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ON SPECIFIC CONSTANCY AND SEGREGATION INTO RACES IN SEA-FISHES

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CONTENTS

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I.

Race-forming species.

In 1901 the present author showed that the species *Lycodes vahlii* Reinhardt belonging to the subfamily *Lycodinae* (family *Zoarcidae*) falls into three races each of them inhabiting a distinct geographical area, viz. South Scandinavia, Iceland and Greenland. These races are very much alike inter se, only differing from each other by the number of vertebrae and rays in the median fins, as will appear from the table below quoted from the above paper:[1]

	Scandinavia	Iceland	Greenland
Number of vertebrae............	98—101	105	112—116
— - rays in dorsal fin. . .	95—96	103—105	113—117
— - - - anal fin......	85—86	90	90— 98

It will be seen that the number of vertebrae and rays in the median fins increases from warmer to colder regions. In harmony with this variation there is an increase in the body size; measurements of a great number of individuals showed that no specimen larger than 196 mm was known from the Kattegat, the Skagerrak and southern Norway, while the largest specimen from Iceland was 355 mm long and the largest specimen from Greenland 520 mm.

These races had earlier been regarded and described as distinct species, the Scandinavian as *Lycodes gracilis* M. Sars (1866), the Icelandic as *L. lugubris* Lütken (1880) and the Greenland race as *L. vahlii* Reinhardt (1831), but were by me referred as races to one and the same species and called *L. vahlii gracilis*, *L. vahlii lugubris* and *L. vahlii typica*.

In my monograph: "The North-European and Greenland

[1] The notes will be found in the appendix to the paper.

Lycodinae"[2] the question has been resumed and treated in more detail on pages 13—21, and the correctness of my preliminary notice has been confirmed.—In the appendix on page 21 it is stated that I had the opportunity to examine a specimen from northernmost Norway (Baas Fjord in East Finmark) which differed from *L. vahlii gracilis* by having 101 rays in the dorsal fin, 89 in the anal fin, and by its considerable size, 268 mm, and which approached the Icelandic *L. vahlii lugubris*; this was explained by the fact that in the fjords of East Finmark "the conditions are half arctic."

In the common Gunnel, *Pholis gunellus* L. (syn. *Centronotus gunellus*) I found similar conditions as in *Lycodes vahlii*, the number of vertebrae and rays in the dorsal and anal fins being somewhat greater in the Greenland than in the European specimens, while the Icelandic specimens form a transition. This will be seen from the table below which is based on 12 specimens from Denmark, 19 from Iceland and 12 from Greenland.

	Number of vertebrae	Mean	Number of dorsal fin rays	Mean	Number of anal fin rays	Mean
Denmark .	84—87	85.2	77—80	78.8	42—46	43.7
Iceland. . .	85—88	86.5	78—81	80.1	43—46	44.3
Greenland	85—89	87.5	79—82	81.1	44—48	45.1

As regards this fish also we are confronted with the phenomenon that colder conditions—from Denmark via Iceland to Greenland—are correlated with a higher number of vertebrae and fin rays[3].

As a third example of the fact that the sea area from the Kattegat towards the northwest across the Faroes and Iceland to Greenland, with its gradually decreasing temperature of the water, caused the segregation of a species into races may be mentioned the species *Triglops pingelii* Reinhardt belonging to the Sculpins (*Cottidae*). An investigation of 240 specimens for number of vertebrae and rays in the 2nd dorsal fin and the anal fin recently published by me[4] shows that within this area four races can be distinguished, the average numerical values of which will appear from the table below:

	Vertebrae	2nd dorsal fin	anal fin
1. *T. pingelii murrayi:* Kattegat, Skagerrak, North Sea, Scotland, Shetland and Faroes	42.7	20.4	20.0
2. *T. pingelii islandicus:* Iceland . .	43.6	21.4	21.0
3. *T. pingelii pietschmanni:* Davis Strait and central West Greenland	45.0	22.3	22.2
4. *T. pingelii pingelii:* Southern and northern West Greenland and East Greenland	48.5	24.8	24.8

Moreover, in a number of specimens which had to be spared, only the fin rays were counted and there was no change in the result.

Considered as a whole the number of vertebrae in *Triglops pingelii* may vary from 42 to 51, the number of rays in D_2 from 18 to 28 and in A from 18 to 28, which is a considerable range of variation.

It will be seen from the table that the average number of vertebrae and fin rays in D_2 and A increases gradually as we proceed from warmer to colder seas. There is a distinct correlation between the temperature of the water and the average values both for vertebrae and rays in D_2 and A.

It also appeared that the body size increases in arctic areas, the largest individuals available from the area of the Kattegat-Faroes and Iceland being 125 mm, while individuals from Greenland attain a length of 200 mm.

The fact that the race with the highest number of vertebrae and fin rays (*T. pingelii pingelii*) occurs in southernmost West Greenland, while the race with the somewhat lower number of vertebrae and fin rays (*T. pingelii pietschmanni*) is found in central West Greenland might seem to be an exception to the rule that these numerical values increase from south to north. The contrast is only apparent; this agrees precisely with the hydrographic conditions since the cold polar current coming from East Greenland round Cape Farewell has a stronger influence on southernmost West Greenland than on central West Greenland where the polar current is much weakened.

Still another example can be given. The writer has advanced the view[5] that *Ammodytes lancea* Cuv. (*A. tobianus* autt., non Linné), *A. marinus* Raitt and *A. dubius* Reinhardt do not represent separate species, but are only subspecies of one species, characterized by an increasing number of vertebrae and fin rays:

	Number of vertebrae	Mean	Number of dorsal fin rays	Mean	Number of anal fin rays	Mean
A. lancea lancea . .	60—66	62.6—64.5	51—57	52.9 —54.7	26—31	27.1—28.4
A. lancea marinus	66—73	68.5—71.5	55—63	59.05—61.0	28—34	30.27—31.9
A. lancea dubius .	73—80	75.1	60—68	64.71	30—36	33.16

Considered as a whole the number of vertebrae in *Ammodytes lancea* s. lat. may thus vary from 60 to 80, D. from 51 to 68 and A from 26 to 36, a remarkably great range of variation.

It is stated for *Ammodytes lancea lancea* that it spawns in the spring (April to May) and the summer (August to September), at any rate in the Baltic and the North Sea, according to Kändler[6]. I suppose that under the influence of high temperatures its young developed a lower number of vertebrae and fin rays than *A. lancea marinus*, the spawning period of which occurs in the winter (December to February) with the low temperatures (the hydrographical winter temperature falling as low as 3° C. mean or even lower). A still higher number of vertebrae and rays in dorsal and anal fins is found in *A. lancea dubius* which is a pronounced arctic form, since it occurs in Greenland; and it is the predominant form there, since 233 specimens have been available for counting the vertebrae against only 38 specimens of *A. lancea marinus*.

Simultaneously with my paper Kändler published a work in which he holds the same view as in his earlier preliminary notice, viz. that *A. marinus* is a distinct species. I cannot, however, change my view[7].

By the investigation of a huge material of cod (*Gadus callarias* L.), about 20.000 specimens derived from 114 localities, Johs. Schmidt[10] came to the result that the number of vertebrae, at any rate in open waters, decreases as we proceed from north to south. This applies both to the western part of the area from Labrador and southward to U.S.A., and to the eastern part from northern Norway to the North Sea, and from Iceland to western Scotland and England. The average number of vertebrae proved to be influenced—directly or indirectly—by the temperature of the water, in such a manner, that the populations under lowest temperatures have the highest number of vertebrae and vice versa. The 2nd dorsal fin also, like the vertebrae on the whole, showed correlation between the number of rays and the temperature.

The expression "north to south" used by Schmidt should not be understood to mean that the geographical degree of latitude is the decisive factor, it is the temperature conditions in the locality which are of importance; this appears from Schmidt's own account and is also expressed in the above brief summary of his paper. A table of the average number of vertebrae with a table of the surface isotherms in the whole area discussed is given by Schmidt in his Pl. II, l. c.

A striking example showing that it is hydrographical conditions and not the degree of latitude which are decisive is clearly shown by Sven Runnström in his paper: "Racial Analysis of the Herring in Norwegian Waters"[11], in which he writes on p. 86: "As regards the Norwegian spring-herring we found a decreasing number of vertebrae from south to north, which is apparently in contradiction to the general rule. However, we have stated that the salinity and temperature along the Norwegian coast increases northwards and thus the variation in the vertebral number is in good accordance with the presumed effect of these factors[12]. In the same manner we found that the vertebral number of the spring spawning groups in northern North Sea increases from west to east with falling salinity and temperature".

As mentioned on p. 5 I found a parallel to this in *Triglops pingelii*: In southernmost West Greenland which is strongly influenced by the cold polar current coming from East Greenland the number of vertebrae and rays in D_2 and A is greater than in central West Greenland, where the polar current is much weakened.

In several fishes a correlation has thus been proved to exist between the temperature of the sea water and the number of vertebrae, and sometimes also the rays in certain median fins.

That the number of vertebrae in races of the herring (*Clupea harengus*) may even vary with the fluctuations in environmental factors[13] has, so to speak, been proved by Nature herself in recent years by a large-scale experiment. In 1936 Runnström[14] called attention to the fact that the number of vertebrae in the herring of Iceland which he examined in 1932 and 1933 was lower than that found by A. C. Johansen[15] on the Icelandic herring for the years 1919—1924. Runnström adds: "perhaps this phenomenon can be explained by changes in the hydrographical conditions on the spawning grounds". Further I may quote the following statement in Runnström's above-mentioned work from 1941 (pp. 92—93):

"..... the mean vertebral number of the Norwegian spring herring in present time is lower than that found by Broch in the years 1904—1906[16]. Also the vertebral number of the Icelandic spring herring in the period 1932—34 was considerably lower than the mean found by Johansen in the year 1924. Also as regards the Faroe herrings Wood[17] found a much lower vertebral number than earlier stated by Johansen, and according to Lissner[18] the autumn spawning herring in the North Sea also seems to have a lower mean value than the commonly accepted one. Undoubtedly the northern waters have had a rather "warm" period in recent years, as pointed out by Ad. S. Jensen[19], which may have lowered the vertebral number of the herring in these waters".

It can be added that Vedel Tåning[20] who examined samples of herrings caught in Iceland in 1936 came to the same result as Runnström, viz. that the average number of vertebrae in these quite young herring, both spring and summer spawning herring, was equal to that recorded by Runnström in mature herring a few years ago, but lower than the value found by Johansen in 1919—1924.

Runnström further states that Rounsfell and Dahlgren[21] and Tester[22] have found that the mean vertebral count of successive year classes of the Pacific herring (*Clupea pallasii*) along the west coast of North America varies inversely with the temperature of the water during the period of spawning and early development.

It might be asked whether the temperature is the only factor capable of influencing the average values of the number of vertebrae and fin rays, since it might be presumed that the salinity might also be of importance. To clear up this question JOHS. SCHMIDT examined the cod and came to the conclusion thal the salinity in the North Atlantic area does not seem to point to any closer connection between the variations of this factor and of the characters investigated, as was the case in respect of the temperature[10].

While no experiments have been made with a view to changing the number of vertebrae and fin rays by changing the temperature at a very early stage in the development of the fishes mentioned above, many investigators have studied the influence of the temperature on the rate of development of the eggs of fishes. The results all show that high temperatures increase the rate of development and that low temperatures delay it. Worth special mention is a series of accurate measurements of the average rate of development of the eggs made by DANNEVIG[23] on five species of salt water fishes; the results were as follows:

Temp. in °C.	−1°	3°	4°	5°	6°	8°	10°	12°	14°	
Gadus callarias	42	23	$20^1/_2$	$17^1/_2$	$15^1/_2$	$12^3/_4$	$10^1/_2$	$9^2/_3$	$8^1/_2$	Time of incubation in days (24 hours).
— *merlangus*	..	..	..	$15^1/_3$	$13^1/_2$	$10^1/_4$	8	$6^1/_2$	$5^3/_4$	
— *aeglefinus*	42	23	$20^1/_2$	$17^3/_4$	$15^1/_2$	13	$10^3/_4$	$9^2/_3$	$8^3/_4$	
Pleuronectes platessa	..	..	..	..	$18^1/_4$	$14^1/_3$	12	$10^1/_2$	..	
— *flesus*	..	..	..	..	$6^1/_2$	$5^1/_2$	$4^1/_2$	$3^2/_3$	..	

Cf. also WORLEY whose experiments on the development of the egg of mackerel (*Scomber scombrus*) at different temperatures (10°—24° C.) showed that typical development could be realized only between 11° and 21°; the length of the developmental period increases from $49^1/_2$ to 207 hours when the temperature is lowered from 21° to 10° C.[24]

In this country JOHANSEN and KROGH[25] by their studies on the influence of the temperature on the development of eggs of cod and plaice partly confirmed the result of DANNEVIG's experiments, partly continued them. But they explain the influence of the temperature on the rate of development of the eggs on the basis of the following quite new views: "There is no reason to believe that a supply of energy in the form of heat could be utilized at all by the embryos. The energy, which is undoubtedly necessary for the development, is derived in the case of fish eggs, as in all other eggs, from the chemical processes involved in the metabolism of the eggs, and an outward sign of this is that a certain proportion of the nutritive material contained in the eggs, disappears during development, being oxidized to carbon dioxide and water and yielding energy. The temperature must be looked upon as a factor which will have a certain influence upon the velocity of the chemical reactions and other processes involved in the development".—As far as I know, nobody has studied this part of the problem since Johansen and Krogh's paper appeared in 1914.

II.

Constant species.

In the preceding part we have mentioned fishes in which there is correlation between the temperature of the sea water and the number of vertebrae and rays in the median fins, whereby local races can be distinguished.

We shall now consider two species of fish, each having a wide geographical distribution, where the individuals live under very different conditions without forming races.

In the first place the European eel (*Anguilla anguilla* Linné[26]) should be mentioned, on which Johs. Schmidt has undertaken a comprehensive racial study[27]. After examining 5—6000 specimens from its vast area of distribution—from Iceland, the Faroes and the White Sea along Europe down to North Africa and from the adjoining seas, the Baltic and the Mediterranean with the Black Sea and the Sea of Azov and from the rivers and lakes connected with all the areas mentioned here—he was able to show that all eel populations, even those from the most far-away corners of Europe displayed identical average values as regards the number of vertebrae; all European eels belong to one and the same species, within which it was impossible to demonstrate the existence of local races[28]. This, Schmidt says, is due to the fact that all European eels are born in the same locality. By purposeful and untiring exploration, through 25 years, of the Atlantic, from Iceland to Morocco and from Egypt to

America, Schmidt succeeded in demonstrating that the eels from Europe travel over the Atlantic to the Sargasso Sea where they spawn in the spring. The spawning region of the European eel lies in an area to the north-east of St. Thomas and south-east of the Bermudas, where the depth is more than 6000 m, for here, and only here, were the newly hatched larvae found, their length being 5 to 7 mm; they float 200—300 m below the surface in water layers, the temperature of which is about 20° C. The larvae (*Leptocephalus brevirostris*) gradually rise to the upper water layers, and are then carried towards Europe by the east-going movement of the North Atlantic current, and later on, when the youngest stages of development have been passed, also by their own active movements—a journey that lasts between two and three years. The first development of the eel, including the formation of the vertebrae, takes place under quite uniform hydrographic conditions[29].

The same view may be applied to the other species of *Anguilla* of the Atlantic, the American *A. rostrata* Le Sueur[30]. It occurs in south-western Greenland and Labrador; it is abundant in Canada and the United States, in the northern part of Mexico, partly also in the West-Indian archipelago; it is also found in the southern part of Mexico and in Panama and in South America in Guiana[31]. Of the American eel 863 specimens were examined and it appeared that it is distinguishable from the European eel, of which 2775 specimens were examined, by means of the average number of vertebrae: *A. rostrata* 107, 250, *A. anguilla* 114, 728[32]. In *A. rostrata* too Schmidt could not demonstrate races. This is due to the fact that all the American eels have common breeding grounds, situated in a small section of the warm, deep Sargasso-Sea north of the West-Indian Islands, for the most part somewhat farther west and south than the European Eel, and that they spawn a couple of months earlier in the year, as early as January and February; here hundreds of the early tiny larvae, 7—8 mm long, were caught. Gradually as the larvae (Leptocephals)[33] increase in size they spread out in the western Atlantic to the north and to a smaller extent to the south. The full development from egg[34] to elver is completed in only about one year; the elvers are then close to the American coast and seek the shores and river mouths. The European eel, on the other hand, has many months in which to exist as larva before the metamorphosis, and during this time it is carried towards and makes for Europe[35].

III.

Correlation between temperature and number of vertebrae in genera.

In section I it was exemplified how the temperature of the water influences countable characters in certain marine fishes, viz. vertebrae and rays in the median fins, which are the characters by which races within these species are distinguishable from each other. It was also exemplified how fishes which had previously been described as distinct species, actually belong to a single species, the presumed species corresponding to races, the distinctive features of which, the number of vertebrae and fin rays, are also correlated with the different temperature conditions under which these fishes breed.

But not only this. Within certain families the genera of which are distinguishable from each other by good characters usually employed in ichthyology, some genera belong to tropical, others to temperate seas. The species within the genera distributed in warm seas have been found to possess a low number of vertebrae, while the species of genera from colder seas have a high number of vertebrae. As these investigations, which were made in the latter half of the last century, throw light on the development of higher systematic units, they will be briefly dealt with in the following.

The first to direct attention—in 1862—to this was the famous German-English zoologist Albert Günther. In the 4th volume of his monumental work in eight volumes on the fishes of the world Günther writes as follows in the introduction to the family Lip-fishes (*Labridae*): "A character which has been entirely overlooked, but which, for the further division of Labridae, is as important as that taken from the dentition or from the structure of vertical fins, is that of the number of the vertebrae, the value of which has been maintained by me on several occasions. It will be evident, from the numerous statements contained in the following pages (65—244), that in those genera which are composed entirely or for the greater part of tropical species, the vertebral column is composed of 24 or nearly 24 vertebrae, whilst those which are chiefly confined to the temperate seas of the northern or southern hemisphere have that number increased[36]".

In the following years several of the leading ichthyologists of America, GILL, JORDAN, GOSS, GILBERT and EIGENMANN, gave notice that they too had found that there existed a correlation between temperature and vertebrae in many other families and genera of bony fishes; *Clupeidae, Labridae, Scorpaenidae, Blennidae* and *Pleuronectidae* were pointed out as examples hereof.

In 1891 JORDAN gave a statement of what was known of this subject and he drew the following conclusion from the last 30 years' investigations in this field: "In many groups of fishes the northern or cold-water representatives have a larger number of vertebrae than those members which are found in tropical regions[37]".

In these papers JORDAN has a small section on the variations in fin-rays and he writes about this: "In some families the number of rays in the dorsal and anal fins is dependent on the number of vertebrae. It is therefore subject to the same fluctuations". As examples hereof he mentions some genera within the family *Scorpaenidae.*

As a striking example showing that there is a relation between the number of vertebrae and geographical distribution JORDAN and EVERMANN in their large work mention the family *Pleuronectidae*[38] and write in the introduction (p. 2603) that in no group of fishes is it more striking that the northern representatives have the number of vertebrae increased. They give numerous examples of this and attach so much importance to the number of vertebrae that they include this character in the subdivision of the flounders into genera.

Summary.

I.

In a series of species of marine fishes, *Lycodes vahlii, Pholis gunellus, Triglops pingelii, Ammodytes lancea, Gadus callarias* and *Clupea harengus,* with a wide geographical distribution, there is a correlation between the hydrographic conditions and the vertebrae, the latter increasing in number with decreasing temperature. Within these species local races can be distinguished which are characterized by the average numbers of vertebrae. Since the formation of the vertebrae takes place at a very early stage in the development, and as the vertebrae remain unchanged throughout life, the formation of races within each species is correlated with the temperature conditions prevailing in its different breeding areas. What has been said here of the vertebrae partly applies also to the number of rays in the dorsal and anal fins. In *Lycodes vahlii* and *Triglops pingelii* an increase of body size in relation to decreasing temperature has likewise been shown to exist.

II.

For two other species of fish which also have an enormous geographical distribution, viz. *Anguilla anguilla* and *Anguilla rostrata*, no local races can be demonstrated on the basis of the vertebral number or other characters although these species live under very different hydrographic conditions. When these fishes are going to propagate they do not breed in the places where they grew up, but all of them migrate to the same area, the Sargasso Sea, where egglaying and the very first stages of development, thus also the formation of vertebrae, take place; this explains why these fishes, no matter how far they migrate, preserve their constancy of species and do not segregate into races.

III.

In the latter half of the last century the leading ichthyologists of Europe and America called attention to the fact that in many genera of bony fishes erected on the usual good characters there is a correlation between temperature and vertebrae, so that the species within genera distributed in warm seas have a low number of vertebrae, while species of genera from cold seas have a high number of vertebrae. These conditions throw light on the development of higher systematic units.

Notes.

[1] Ad. S. Jensen: Ichthyologiske Studier, II: Om en mærkelig Variationsrække af *Lycodes vahlii* Reinh. Vidensk. Meddel. fra den naturhist. Foren. i Kbhvn. 1901, pp. 202—204.

[2] The Danish Ingolf Expedition, II. 4, 1904.

[3] Ad. S. Jensen: Contributions to the Ichthyofauna of Greenland, I—III, p. 40. Spolia Zoologica Musei Hauniensis, II, 1942.

[4] Ad. S. Jensen: Contributions to the Ichthyofauna of Greenland, IV—VI, p. 13-23. Spolia Zoologica Musei Hauniensis, IV, 1944.

[5] Ad. S. Jensen: On subspecies and races of the Lesser Sand Eel (*Ammodytes lancea* s. lat.). Kgl. Danske Vidensk. Selsk. Biologiske Meddelelser XVI, 9. 1941.—After this paper had been published I received from Mr. Paul Hansen, fishery biologist, 53 specimens of *Ammodytes*, 31.5—48.5 mm long, extracted from the stomach of the charr (*Salmo alpinus*) caught on July 17th 1932 in Amitsuarssuk, a branch of the Godthaabfjord. All these 53 specimens were examined for the number of vertebrae, and the mean figure proved to be 75.07, thus agreeing with that found for *A. dubius*; one of the specimens was however peculiar in having 80 vertebrae, while the highest number previously found in Greenland *Ammodytes* was 78.

[6] R. Kändler: Beobachtungen über die Laichzeiten der *Ammodytes*-Arten in Nord- und Ostsee. Zool. Anz., Bd. 118, 1937, p. 1.

[7] Rudolf Kändler: Untersuchungen über Fortpflanzung, Wachstum und Variabilität der Arten des Sandaals in Ost- und Nordsee, mit besonderer Berücksichtigung der Saisonrassen von *Ammodytes tobianus* L. Kieler Meeresforschungen, Bd. V, Heft 1, 1941, pp. 45—145.

As regards the adult individuals Kändler is of the opinion that the species *A. marinus* and *A. lancea* can be distinguished from each other by the colour, since the former is bluish-green on the upper side, while the latter is generally more yellow-green and lighter. It is however a well known fact that the colours in one and the same species of fish may vary very much, especially in harmony with the surroundings; as *A. marinus* is a high sea fish it is quite natural that the upper side should assume a bluish-green colour, while *A. lancea* which lives in shallow water near the shore acquires a yellow-green and lighter tinge corresponding to this area. Otherwise Kändler as well as Bruun[8] and I cannot accept Duncker and Mohr's statement that *A. marinus* differs from *A. lancea*, besides by the two ventro-lateral skin folds, by possessing a third somewhat lower skin fold in the midventral line, whereas *A. lancea* lacks such a fold; Kändler says about this that he has not been able to prove any essential difference in the numerous specimens which he had before him, a low keel-like skin fold is found in both species.

In this paper Kändler reports an interesting observation which he has made: The young stages of *A. marinus* are easy to distinguish from those of *A. lancea* by the different pigmentation; this feature is described on pp. 64—66 and illustrated by a series of text figures. Kändler attaches much importance to this and believes that the different distribution of the pigment in these larvae shows that they belong to two different species. In this connection I call attention to the fact that JOHS. SCHMIDT in his great work: "The pelagic postlarval stages of the Atlantic species of Gadus", Part II, pp. 4–5[9] states that larvae of the common cod (*Gadus callarias*) from the southern North Sea and the inner Danish waters deviate from those of the northern North Sea, the Skagerrak, the Faroes and Iceland in that the pigment is much weaker and in that the hindmost postanal pigment band, which in the more northern sea areas in the small young of cod is an important mark of recognition, is quite lacking in several specimens. I doubt therefore that a difference in the distribution of the pigmentation in the two larval forms of *Ammodytes* should be interpreted to mean that the two forms belong to two species.

The young stages of *A. marinus* from the Baltic are considerably more slender than equally large specimens from the North Sea and than young *A. lancea* according to KÄNDLER; consequently no specific difference can be traced in that respect.

There only remain the differences in the number of vertebrae and rays in the dorsal and anal fins; as will be seen from the table on p. 6 they clearly show a division, although with transitions, of the species into three groups which I called subspecies in my earlier paper, but which I now consider it more correct to designate as races. As shown by KÄNDLER, there exist again two races of *A. lancea lancea* which have different breeding times (spring and summer) and which show considerable differences in the number of vertebrae and fin rays, although it comes within the limits for *A. lancea lancea.*

KÄNDLER studied the structure of the otoliths most thoroughly and it proved to differ according to different breeding times. Thereby it became possible to distinguish the *Ammodytes* forms from each other, and age and growth conditions could now be determined.

In 1941 (Fauna och Flora, p. 24) the Swedish zoologist YNGVE LÖWEGREN gave his view on *Ammodytes.* In catches with a seine on the south and east coast of Skåne he found 955 *A. lancea* ("*A. tobianus*") and only 29 *A. marinus*, but he emphasizes himself that this is due to the fact that *A. marinus* prefers deeper water. Only by the study of the number of vertebrae and fin rays can the two species be distinguished, in outer appearance they are practically alike, according to LÖWEGREN.—A small correction may be made in L.'s map fig. 4; it shows that *A. marinus* occurs in eastern Greenland, but in my paper I write on p. 17: "*Ammodytes* is not known from the east coast of Greenland".

[8] ANTON FR. BRUUN: The *Ammodytes lancea* group. Vidensk. Meddel. fra Dansk naturhist. Foren., Bd. 104, 1941, p. 329.

[9] Meddel. fra Kommiss. f. Havundersøgelser, Serie: Fiskeri, Bd. II, No. 2, 1906, pp. 4—5.

[10] JOHS. SCHMIDT: The Atlantic cod (*Gadus callarias* L.) and local races of the same. Comptes-rendus des travaux du Laboratoire Carlsberg, 18° volume, no. 6, p. 1—71, Pl. I—X. Copenhague 1930.

[11] Report on Norwegian Fishery and Marine Investigations, Vol. VI, No. 7, 1941.

[12] The rising temperatures and salinities of the coastal water from south to north are due to an inflow of cold Baltic water with low salinity from the south, which is gradually intermingled with warmer and more saline Atlantic water along the coast (RUNNSTRÖM l. c. p. 92).

[13] This should not be understood to mean that the vertebral number of the adult fishes can be altered; it is a well known fact that the formation of the vertebrae takes place at a very early stage of the development, and that the vertebral number hereby is fixed for the rest of the life of the fish.

[14] SVEN RUNNSTRÖM: The distribution of the Atlanto-Scandian Spring-Herring. Rapp. et Proc.-Verb. du Conseil Internat. pour l'explor. de la Mer, Vol. C, 2. Part, pp. 25—26.

[15] A. C. JOHANSEN: On the summer-spawning herring of Iceland. Meddel. fra Kommiss. f. Havundersøgelser, Bd. VI, No. 3. 1921—*Idem*: Investigations on Icelandic herrings in 1924 and 1925. Rapp. et Proc.-Verb. du Conseil Internat. pour l'explor. de la Mer, Vol. XXXIX, 1926.

[16] Hj. Broch: Norwegische Heringsuntersuchungen während der Jahre 1904—1906. Bergens Museums Årbok 1908.

[17] M. A. Wood: In "Report of North-Western Area 1934". Rapp. et Proc. Verb. du Conseil Internat. pour l'explor. de la Mer, Vol. XCIV. 1935.

[18] H. Lissner: On races of herrings. Journal du Conseil, Vol. IX, 1934.

[19] Ad. S. Jensen: Concerning a change of climate during recent decades in the Arctic and Subarctic regions, from Greenland in the west to Eurasia in the east, and contemporary biological and geophysical changes. Kgl. Danske Vidensk. Selskab, Biol. Meddel. XIV, 8, 1939.

[20] Å. Vedel Tåning: Rapp. et Proc.-Verb. du Conseil Internat. pour l'explor. de la Mer, Vol. CIX, p. 16. 1938—39.

[21] G. A. Rounsefell and E. H. Dahlgren: Fluctuations in the supply of herring (*Clupea pallasii*) in Prince William Sound, Alaska. U. S. Bur. Fish. Vol, 47, Bull. no. 9, 1932.

[22] A. L. Tester: Variation in the mean vertebral count of herring (*Clupea pallasii*) with water temperature. Journal du Conseil, Vol. XIII, 1938.

[23] Harald Dannevig: The Influence of Temperature on the Development of the Eggs of Fishes. 13. Ann. Rep. of the Fishery Board for Scotland, being for the year 1894, Part III, p. 149. 1895.

[24] Leonard G. Worley: Development of the eggs of mackerel at different temperatures. The Journal of General Physiology. Vol. 16, 1933, p. 841.

[25] A. C. Johansen and A. Krogh: The influence of temperature and certain other factors upon the rate of development of the eggs of fishes. Cons. perm. internat. pour l'explor. de la Mer, Publ. de Circonstance, No. 68, 1914.

In a succeeding paper Krogh continued the investigations on other groups of animals (eggs of frogs, an insect and a few sea urchins) and in all cases found a straightlined relation between the temperature and rate of development within the temperature interval in which development normally takes place. At the lowest temperatures at which development is possible the rate seems to be relatively a little greater. As the determination applies to very different types Krogh is of the opinion that there is reason to believe that this relation will have general validity. It is the same relation which is expressed by the so-called heat sums or day degrees. Aug. Krogh: On the influence of the temperature on the rate of embryonic development, Zeitschr. f. allg. Physiol. 16, 1914, p. 163.

[26] Synonym: *Anguilla vulgaris* Turton.

[27] Johs. Schmidt: First report on Eel investigations 1913. Rapports et Procès-Verbaux du Conseil International pour l'Exploration de la Mer, Vol. XVIII, p. 1—30 (1914).—*Idem*: Second report on Eel investigations 1915. Ibid. Vol. XXIII, p. 1—24 (1916).

[28] In a paper from 1925: On the distribution of the Fresh-Water Eels (*Anguilla*) throughout the world, II, p. 335. K. D. Vidensk. Selsk. Skr. nat.-mat. Afd. 8, X, 4) Schmidt records that from the Museum of Genova he has received a number of specimens of *Anguilla* from Massawa on the Red Sea, and that they belong to *A. anguilla*. In his paper: "A revision of the genus *Anguilla*" Vilh. Ege ("Dana-Report" No. 16, 1939, p. 149) states that he received six specimens from East Africa whose exact origin is unknown, and three specimens taken at Nairobi in Kenya; these specimens too belong to *A. anguilla*. All the East African specimens may be supposed to have immigrated from the Mediterranean through the Suez Canal. It should be mentioned in this connection that through the Suez Canal which was opened in 1869, some animals have migrated in the opposite direction, from the Red Sea into the Mediterranean. According to Steinitz ten species of fish have penetrated into the Mediterranean through the Suez Canal. Of the evertebrates the pearl-oyster (*Meleagrina margaritifera*) which occurs in great numbers in the Red Sea has migrated through the Canal into the Mediterranean and has spread there to such an extent that it is common on the North African coasts right on to Algeria. The swimming crab *Neptunus pelagicus* reached the Mediterranean at

the end of the nineties and is now so common that it is generally sold on the fish market in Alexandria. In addition immigration of the echinoderm *Ophiactis Savignyi* has been ascertained. On the other hand, no evertebrate is known with certainty to have migrated from the Mediterranean to the Red Sea through the Suez Canal. (Litt. WALTER STEINITZ, Publ. d. Staz. Zool. di Napoli, 8, 1927. TH. MORTENSEN: Dyrevandringer gennem Suez-Kanalen; Naturens. Verden, XII, 1927. TH. MORTENSEN: *Echinoderma*; Ministry of Commerce and Industry, Egypt, The fishing Grounds near Alexandria, XIII, 1937).

[29] JOHS. SCHMIDT: The breeding places of the Eel. Philosoph. Transact. Roy. Soc. London, Series B, Vol. 211, pp. 179—208. 1922.—*Idem*: Die Laichplätze des Flussaals. Internat. Rev. der ges. Hydrobiol. u Hydrographie, Bd. 11, Heft 1—2, pp. 1—40, 1923.—*Idem*: The breeding places of the Eel. Smithson. Rep. for 1924, pp. 279—316 (1925). *Idem*: Danish Eel investigations during 25 years, 1905—1930. Published by the Carlsberg Foundation. Copenhagen, 1935.

[30] Syn. *Anguilla chrysypa* Rafinesque, cf. BEAN in "Science" N.S.Vol. XXIX, p. 871, New York, 1909.

[31] As regards the distribution of the American Eel and its spawning region see the litterature given under JOHS. SCHMIDT[29].—In the above mentioned paper[28] VILH. EGE (p. 149) records that SEALE "had examined eels from Panama and the West-Indies, which were said not to differ in the least from *A. anguilla*. But it became clear later that the four specimens reported as coming from Panama had really come from Cadiz in Spain, whilst an examination of the specimens from St. Thomas, West Indies, undertaken for the present work, has proved that they belong to *A. rostrata*".

[32] Later on EGE (29, p. 132) further examined one hundred *A. rostrata*, and the average number of vertebrae in the 962 specimens was so to say unchanged, viz. 107, 233. It is true that the numbers of vertebrae in the two species overlap: in *A. rostrata* 103 to 111, in *A. anguilla* (110) 111 to 119, but only very few specimens per thousand cannot be referred with certainty to the one or the other of the two species. In his comprehensive monograph on the genus *Anguilla*, which is based on a very large collection and prepared with minute care, EGE has amplified the specific distinction between *A. rostrata* and *A. anguilla* by demonstrating the following specific differences:

A. rostrata: Average maximum value of distance between verticals through anus and origin of dorsal fin, in % of total length, about 9.1. Number of prehaemal vertebrae 41—45.

A. anguilla: Average maximum value of distance between verticals through anus and origin of dorsal fin, in % of total length, about 11.2. Number of prehaemal vertebrae 44—47.

Nowhere in the paper does EGE utter the least doubt that *A. rostratra* and *A. anguilla* are good species, though in several cases he unites forms which were previously regarded as species into subspecies of a single species. Further the very essential difference should be added that the average length of fully grown larvae of *A. rostrata* is about 60—65 mm, of *A. anguilla* about 75 mm, and that the former develops from egg to elver in the course of about 12 months, whilst the latter takes 3 years to carry through the same development.

[33] The Leptocephals of the two species, like the adults, are distinguishable from each other by the number of vertebrae (or myomeres). Of the European eel more than 11000 larvae were examined, of the American eel more than 2300 larvae.

[34] When it is recorded in current literature on the basis of M. P. FISH's paper: "Contributions to the embryology of the American eel, *Anguilla rostrata*" (Zoologica, Vol. VIII, No. 5, New York, 1927) that the eggs of the American Eel have been identified, it should be pointed out that JOHS. SCHMIDT (The Danish "Dana" Expedition 1920—22, Vol. I, No. 1, 1929, p. 16) has commented as follows on the eggs, supposed to be of *Anguilla*, collected in April—May 1923 during the work of the expedition in the Sargasso Sea: "These are altogether different from the ova which Mrs. MARIE POLAND FISH has referred

to the American Eel, and which, in the opinion of Dr. Tåning and myself, have nothing whatever to do with *Anguilla*". Unfortunately Prof. Schmidt did not get an opportunity to revert to this matter. On my request Dr. A. F. Bruun however informed me that most likely the eggs determined by Mrs. Fish belong to *Leptocephalus similis* Lea, which, as will be seen from Bruun's paper (Dana Report, Vol. II, No. 9, 1937, p. 26) has the same number of myomeres as the Leptocephal of *A. rostrata*, and otherwise, to a less trained eye can easily be confounded with young Leptocephals of *Anguilla* on account of its appearance. *L. similis*, according to Bruun (l. c.), belongs to a genus nearly allied to the *Muraena*, and it is natural to mention here that a similar confusion of a Leptocephal of this type with the *Anguilla*-Leptocephal has been made by Uchida, as stated by Bruun (l. c. p. 9).

[35] The central part of the breeding area of the American Eel lies somewhat to the west and south of the central part of the breeding area of the European Eel, but the areas of the two species are apparently not separated, but seem to overlap. It is conceivable, therefore, that some larva of the American Eel took the "wrong way" to Europe, but in that case it might perhaps perish, as its pelagic larval life which only lasts 12 months would come to an end in the middle of the Atlantic ocean. Nevertheless, it has happened once that an American Eel has been found to have landed in Europe among thousands of specimens examined. A. Bruun says in his paper: "Contributions to the life histories of the Deep Sea Eels *Synaphobranchidae*" p. 26 (Dana Report, Vol. II, No. 9, 1937), "that a specimen of *A. rostrata* was taken at San Sebastian in North Spain in December 1930; it was a glass-eel with 108 vertebrae and 68 mm long, taken along with several hundred glass-eels of *A. anguilla* sent to the late Prof. Johs. Schmidt from Dr. Gandolfi Hornyold". A similar case occurred in south western Greenland, where three young *Anguilla rostrata*, 109—110 mm long, were collected in 1841, according to Ad. S. Jensen (Meddel. om Grønland, Bd. 118, No. 9, p. 7, 1937); these too might have made their way to Greenland as elvers.

[36] Albert Günther: Catalogue of the Fishes in the British Museum, Volume Fourth. London 1862.

[37] David Starr Jordan: Relations of Temperature to Vertebrae among Fishes, Proc. U. S. Nat. Museum, Vol. XIV, No. 845. 1891. A modified reprint, with some additional matter, has been given by Jordan in The Wilder Quarter-Century Book, Ithaca, N.Y. 1893.

[38] David Starr Jordan and Barton Warren Evermann: The Fishes of North and Middle America, Part III, Washington, 1898.

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