesser Sandeel fry smaller than 10mm. June.

that *conditions must have been very abnormal.* In this series of hauls larvae of *Mallotus villosus* were the only ones that were of frequent occurrence, 1218 specimens being caught in 27 positive 15 minutes hauls. Beside this only 6 larvae of *Sebastes marinus* in 3 hauls and 14 of *Clupea harengus* in 9 hauls. No other fish larvae were caught during this period.

From the year 1904 we have at disposal 29 larvae from 6 stations off the south-east coast which were 5—26 mm. long, taken 24/5—30/5.

June.

Samples from a cruise round Iceland from the southeast coast to Faxaflói in the beginning of June 1924 gave the result shown in fig. 30. Ammodytes larvae of the lancea-group were most abundant at three stations viz. south of Héraðsflói, off Cape Horn and in Faxaflói. *Newly hatched larvae were frequent off the east coast,* westwards to Grímsey but off the remaining part of the north coast and along the west coast they were further developed, average sizes from 13,90 mm. to 17,99 mm. being observed here (see fig. 44).

The hauls made later in this month (11/6—21/6 1926, 19/6—2/7

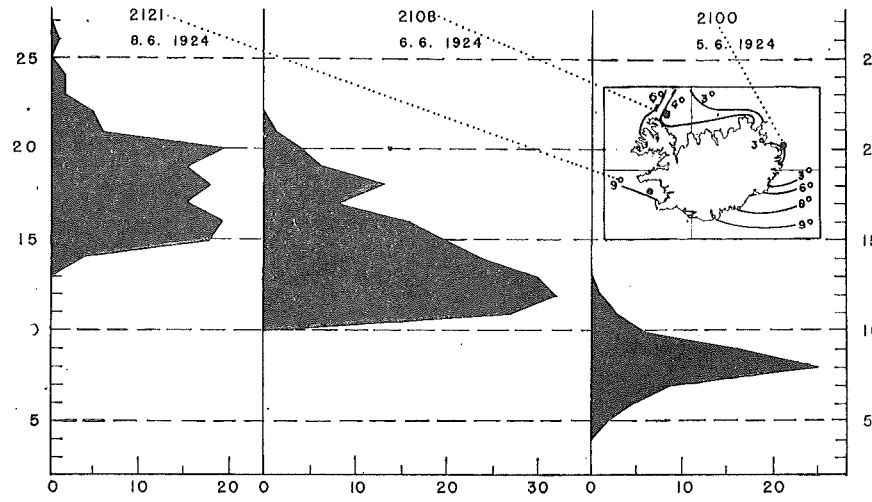


Fig. 44. Length distribution of post-larval stages of *Ammodytes* (*lancea*-group) during June 5th—8th 1924 in different areas of the Icelandic costal waters. Isotherms in the period of observation in the rigth hand corner. Length in mm. (ordinate). Number measured (abscissa).

1924 and 22/6—13/7 1936) usually gave low numbers of larvae (see fig. 31—33) and from the sizes encountered (10—30 mm.) it is evident that *no hatching took place off the west and western part of the north coasts at this time.*

July.

Throughout this month the catch numbers of larvae of the *lancea*-group are very small as will be seen by the distribution charts shown in figs. 34—39. The observations cover 6 years and most years samples are at disposal from all the coasts of the country. *No recently hatched larvae of the lancea-group have ever been found in this month.*

August.

Fairly complete series of hauls were made in three different years in the month of August. Positions of stations operated are shown in figs. 40—42. In 1927 no larva was caught. In 1933 no larva but one young specimen 60 mm. long. And lastly in 1939 24 specimens were caught in two localities off the south coast, the average size being 37,77 mm. (22 specimens) and 33,50 mm. (2 specimens). *Evidently it is only by chance that we get larvae of the lancea-group in the nets at this time of the year.*

Discussion.

1. ***The Distribution of A. lancea lancea and A. lancea marinus.***

Unfortunately I have not been able to distinguish the small larvae of these forms. But the distribution of larvae > 20 mm. in length, in which the vertebrae have been counted, gives us some information of the distribution as will be seen from the charts figs. 44 and 45.

A very striking difference appears. *A. lancea lancea is entirely confined to the south and west coast waters, i. e. the boreal area.* On the other hand, *A. lancea marinus is found off all the coasts of the country.*

It is difficult to draw any further conclusions as the larvae may have drifted a considerable distance from the spawning grounds.

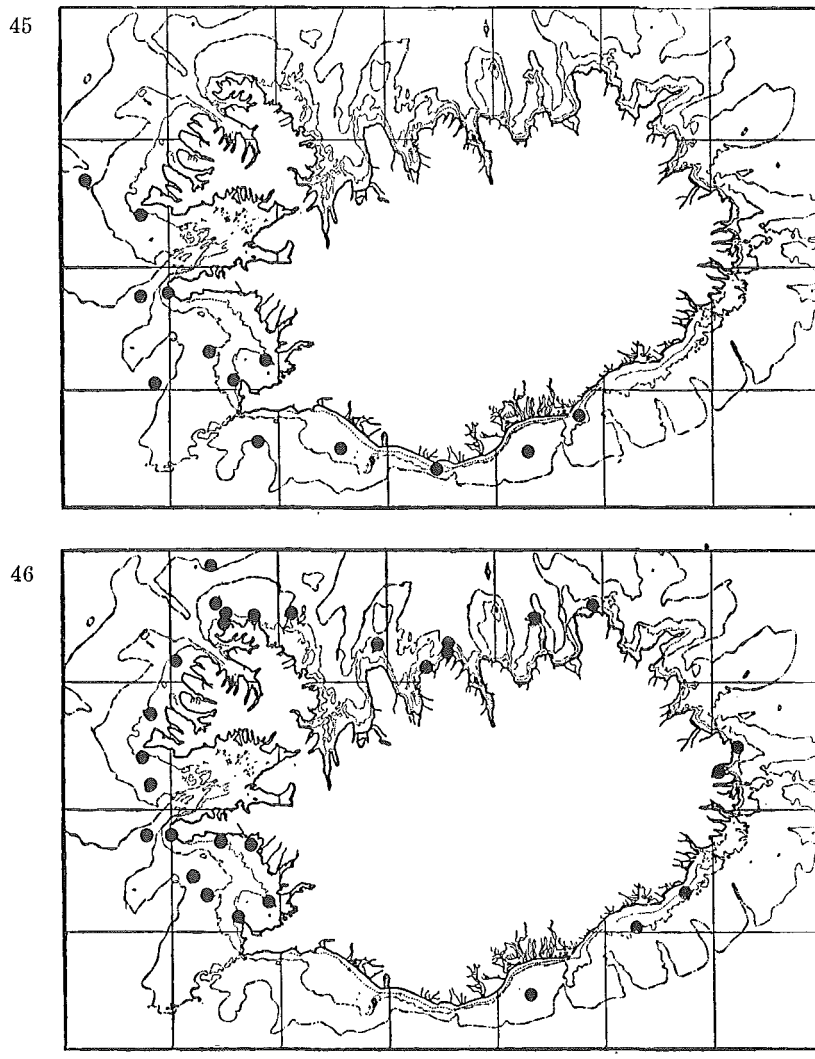


Fig. 45—46. Distribution of post-larval stages of *Ammodytes* in Icelandic waters, identified by means of vertebrae counts. Fig. 45. *A. lancea lancea.* Fig. 46. *A. lancea marinus.*

2. *Hatching period.*

The present collections do not include any samples from the height of the hatching period. But the April samples from 1904, recorded above, show, that spawning must have begun earlier, *probably in*

late March and the beginning of April off the south and west coast.

From the Appendix showing size distribution of all fry, it will be seen that *off the north and especially the east coast hatching begins a little later, probably about the beginning of May.*

The difference in the time of hatching is well illustrated in the graph fig. 44 showing the size distribution at three different stations off the southwest, north and east coast respectively. In the middle of June hatching has come to an end everywhere. A few newly hatched larvae are found off the east coast, and in view of the low temperature still prevailing we must assume that some time has elapsed from the height of hatching although the average size has the low value of 7 mm.

There is no indication of more than one spawning period of Ammodytes of the lancea-group as will be seen from the size distribution shown in the Appendix.

In later years collections have been made in the summer months only as will be seen from table 6. The average number per 1^h

TABLE 6.

Number of post-larvae of Ammodytes (lancea-group), taken in Icelandic waters in each month 1924—1939.

	May	June	July	August	Total
No. of pos. hauls	0	72	49	2	123
Total no. of larvae	0	757	183	2	942
Av. no. per 1^h pos. haul		42,0	14,0	4,0	30,2
Larvae < 10 mm.		87	1	0	88
— — %		11,5	0,5		9,3

positive haul is largest in June, i. e. 42 specimens. In August larvae were only found occasionally. As a consequence of this the small larvae are much too poorly represented in our material as seen from the number of fry in the different size categories.

TABLE 7.

Number of post-larvae of Ammodytes (lancea-group) in different size categories, taken in Icelandic waters 1924—1939.

Size in mm.	< 10	10—14	15—19	20—24	> 25	Total
Number	88	272	263	144	163	930[1])
%	9,5	29,2	28,3	15,5	17,5	100,0

3. ***Vertical distribution of fry.***

Quite newly hatched larvae were found in the surface hauls made in April 1904. The collections from later years, on the other hand,

TABLE 8.

Number of post-larvae of Ammodytes (lancea-group), taken in Icelandic waters, according to depth of haul.

Metres of wire out	10—30	40—65	100—300
No. of pos. hauls	48	69	6
Total no. of larvae	238	659	45
Av. no. per 1h pos. haul	19,8	38,2	22,0
No. < 10 mm.	73	15	0
— — %	30,7	2,3	

show, that *older larvae were found mainly in the hauls with 40—65 meters of wire out, i. e. in about 15—20 m. depth.* Nearer the surface they were fewer in numbers and this also applies to the deeper hauls.

4. ***Horizontal distribution.***

a. Distribution of fry < 10 mm.

The few records of small fry are shown in fig. 43. It does not give a true picture of the location of the spawning grounds, as it shows only the last phase in the hatching.

1) + 12 of doubtful length.

b. Distribution of all fry.

The size-distribution of all the fry taken in Icelandic waters 1924—1939 is shown in the Appendix. We distinguish between the four coastal areas off Iceland and then the material is divided according to time of capture.

The west coast waters show the largest numbers caught with the highest average size of the larvae in July. Otherwise the material is too scanty to give definite answer to the question of growth.

c. Distribution according to depth of locality.

Table 9 shows that *numbers of all fry per 1 hour positive haul are highest inside 50 m. depth.* On the other hand it is extremely characteristic that fry < 10 mm. in length are most frequent in deeper areas, i. e. between 75 and 150 m. depth.

TABLE 9.

Number of post-larvae of Ammodytes (lancea-group), taken in Icelandic waters 1924—1939, according to depth of locality.

Depth in m.	No. of pos. hauls	Total no. of larvae	No. per 1h pos. haul	Larvae < 10 mm.	% of small larvae
< 50	14	154	44,0	1	0,6
50— 75	50	358	28,6	7	2,0
75—150	39	336	33,3	80	23,8
150—250	9	58	25,8	0	0,0
> 250	7	32	18,3	0	0,0

Now we must bear in mind that as earlier shown the distribution of fry < 10 mm. in length did not show the true situation of the spawning grounds (see p. 47 and fig. 43), but only those localities where the hatching process lasted till the beginning of June. From this fact we may therefore conclude that *in deeper water the hatching either takes longer time or begins and ends a little later than in shallower water.*

Where the depth is more than 150 m. spawning seems not to occur.

C. W.-GREENLAND.

The collection treated here originates from the cruise af „Dana" in W.-Greenland waters in 1925. The gear used was the 2 m. stramin net. Usually two hauls were made, with 50 and 100 meters of wire out respectively.

June.

Most of the collection was caugth in this month. Positions of stations and numbers caugth are shown in fig. 47 a and the material is listed in the Appendix, where W.-Greenland waters are divided into different areas along the coast from south to north. The average number per 1 hour positive haul increases from south to north. The average size decreases in the same direction, but with the exception that it is lowest in the area between 66° and 68° N. Lat. *Baggesgaard Rasmussen & Jacobsen's* (1930) description of the hydrographical conditions during the period of investigation, shows, that in this sector a tongue of cold water stretches from the Davis Strait towards the coast. (l. c. fig. 24 and 25).

July.

North of 66° N. Lat. we have no samples from this month, while stations were operated in all the more southern sectors. In the beginning of this month post-larvae are still numerous between 64° and 66° N. Lat., but to the south of 64° N. Lat. post-larvae were practically absent, as seen from the chart fig. 47 b.

Discussion.

The few larvae in which vertebrae could be counted all belong to *Ammodytes lancea dubius.*

1. ***Hatching period.***

Presumably hatching begins in late April or the beginning of May in the southern areas and has ceased in the beginning of June, while in the two northernmost areas hatching is still going on at this time.

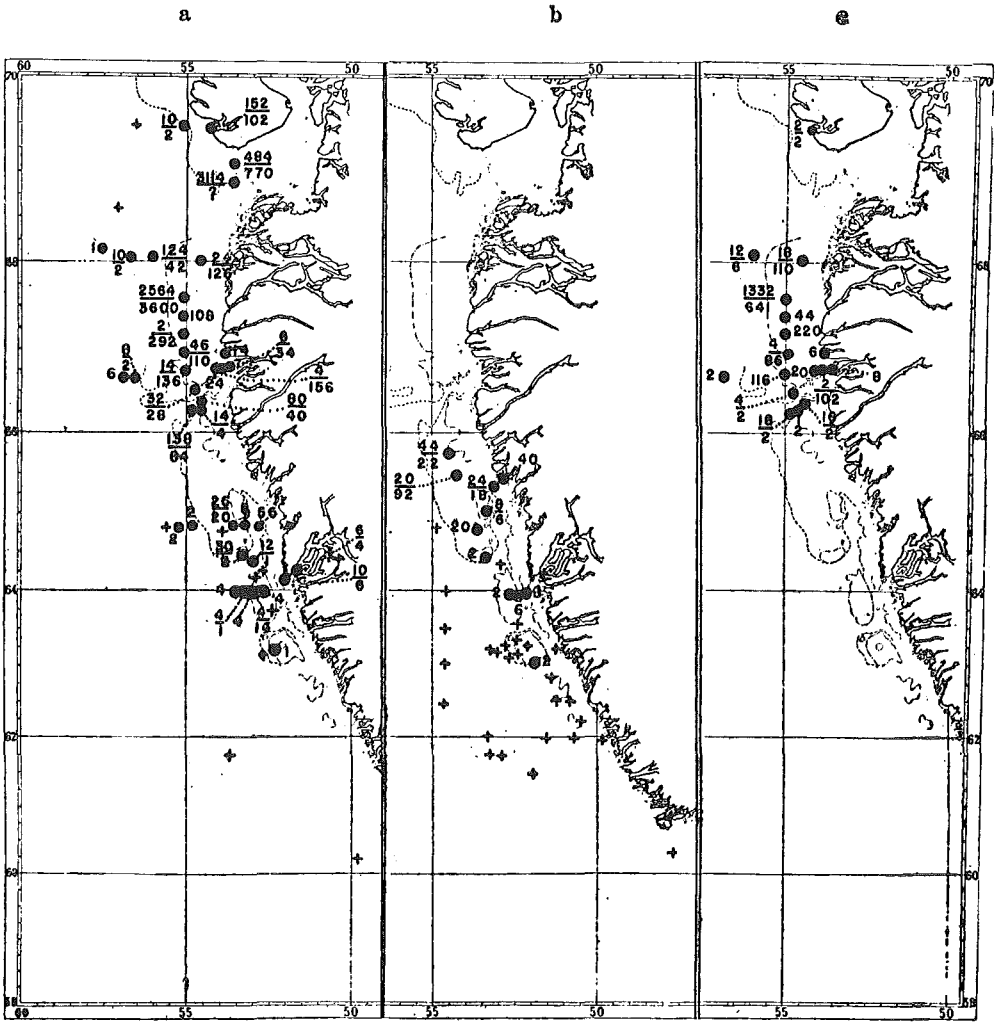


Fig. 47. Distribution of post-larval stages of Lesser Sandeel (the *lancea*-group) in W-Greenland waters.
a. June 7th—30 th 1925.
b. July 1st—14th 1925.
c. Distribution of post-larval stages smaller than 10 mm. Numbers per 1 hour haul.

Although the size distribution in the area between 66° and 68° N. Lat. gives a curve with two peaks, viz. about 9 mm. and 15 mm., this does not necessarily mean that we have to deal with two breed-

ing periods. Perhaps this can be explained by the variations in temperature in the area, the larvae inside the cold tongue of water being smaller than those growing up outside it.

In July no larvae < 10 mm. in length were caught, i. e. hatching had ceased everywhere.

2. ***Vertical distribution of fry.***

The average number of fry caught with respectively 50 and 100 meters of wire out is about the same (see table 10). On the other

TABLE 10.

Number of post-larvae of Ammodytes (lancea-group), taken in Greenland waters, according to depth of haul.

Metres of wire out	50 m.	100 m.	> 100 m.	Surf.
No. of pos. hauls	39	35	2	2
Tot. no. of larvae	3570	2941	2	25
Av. no. per 1h pos. haul	18,2	16,8	1,5	25,0
No. < 10 mm.	693	1683	0	0
— — %	19,4	57,2	0,0	0,0

hand *the small larvae, < 10 mm. in length, are much more numerous in the deeper hauls.* Too few hauls have been made in other depths to give reliable information.

3. ***Horizontal distribution of fry.***

a. Distribution of fry < 10 mm.

Fig. 47 c shows the positions of stations where small larvae were encountered during the period of investigation. This chart shows the hatching grounds where the hatching process lasts longest in W.-Greenland waters.

b. Distribution of all fry.

Information on the distribution according to time, size and area is given in the Appendix which was discussed above.

c. Distribution according to depth of locality.

Table 11 gives us very interesting information on this feature. *The numbers of larvae are exeedingly high inside 50 m. depth,* viz.

892 specimens per hour positive haul and they decrease as we move into deeper waters. The same applies to the tiny fry < 10 mm. in

TABLE 11.

Number of post-larvae of Ammodytes (lancea-group), taken in Greenland waters, according to depth of locality.

Depth in m.	No. of pos. hauls	Total no. of larvae	No. per 1h pos. haul	Larvae < 10 mm.	% of small larvae
< 50	7	3123	892,6	1986	63,6
50— 75	14	379	68,4	176	46,4
75—150	21	470	44,4	174	37,0
150—250	13	126	19,4	3	2,4
> 250	18	2377	263,6	14	0,6

length. The percentage figures show a steady decreasing to about 150 m. depth and in still deeper water the percentage figures go down to 2,3 and 0,6%. This same fact was established as regards the Icelandic material.

On the other hand, larger post-larvae are also found numerously in deeper water, 263 specimens being caught per 1h positive haul. Whether this phenomenon can be explained by the fact that two sub-species, *A. lancea marinus* and *A. lancea dubius*, occur in W.-Greenland waters, is at present uncertain as the post-larvae could not be distinguished.

2. AMMODYTES LANCEOLATUS.

A. THE FAR ES.

The fry of *A. lanceolatus* is far less frequent than that of the *lancea*-group. The collections from the Faroes include 235 post-larval specimens of this species against 6975 of the *lancea*-group, or 11 specimens against 147 specimens per 1^h positive haul.

Figs. 48—51 show the localities where these positive hauls were made in the various months.

The larval stages of this species have not been found prior to May, but from then on and during the whole summer larvae have been encountered.

In May they are especially found in the fjords of *Suðuroy*, but in subsequent months they occur in the northern fjords as well. *The largest numbers are found in the fjords, as will be seen from the chart, whereas the outer areas are poor in larval stages.*

Many stations have been repeatedly operated during the summer and at many of these stations we encounter larval stages of this species in the different months.

Discussion.

1. ***Hatching period.***

The finds of larvae indicate that *hatching begins in the last part of May.* But the few records, in spite of a great number of hauls being made in that month, show, that the spawning intensity is very low in this month as well as in June. This is well borne out by the following table, showing number of *A. lanceolatus* larvae in each month 1924—1939.

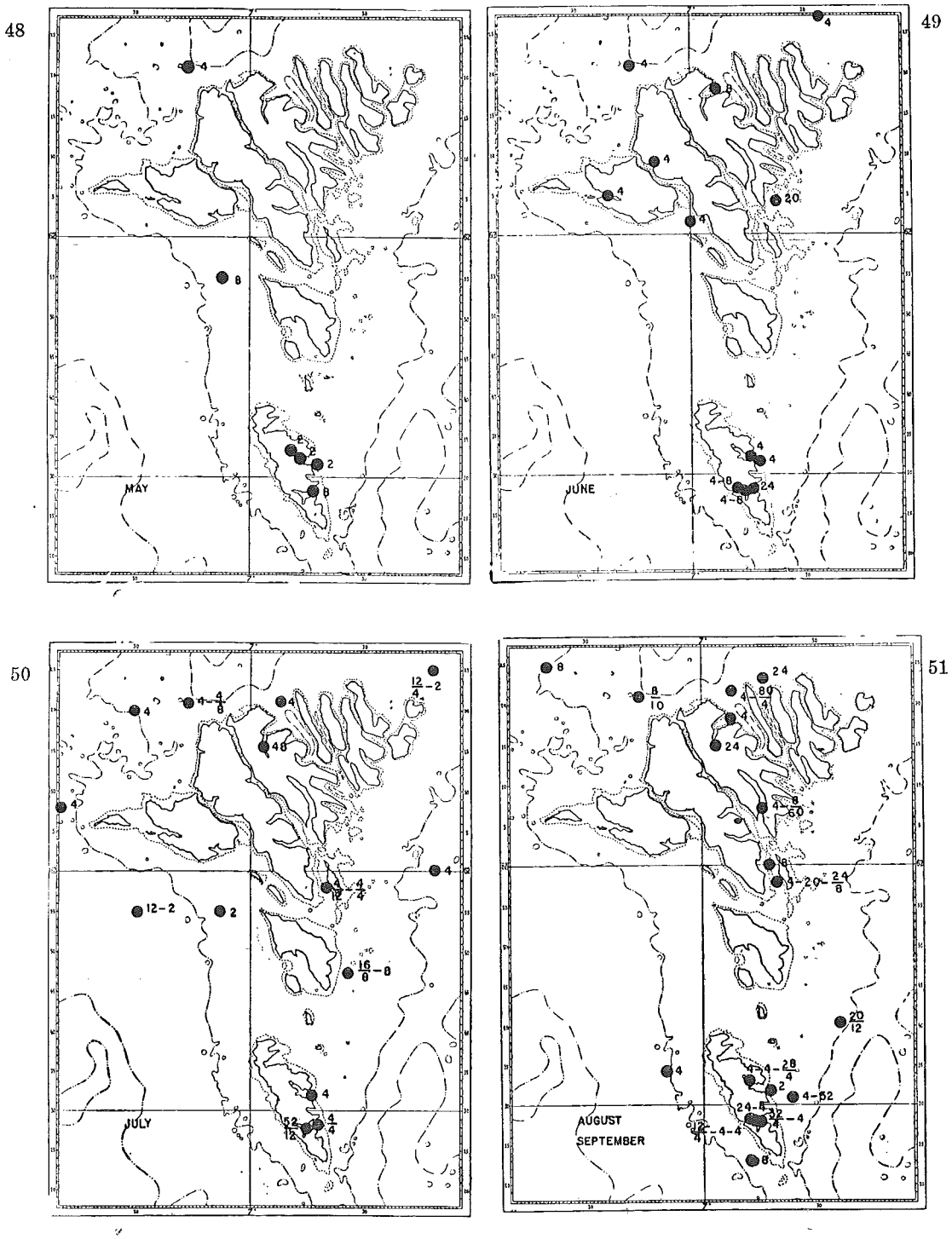


Fig. 48—51. Distribution of post-larval stages of *A. lanceolatus*, in Faroese waters, during May—September 1924—1939. Numbers per 1 hour haul. Positive stations only.

TABLE 12.

Number of post-larvae of Ammodytes lanceolatus in each month taken in Faroese waters 1924—1939.

	March	April	May	June	July	August	Sept.	Total
Total no. of larvae	0	0	8	26	64	116	21	235
No. of pos. hauls	0	0	6	14	26	35	3	84
Av. no. per 1h pos. haul			4,3	7,4	9,5	13,2	28,0	11,0
Larvae < 10 mm.			8	6	39	51	5	109
— — % ..			100,0	23,1	60,9	44,0	23,8	46,3

The main spawning seems to take place in July and August, when respectively 60,9% and 44% of the larvae are less than 10 mm. long. The average number per 1h positive haul increases steadily towards the close of the period of observation, i. e. till the beginning of September. But throughout the season these numbers remain very low.

The numbers of larvae in different size categories give very much the same result as with regard to the *lancae*-group larvae. There is a sudden fall off in numbers of post-larvae above 10 mm. in length and the post-larvae seem to evade the net after having grown to about 20 mm. in length.

TABLE 13.

Number of post-larvae of Ammodytes lanceolatus in different size-categories, taken in Faroese waters 1924—1939.

Size in mm.	< 10	10—14	15—19	20—24	> 25	Total
Number	109	68	40	14	3	234[1])
%	46,6	29,1	17,1	6,0	1,3	100,0

2. ***Vertical distribution of fry.***

The following table shows the numbers of fry caugth in hauls of varying depth.

1) + 1 of doubtful length,

TABLE 14.

Number of post-larvae of Ammodytes lanceolatus, taken in Faroese waters according to depth of haul.

Metres of wire out	10—35 m.	40—65 m.	100—300 m.	Surf.
No. of hauls	52	26	4	1
Total no. of larvae	163	66	4	1
Av. no. per 1h pos. haul	12,3	10,0	2,5	12,0
Larvae < 10 mm.	69	37	2	1
— — %	42,3	56,1	50,0	100,0

The material is too scanty to give conclusive evidence on this issue. It may be stated, however, that *the fry occurs quite near the surface.* But we need further observations on its occurrence near the bottom for comparison with the records here given.

3. ***Horizontal distribution of fry.***

Most larvae have been caught in the more extensive fjord areas in the northern part of the islands, as seen by the Appendix which gives the size-distribution at various times in the northern and southern areas respectively. The collection from the Suðuroy area indicates that the spawning period may be divided into an earlier in May and a later one which begins in July. An indication of this is also seen in the material from the northern islands. In both cases the average size becomes lower in July than it was in the preceding mounth.

As to the growth of the larvae during the summer the material is too poor.

4. ***Distribution of fry according to depth of locality.***

Table 15 showing the distribution of fry according to depth of locality gives us valuable information. It will be seen that *all the fry has been taken inside 150 m. of depth and the percentage of small larvae is highest inside 50 m. of depth, decreasing with increasing depth.* The numbers per 1h positive haul are also highest in quite shallow water.

TABLE 15.

Number of post-larvae of Ammodytes lanceolatus, taken in Faroese waters, according to depth of locality.

Depth in m.	No. of pos. hauls	Total no. of larvae	No. per 1h pos. haul	Larvae < 10 mm.	% of small larvae
< 50	19	62	12,8	46	74,2
50— 75	24	68	11,5	29	42,6
75—150	35	95	10,7	28	29,5
150—250	—	—	—	—	—
> 250	—	—	—	—	—

B. ICELAND.

Only 260 larvae of *A. lanceolatus* have been found in Icelandic waters in the period 1924—1939 in 47 positive hauls or 20 larvae per 1 hour positive haul. This against 942 larvae of the *lancea*-group in the same period, in 123 positive hauls or 30 larvae per 1 hour positive haul. This shows that the fry of *A. lanceolatus* in Icelandic waters is far less common than the fry of the *lancea*-group.

On the chart fig. 52 all these records are shown, while the distribution of larvae less than 10 mm. in length is shown in fig. 53.

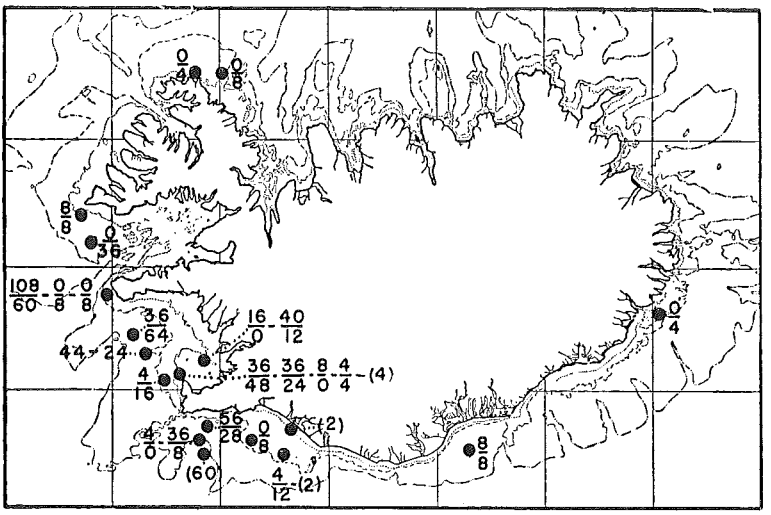
It will be seen that *the larvae of A. lanceolatus are entirely confined to the south and west coasts of Iceland,* and have never been observed off the east coast or east of the north-western peninsula.

Discussion.

1. ***Hatching period.***

Presumably hatching begins in May, but we only have May collections available for 1934, when conditions were somewhat abnormal as stated above. As seen from table 16, showing numbers of larvae in each month, they are comparatively high in June and July, but

52



53

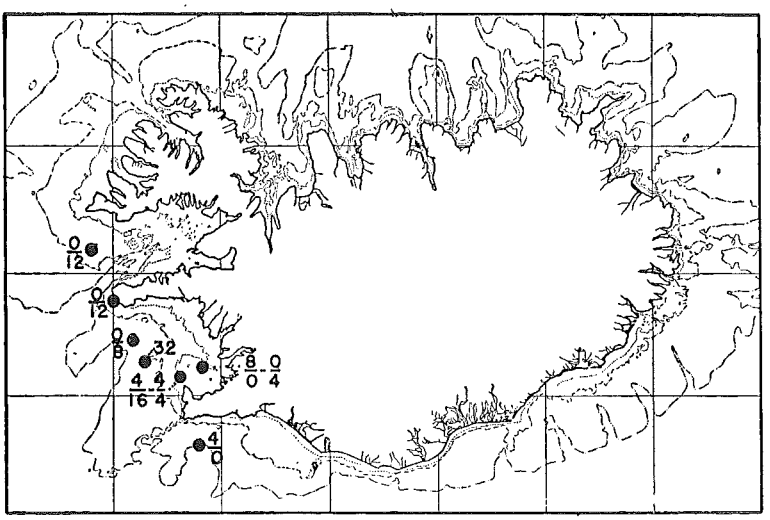


Fig. 52. Distribution of post-larval stages of *A. lanceolatus* in Icelandic waters during 1924—1939. Numbers per 1 hour haul. Positive stations only.

Fig. 53. Distribution of post-larval stages of *A. lanceolatus* in Icelandic waters smaller than 10 mm.

fall off rapidly in August. The percentage of small larvae is, however, greatest in June and hatching has ceased altogether in the beginning of August.

TABLE 16.

Number of post-larvae of Ammodytes lanceolatus, taken in Icelandic waters in each month 1924—1939.

	May	June	July	August	Total
No. of pos. hauls	0	13	31	3	47
Total no. of larvae		95	161	4	260
Av. no. per 1^h pos. haul		29,2	18,1	3,3	20,3
Larvae < 10 mm.		18	9	0	27
— — %		18,9	5,6	0,0	10,4

That the sampling is not adequate is borne out by table 17 showing number of fry of *A. lanceolatus* in different size groups. The small larvae are far too poorly represented.

TABLE 17.

Number of post-larvae of Ammodytes lanceolatus in different size-categories, taken in Icelandic waters 1924—1939.

Size in mm.	< 10	10—14	15—19	20—24	> 25	Total
Number	27	80	63	49	39	258[1])
%	10,5	31,0	24,4	19,0	15,1	100,0

2. ***Vertical Distribution.***

The larvae recorded were chiefly caught in the upper layers of water, as seen by table 18.

TABLE 18.

Number of post-larvae of Ammodytes lanceolatus, taken in Icelandic waters, according to depth of haul.

Metres of wire out	10—30 m.	40—65 m.	100—300 m.
No. of pos. hauls	18	23	6
Total no. of larvae	117	104	39
Av. no. per 1^h pos. haul	25,8	17,8	13,0
Larvae < 10 mm.	13	14	0
— — %	11,1	13,5	0,0

1) + 2 of doubtful length.

The average number per 1 hour positive haul is highest nearest the surface, but smaller larvae, < 10 mm., are equally frequent in 15—20 m. depth, but totally absent in hauls taken with 100—300 metres of wire out.

3. ***Horizontal Distribution.***

The small larvae were found exclusively off the south-west coast as shown in fig. 53. The whole material is listed as to areas, time and size in the Appendix.

Most of the fry were caught off the west and a great number off the south coast, as previously shown. Off the west coast the average size increases from 9,09 mm. in the beginning of June to 17,21 mm. in July. The growth is a little ahead in the south coast waters as will be seen from the table.

4. ***Distribution according to depth of locality.***

It is remarkable that *the average number per 1 hour positive haul reaches its maximum in about 250 m. depth.* This is contrary to what was found in Faroese waters. The numbers are shown in table 19.

The small larvae are, on the other hand, mostly found within 150 m. depth. But we must bear in mind that we have to deal with very small numbers.

TABLE 19.

Number of post-larvae of Ammodytes lanceolatus, taken in Icelandic waters, according to depth of locality.

Depth in m.	No. of pos. hauls	Total no. of larvae	Av. no. per 1h pos. haul	Larvae < 10 mm.	% of small larvae
< 50	8	45	21,7	7	15,6
50— 75	16	84	20,6	9	10,7
75—150	14	57	16,1	8	14,0
150—250	6	67	34,7	3	4,5
> 250	3	7	4,7	0	0,0

GENERAL REMARKS.

1. ON THE GEOGRAPHICAL DISTRIBUTION OF THE NORTH-ATLANTIC AMMODYTES.

Sufficient knowledge has been gained in recent years on the distribution of the *Ammodytes* species to enable us to refer them to zoogeographical groups. A short summary of the results will be given in the following:

The lancea group.

A. lancea lancea.

In Kändler's (1941, p. 117—118) material of adult *Ammodytes* from the *Baltic and North Seas* this form is most frequent. *It lives predominantly in the shallow coastal waters.* In the coastal waters *round Denmark, A. lancea lancea* is by far the most common form (*Jensen* 1941, p. 13—14, fig. 1). *Off Scotland, „A tobianus* has so far been found only at inshore positions from the Moray Firth to the Firth of Forth on the east of Scotland, and in Loch Striven on the west". (*Raitt* 1934, p. 370, chart no. 3). *Soleim* (1945, p. 9) mentions 1 sample only from *Norwegian waters* (Djupedal, Herdla, near Bergen). From *the Faroes, Bruun* (1941, p. 331) records 1 locality (Kvalbö) and from *Iceland* he records 2 localities (Portland and Hornafjörður). All these localities lie inshore. In the present paper it was shown that the larvae found were confined to the south and west coasts of Iceland. 1 specimen was recorded from the Faroes.

A. lancea lancea is thus a boreal form.

A. lancea marinus.

Kändler (1941, p. 117) shows that in the *North and Baltic Seas* this form is common and *occurs mainly offshore.* In *Danish waters*

it is very rare (*Jensen* 1941, p. 15). In *Scottish* waters it is the most common form, „a total of 3.357 adult specimens of *A. marinus* has been collected during the past six years, as against only 364 *A. tobianus*. *A. marinus* has much the wider distribution, having been encountered both inshore and offshore from the Faroes to St. Kilda, and from the Shetlands to the Firth of Forth". (*Raitt* 1934, p. 370). From *Faroese waters*, *Bruun* (1941, p. 331) records 4 localities, and *off Iceland* he found this form in 6 localities. In the present paper it was shown that this form is very common, both off the Faroes and off Iceland. From *the fjords of W.-Greenland*, *Jensen* (1941, p. 22) gives several records of its occurrence.

A. lancea marinus is thus a subarctic-boreal form.

A. lancea dubius Reinhardt.

So far *A. lancea dubius* has only been met with in *W.-Greenland waters*, where it seems to prefer deeper water than *A. lancea marinus* according to *Jensen* (1941, p. 21). It seems to be more common than *A. lancea marinus* in these waters.

A. lancea dubius is thus a subarctic form.

A. lanceolatus *Lesauvage.*

This species is recorded from *south of Ireland* by *Fage* (1918, p. 17), from the Atlantic coast of France by *Moreau* (1880, p. 217), from various localities *off the British Isles* by *Day* (1884, p. 331). *Kändler* (1941, p. 117) found it of common occurrence in the *Baltic and North Seas* both in offshore and inshore waters. It is common in *Danish coastal waters* (*Otterström*, 1914, p. 48). According to *Raitt* (1934, p. 37) it seems to be fairly common in *Scottish waters*. In *Norwegian coastal waters* it is distributed northward to Tromsö (*Wollebæk* 1924, p. 216). A sample of adults from *the Faroes* (Hvalböur) was recorded in the present paper and according to the finds of larvae it is not infrequent here. *Sæmundsson* (1925, p. 291) records it from all the coasts of *Iceland* but according to the present investigation its breeding area is restricted to the south and west coasts of Iceland.

A. lanceolatus is thus a boreal species.

2. ON HATCHING PERIODS AND TEMPERATURE.

From our records on the seasonal occurrence of larvae in the area investigated it will appear that:

1. The hatching period of the larvae of the *lancea*-group (probably *A. lancea marinus*) in Faroese, south and west Icelandic waters is from the beginning (Faroes) or middle (Iceland) of March to May.
2. Off the north and east coasts of Iceland this period is probably from the beginning of May to the middle of June (cf. fig. 43).
3. The hatching of larvae in W.-Greenland waters (probably *A. lancea* dubius) takes place during the spring months, May and June.
4. The hatching period of *A. lanceolatus* is from May to the end of summer (at least in Faroese waters). An indication of two phases in the spawning was observed.

The difference in time of hatching between the larvae of the *lancea*-group and those of *A. lanceolatus* is clearly shown in fig. 54.

In Faroese waters most of the larvae of the *lancea*-group will

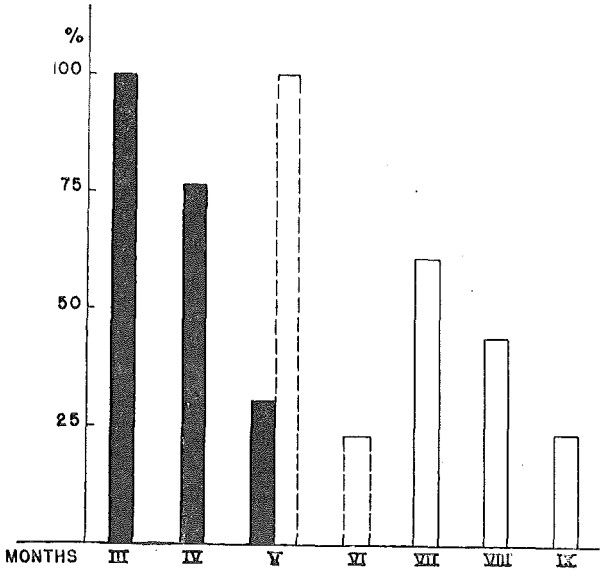


Fig. 54. Percentage frequency of post-larval stages of *Ammodytes* in Faroese waters, smaller than 10 mm. Black — the *lancea*-group. White — *A. lanceolatus*. Stipled columns — only few post-larval stages found.

hatch in temperature of about 5°—7° C (see *Tåning* 1936 a, p. 16, fig. 10). Off S.-Iceland these temperatures will also be prevailing in spring (see *Thomsen* 1938, p. 9, fig. 8). In the western fjords and bays they will be still lower, i. e. about 3°—5° C (*Thomsen* l. c., p. 17). And off the north and east coasts hatching may even begin in spring in water with temperature of about 2° C.

On the hydrographical conditions during the cruise of the „Dana" in W.-Greenland waters in 1925, *Baggesgaard-Rasmussen* and *Jacobsen* (1930) have given a clear account. It seems evident from their records that the hatching takes place in waters of negative temperatures or temperatures just above zero.

With regard to *A. lanceolatus* the larvae hatch at temperatures of 7°—10° C in shallower and 7°—8° C in deeper water off S.-Iceland. Off the Faroes similar conditions are met with.

APPENDIX TO PART II.

Distribution of all material of post-larval *Ammodytes* according to months, areas and size categories (5 mm. groups).

The lancea-group.

The Faroes 1924—1939.

Size groups	4	5–9	10–14	15–19	20–24	25–29	30–34	> 35	?	Average size	Total number
Northern Islands (N. of 61° 45′ N. Lat.)											
Late March	2	33								5,17	35
April	129	3014	955	18					2	77,59	4116 + 2
Early May		212	250	28					1	10,19	490 + 1
Late —		77	122	149	125	10				15,68	483
June			3	3	3	3	3		1	22,33	15 + 1
July				3	1	2	2	7	1	36,60	15 + 1
											5154 + 5
Suðuroy (S. of 61° 45′ N. Lat.)											
Late March	74	59								4,52	133
Early May		330	205	22						8,86	557
Late —		178	525	300	64	6	9	1		13,43	1083
June			3	13	9	3		5		22,15	33
July				1	2	3	1	3		27,80	10
											1816

Iceland 1924—1939.

Size groups	5–9	10–14	15–19	20–24	25–29	30–34	> 35	?	Average size	Total number
W.-Iceland										
June 1—15th		56	106	39	4			4	16,48	205 + 4
— 16—30th	2	41	60	63	24	3	1	1	19,05	194 + 1
July		3	11	24	27	22	1	3	24,33	88 + 3
August							1		(60,00)	1
										488 + 8

Size groups	5–9	10–14	15–19	20–24	25–29	30–34	> 35	?	Average size	Total number
N.-Iceland										
June 1—15th	3	135	74	6	1				13,96	219
— 16—30th				2	2				(23,50)	4
July			2	3	11	20	4		29,75	40
August							1	3	(42,00)	1 + 3
										264 + 3
E.-Iceland										
June 1—15th	73	20						1	8,56	93 + 1
July						1	1		(35,00)	2
										95 + 1
S.-Iceland										
June 1—15th	9	16	7	4			1		13,73	37
— 16—30th					1				(25,00)	1
July	1		3	5	8	5	23		31,38	45
										83

W.-Greenland 1925.

Area N. Lat	Date	5–9	10–14	15–19	20–24	25	> 25	?	Average size	Total number
60°—62°	5—6/6									
62°—64°	7—9/6			16	1			2	17,12	19 + 2
64°—66°	10—20/6		16	72	9			4	16,77	101 + 4
	1—14/7		13	60	77	4	4		19,59	158
66°—68°	21—30/6	390	284	113	4			2987	10,46	3778 + 2987
68°—70°	26—29/6	75	612	52	1			1742	11,91	2482 + 1742
										6538 + 4735

A. lanceolatus.

The Faroes 1924—1939.

Size groups	5–9	10–14	15–19	20–24	25–29	?	Average size	Total number
Northern Islands (N. of 61° 45′ N. Lat.)								
Early May	1						(6,00)	1
Late —	2						(8,00)	2
June	3	3	2	4			14,25	12
July	21	15	6	2		1	11,20	45
August	31	21	20	5			11,64	77
								137

Size groups	5–9	10–14	15–19	20–24	25–29	?	Average size	Total number
Suðuroy (S. of 61° 45′ N. Lat.)								
Late May	5						(6,20)	5
June	3	7	3	1			12,79	14
July	18	1					6,21	19
August	20	10	5	2	1	1	10,76	38 + 1
September	5	11	4	1			12,24	21
								97 + 1

Iceland 1924—1939.

Size groups	5–9	10–14	15–19	20–24	25–29	30–34	> 35	?	Average size	Total number
W.-Iceland										
June 1—15th	8	3							9,09	11
— 16—30th	9	21	15	1					13,35	46
July	9	37	28	13	8	7	3	1	17,21	105 + 1
August		1		1	1				(19,33)	3
										165 + 1
N.-Iceland										
July		1						1		1 + 1
August			1							1
										2 + 1
E.-Iceland										
July							1			1
										1
S.-Iceland										
June 16—30th	1	14	13	8	2				16,21	38
July		3	6	28	13	1	1		22,67	52
										90

SUMMARY

The present paper is mainly based in collections of post-larval stages of sandeels (*Ammodytidae*) taken during the years 1924—1939 by the Danish research vessels in Faroe, Iceland and W.-Greenland waters. The first part deals with the identification of post-larval stages of *Ammodytidae*.

1. Two post-larval types were identified in the material at disposal. According to previous identifications (*Ford* 1920, *Kändler* 1941), the one type, (figured on Plate I) is that of *A. lancea marinus* (vide *Kändler*) and the other type (figured on Plate II), that of *A. lancea lancea* (or *tobianus*) (vide *Ford*). The post-larval type described by *Ford* as *A. lanceolatus* was not observed in the collections from the areas considered.

2. A test by means of countings of vertebrae revealed that our second type (Pl. II), previously described as *A. tobianus,* is in fact the post-larva of *A. lanceolatus,* The Greater Sandeel. On the other hand, it was found that the subspecies of the *lancea*-group (The Lesser Sandeels) *A. lancea lancea* (or *tobianus*) *A. lancea marinus* and *A. lancea dubius,* have so similar post-larval stages that they cannot at present be distinguished by other means than by counting the vertebrae in specimens more than 20 mm. in length. This post-larval type proved to be correctly identified by *Kändler* as *A. marinus* and is figured on plate I.

3. Accordingly it is concluded:
   a. that the previous data on post-larval stages of *A. lancea marinus* must apply to *A. lancea lancea* (*tobianus*) as well.
   b. that the previous data on post-larvae of *A. lancea lancea* (*tobianus*) must be referred to *A. lanceolatus,* and
   c. that previous data on post-larvae of *A. lanceolatus* must be referred to another species of *Ammodytidae,* not definitely known as yet, but most probably *Gymnammodytes*

semisquamatus (The Smooth Sandeel), which seems to be fairly common in Scottish and English waters and which post-larval stages have hitherto not been recorded.

4. In the meantime *Corbin & Vati* (1949) published a paper stating that they had observed vomerine teeth in post-larvae described by *Ford* and *Kändler* as *A. lanceolatus,* a result that seemed incompatible with the conclusions of the present paper. In an appendix it is shown that the post-larvae identified by the present author as *A. lanceolatus,* but previously as *A. tobianus,* develop vomerine teeth, the beginnings of which can be seen in post-larvae of about 20—25 mm. length. It is suggested that the vomerine teeth observed in *Ammodytes* sp. by *Corbin & Vati* are larval teeth, and that this post-larval type most probably belongs to *G. semisquamatus.* When this interpretation of the observational data is applied, various discrepancies in vertebral numbers of post-larvae and adults seem satisfactorily explained.

The latter part of the paper contains a detailed analysis of the distribution of post-larval stages of sandeels in the areas considered.

5. The post-larval stages of the *lancea*-group, encountered in *Faroese waters,* belong mostly to *A. lancea marinus,* as indicated by the vertebral counts. The spawning occurs mainly between the islands and in the fjords, but also in offshore waters. The predominance of sandy bottom around the isles favours the existence of extensive spawning areas in these waters. The hatching begins in the latter half of March and continues throughout April until the beginning of May when it falls off rapidly. In certain years, as e. g. 1925, hatching may still occur in the latter half of May, especially in deeper, offshore waters, where the hatching starts later than in the fjords and may also require more time because of the slower vernal warming up of the water masses. The newly hatched post-larvae are most numerously found in the surface layers of the sea, especially where the depth is from 50—150 m.

6. Vertebral counts of advanced post-larval stages show, that both *A. lancea lancea* and *A. lancea marinus* are present in *Icelandic waters,* the former being confined to the south and south-west coasts, while the latter was found off all the coasts of the country. Observations from the beginning of the hatching period are not available, but in the middle of April (1904) hatching has begun off the south

and west coasts and the length distribution of post-larval stages indicates that hatching must have begun in early April or perhaps in late March. In these boreal waters hatching comes to an end in the latter part of May. About the middle of May the hatching seems to begin off the north and east coasts, continuing until about the middle of June. The collections from Icelandic waters contain mainly advanced post-larval stages. These were most frequent in about 10—15 m. depth, the greatest number being found inside the 50 m. depth contour.

7. The few post-larval stages from *W.-Greenland waters*, in which vertebrae could be counted, belong to *A. lancea dubius*. Judged by the size distribution during June hatching begins in late April or the beginning of May in southern W.-Greenland waters. It is still continuing in the area north of 66° N. Lat. at the end of June, but in the beginning of July hatching has ceased everywhere in these waters. The newly hatched fry was mainly found in 20—30 m. depth (100 mw) and predominantly in shallow water, the frequency falling off rapidly when the depth of the sea exceeded about 150 m.

8. The main spawning grounds of *A. lanceolatus* in *Faroese waters* lie inside the fjords and between the isles. The hatching begins in the last part of May and continues throughout summer. Two phases in the spawning are indicated. The one, with low spawning intensity in May—June, and the other, with greater spawning intensity in July—September. The newly hatched post-larvae were found quite near the surface. All the fry was taken inside 150 m. depth of the sea and was most frequent inside 50 m. depth.

9. The post-larval stages of *A. lanceolatus* are confined to the south and west *Icelandic coastal waters*. Presumably hatching begins in May, although positive hauls were not made during that month in 1934. The small percentage of small post-larvae indicates inadequate sampling during the hatching period. The frequency of small post-larval stages was highest in June. Hatching apparently comes to an end in August. The post-larval stages were most frequent quite near the surface and, remarkably enough, reached their maximum frequency where the depth of the sea was about 250 m.

10. A survey of the occurrence of *Ammodytes* in northern waters is given.

11. Temperature conditions in relation to hatching are discussed.

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Plate I.

The lancea-group *(A. lancea marinus)*.

a. Post-larva 4,5 mm. Stat. 5325, 6/4 1935, 30 mw.
b. Post-larva 6,0 mm. Stat. 5325, 6/4 1935, 30 mw.
c. Post-larva 11,0 mm. Stat. 2108 1924, 6/6 1924, 65 mw.
d. Post-larva 16 mm. Stat. 2108 1924, 6/6 1924, 65 mw.
e. Post-larva 33 mm. Stat. 5986, 20/7 1938, 100 mw.
f. Same as e.

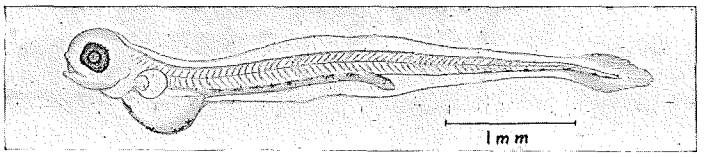
Plate II.

A. lanceolatus.

a. Post-larva 6,0 mm. Stat. 3124, 18/7 1927, 65 mw.
b. Post-larva 11,0 mm. Stat. 3310, 23/8 1927, 35 mw.
c. Post-larva 16 mm. Stat. 3125, 18/7 1927, 65 mw.
d. Post-larva 25 mm. Stat. 3124, 18/7 1927, 65 mw.
e. Same as d.

PLATE I.

1



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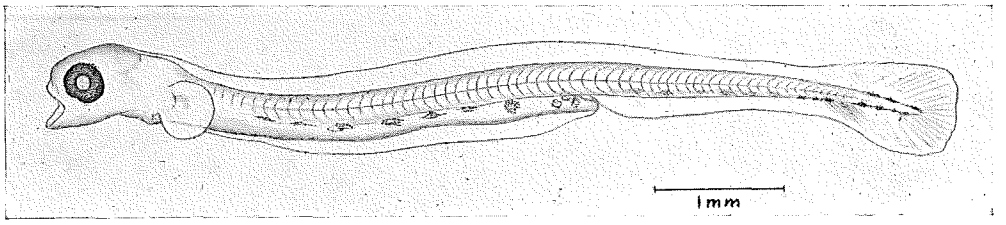

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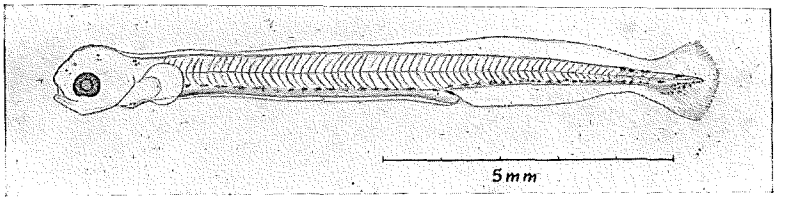

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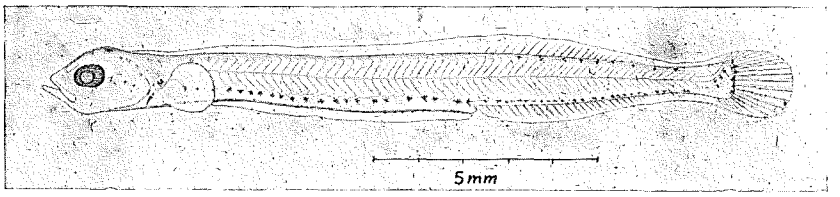

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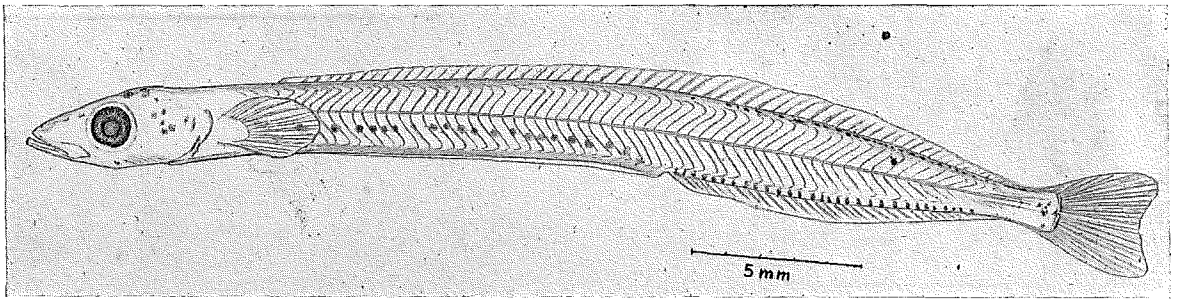

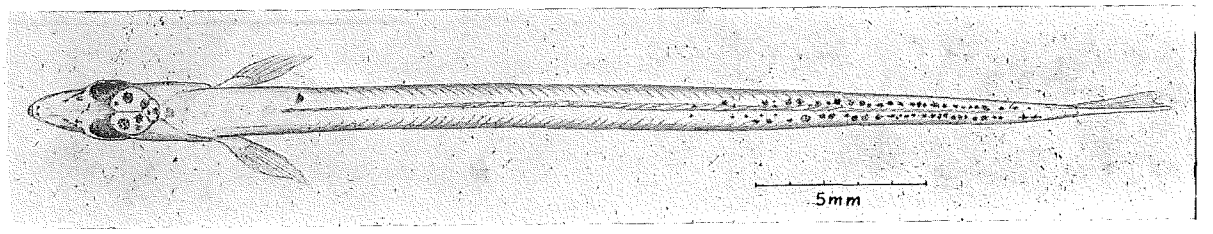

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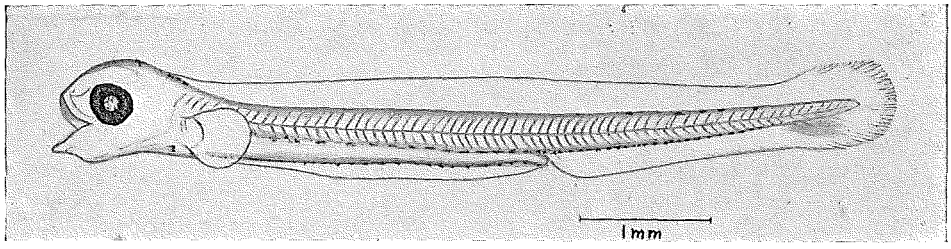
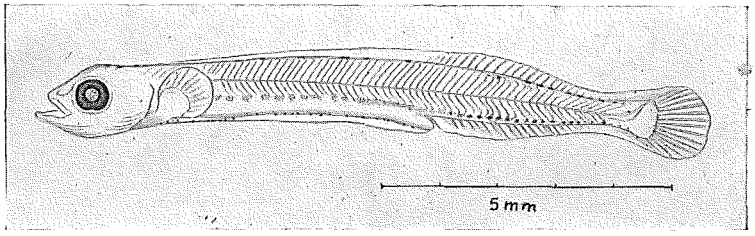
PLATE II.

1



2



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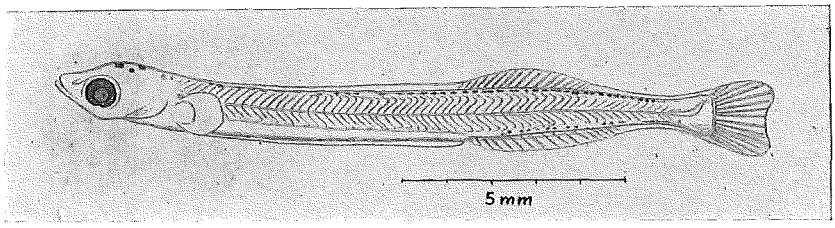

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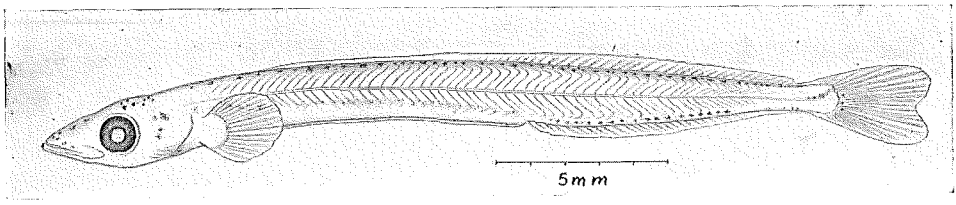

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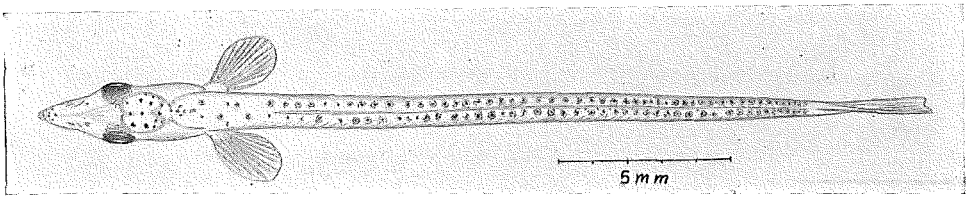

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