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SYNOPSIS OF BIOLOGICAL DATA ON THE COMMON SHRIMP *Crangon crangon* (Linnaeus, 1758)

by

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SYNOPSIS OF BIOLOGICAL DATA ON THE COMMON SHRIMP
Crangon crangon (Linnaeus, 1758)

Exposé synoptique sur la biologie de la crevette
Crangon crangon (Linnaeus, 1758)

Sinopsis sobre la biología del camarón
Crangon crangon (Linnaeus, 1758)

prepared by

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1/ This synopsis has been prepared according to outline Version No.2 (H. Rosa, Jr., FAO Fish Synops., (1)Rev.1, 1965).

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

1 IDENTITY

1.1 Nomenclature

1.11 Valid name

Crangon crangon (Linnaeus, 1758)

1.12 Objective synonymy

Cancer crangon
Linnaeus, 1758, Syst.Nat., ed.10, vol.1, p.632 (original combination)

Astacus crangon
(Linnaeus, 1758) Fabricius, 1775, Syst. Ent., p.417.

Cancer (Astacus) crangon
(Linnaeus, 1758) Herbst, 1792, Versuch Naturgesch. Krabben Krebse, vol.2, p.75.

Crangon vulgaris
Fabricius, 1798, Suppl.Ent.Syst. p.387.

Crago vulgaris
(Fabricius, 1798) Lamarck, 1801, Syst. Anim.s.Vert., p.159.

Astacus (Crangon) vulgaris
(Fabricius, 1798) Moore, 1839, Mag.nat. Hist., n.ser.vol.3, p.290.

Crangon (Crangon) vulgaris
(Fabricius, 1798) Carus, 1885, Prodr. Faunae Mediterr., vol.1, p.482.

Crangon crangon
(Linnaeus, 1758) Sharp, 1893, Proc.Acad. nat.Sci.Philad., 1893, p.125.

Crangon crangon typicus
Doflein, 1900, Fauna Arctica, vol.1, p.325.

1.2 Taxonomy

1.21 Affinities

Suprageneric

Phylum Arthropoda
Class Crustacea
Subclass Malacostraca
Series Eumalacostraca
Superorder Eucarida
Order Decapoda
Suborder Natantia
Section Caridea
Superfamily Crangonoidea
Family Crangonidae

Generic

Crangon Fabricius, 1798, Suppl.Ent. Syst., p.387; type species by absolute tautonymy: Cancer crangon Linnaeus, 1758 (not Crangon Weber, 1795). Crangon Fabricius, 1798 is placed as name no. 807 on the Official List of Generic Names in Zoology (1955, Opin.Decl.Int.Comm.Zool. Nomencl., vol.10, p.1-44, Opinion 334); in the same Opinion Crangon Weber, 1795 is suppressed and placed, as name no.228, on the Official Index of Rejected and Invalid Generic Names in Zoology.

Definition. First pereiopod with strong subchela having a median tooth on the lower margin of the merus. Second leg slender, almost as long as first, with a true chela; carpus unsegmented. Fourth and fifth legs not broadened for swimming. Carapace in the anterior half with three spines, one median two lateral; no other median spines. Recently Zarenkov (1965) revised the genus and split off several genera from the old Crangon s.l. Within the genus Crangon s.s. a new subgenus Neocrangon Zarenkov was established by him.

Objective generic synonyms:

Crago Lamarck, 1801, Syst.Anim.sans Vert., p.159. Type species (by monotypy): Cancer crangon L., 1758.

Crangonus Rafinesque, 1815, Anal. Nature, p.98. Replacement name for Crangon Fabricius, 1798.

Subjective generic synonym:

Steiracrangon Kinahan, 1861, Trans. Roy.Irish Acad., 24(1), p.56 (type species (by monotypy) Crangon allmanni Kinahan).

Specific

Identity of type specimens

The type material of Cancer crangon no longer exists, but the original description leaves no doubts as to the identity of the species.

Type locality

Baltic Sea; "Habitat in M[are] Balthico" (Linnaeus, 1758, Syst.Nat., ed. 10, vol.1, p.632).

Diagnosis

Third maxilliped with an arthrobranch, sixth abdominal somite smooth above, without two distinct carinae, with a longitudinal median groove on lower surface.

Subjective synonymy

Crangon rubropunctatus
Risso, 1816, Hist.nat.Crust.Nice,p.83.

Crangon maculosa Rathke, 1837, Mém.Acad. Sci.Petersb., ser. 6B vol.3, p.366.

Crangon vulgaris maculosa
(Rathke) Czerniavsky, 1868, Trans. Meeting Russian Natural. St.Petersb., vol.1, p.126.

Crangon maculosa typica
Czerniavsky, 1884, Trans.Soc.Univ.Kharkow, vol.13 suppl., p.71.

Crangon maculosus brevirostris
Czerniavsky, 1884, Trans.Soc.Univ.Kharkow, vol.13 suppl., p.72.

Crangon maculosa suchumica
Czerniavsky, 1884, Trans.Soc.Univ.Kharkow, vol.13 suppl., p.72.

Steiracrangon orientalis longicauda intermedia
Czerniavsky, 1884, Trans.Soc.Univ.Kharkow, vol.13 suppl., p.74.

Steiracrangon orientalis brevicauda
Czerniavsky, 1884, Trans.Soc.Univ.Kharkow, vol.13 suppl., p.75.

Crangon vulgaris Shidlovskii
Ostroumoff, 1896, Mem.Soc.Natural.Nouv. Russ., vol.20 pt.2 no.3, p.75.

Artificial key to the European species of Crangon:

1. Sixth abdominal somite dorsally without carinae
Crangon crangon (L.)

2. Sixth abdominal somite dorsally with two sharp longitudinal carinae
Crangon allmanni Kinahan

1.22 Taxonomic status

Crangon crangon is the type species of the genus. The number of species placed by different authors in the genus varies considerably. Zarenkov (1965) who recognizes 2 subgenera within Crangon, assigned 7 species to the typical subgenus. Other authors place more than 30 species in Crangon. The position of the species with regard to the closely related N.E. American Crangon septemspinosa Say, and N.W. American C. alaskensis Lockington, is not certain, they might be subspecies of a single species or even full synonyms of each other.

1.23 Subspecies

Some authors consider the southern form of this species which inhabits the Mediterranean and the Black Sea as a distinct subspecies Crangon crangon rubropunctata Risso, 1816, but as a rule no subspecies are recognized within Crangon crangon.

1.24 Standard common names, vernacular names

Country	Standard common names	Vernacular names
Belgium	crevette	crevette grise
Denmark	Hestereje	Sandhest
England	common shrimp	brown, grey and sand shrimp
France	crevette	crevette grise
Germany	Nordseegarnele	Nordseekrabbe Krabbe, Granat, Kraut, Porre Sanduhl
Netherlands	garnaal	Nordzeegarnaal Garnaat, Garn Garnaal
Norway	Sandreke	
Sweden		Räkhäst

1.3 Morphology

1.31 External morphology

Generalized

Ehrenbaum (1890) gave a thorough description.

Geographic variation

Maucher (1961) carried out comparative measurements on the body, antenna, and extremities of two samples of Crangon crangon from the North Sea and the Baltic Sea.

Morphological definition of subpopulations

No subpopulations have been distinguished so far.

Description of morphological changes which occur during growth including quantitative data

Tiews (1954a) gave detailed information on the mean length of the endopodite of the first pleopod, on the mean number of the olfactory hairs on the olfactory branch of the first antenna, on the mean maximal width and mean number of segments of the olfactory branch of the first antenna, and on the number of segments of the olfactory branch of the first antenna without hairs, for both sexes of different size groups.

2 DISTRIBUTION

2.1 Total area

Geographic distribution

North Sea, Baltic Sea up to the fjords of Finland, coasts of North and West Europe, Mediterranean Sea (Ehrenbaum, 1890).

Biogeographical and natural characteristics

Main distribution in highly productive estuaries with strong tidal movements of brackish water masses, in the temperate climate zones of Europe between 45°N and 57°N, on sandy and muddy substratum.

2.2 Differential distribution

2.21 Spawn, larvae and juveniles

Larvae present from middle of May to early October in the Sound off Ven (Thorson, 1946), and from December to August in the off-shore waters of the southern North Sea (Rees, 1952). During a 14-years observation period in the Elbe estuary, larvae were found in the polyhaline region from April to October, and with maximum abundance during May and June. Not present in January and February when surface water temperatures were below 4°C. During March they were found only after warm winters. Early larval stages were more abundant at some distance from the coast than close inshore. This is supported by other observations in which ovigerous females concentrate before hatching in the deeper off-shore waters. (Meyer-Waarden and Tiews, 1957). In the Elbe estuary C. crangon larvae appear in deeper water later in the year. C. orangon larvae were found to be more abundant during low than during high tide (Kühl and Mann, 1963a, 1963b). According to Plett (1965a, 1965b) off the coast of Ostfriesland, the greatest abundance of larvae was between the 10 m and the 20 m line and decreased considerably both in shallower and deeper waters. In the area covered by the outer Elbe, and between Helgoland and Büsum, the distribution of larvae was considerably more seaward, extending to Helgoland. During the summer of 1963, off the coast of Ostfriesland, 100 to 450 shrimp larvae were counted under 1 m², as compared with 800-2500 in the Elbe area. A reversed picture was obtained in 1964 (Plett, 1965a, 1965b), when considerably more larvae were found off the coast of Ostfriesland in the Elbe area.

The general distribution pattern of shrimp larvae in the two areas appears to depend on the system of coastal currents which flow in the outer Elbe-Büsum-Helgoland area towards the west and northwest, and therefore transport C. orangon larvae more off-shore, while a west-east current off the coast of Ostfriesland transports the larvae parallel to the coast and thus concentrates the larvae in a relatively narrow strip.

No correlation could be found between larval distribution and water temperature and salinity. Kühl and Mann (1963a) however, stated that the differences observed in the abundance of larvae during the month of May in various years might be positively correlated with water temperatures.

Larvae of C. orangon and C. allmanni occurred irregularly and sparsely from May to September in the area off Newcastle-on-Tyne. All five larval stages were found, the first disappearing from samples after July (Jorgensen, 1923).

2.22 Adults

See Section 3.51.

In the Baltic Sea the main distribution is near the coast, bights and fjords, but it has also been observed far off shore in the center of the Baltic and near Gotland (Henking, 1927). It is found all around the English and Welsh coastline but its density varies from area to area (Mistakidis, 1960). During the winters 1959 to 1961 C. orangon could be caught simultaneously on the usual German fishing grounds and in the deeper waters at some distance from land. However, even the best catches taken in this period were about the same as the average catches obtained during the end of the usual fishing season. Moreover, they have been obtained only in restricted areas at depths between 10 and 20 m. (Meyer-Waarden and Tiews, 1962, 1963a). Wollebaek (1908) found C. crangon in the Brevik Fjord during November and December as deep as 120 m.

2.3 Determinants of distribution changes

See Section 3.51.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

Hermaphroditism, heterosexuality, intersexuality

According to Ehrenbaum (1890), Havinga (1929), Meyer-Waarden (1934, 1935a, 1935b), Nouvel et van Rysselberge (1937), Lloyd and Yonge (1947), and Tiews (1954a) Crangon is heterosexual. Boddeke (1961, 1962a, 1962b, 1966a), on the basis of histological gonad studies and intersexual stages of the endopodites of the first pair of pleopods, concluded that C. crangon is a protandric hermaphrodite and exhibits sex reversal. Meixner (1966a), who bred C. crangon from the 3rd larval stage up to sizes of 55-60 mm (20 males) and 65 mm (5 females) within 14 to 15 months, did not observe any sex change, which is supposed to take place according to Boddeke (1961) at a length between 42 and 46 mm.

Nature and extent of hermaphroditism

Boddeke (1961) stated that sex change from male into female occurs at a length between 42 and 46 mm with a possible sex change at a later stage.

According to Boddeke (1962a, 1962b): "A sex change takes place in August and September. In these months egg production begins in the gonads of the spent male. At the same time, the appendices of the first pleopods of these spent males are increasing in length to enable the attachment of eggs in due course. There are indications that sex change may also take place in February/March. The almost total absence of egg-bearing shrimps in the period 15 September to 15 October can be explained in terms of absence of functioning males in August and September. Obviously this makes fertilization impossible in these months." Boddeke (1966a) reported: "Male shrimps taking part in the mating in October to February change their sex to female in March. Male shrimps taking part in the mating in March to June change sex in April to July."

Sexual dimorphism

The endopodites of the first pair of pleopods are much shorter in the males than in the females. In the females they are always clearly visible and look like narrow spoons, which are twisted along their longitudinal axis. In the males this appendix is spine-like and, because of its small size, hardly visible without a hand lens (Ehrenbaum, 1890). In animals up to 20 mm long the endopodite of the first pair of pleopods is of similar size in both sexes, but in the males it is bent in a hooked position over the joint between basipodite and exopodite. At a body length of 35 mm it has lengthened and possesses three hooked and two straight spines. Finally, at sexual maturity, it is bent more acutely and bears twelve hooks and eighteen spines along the outer side (Lloyd and Yonge, 1947). The length of these endopodites cannot be used for exact sex separation at animals below 40 mm in length (Tiews, 1954a). Boddeke (1961, 1962a, 1962b) confirms this. An appendix masculina (Fig. 1) is attached to the endopodite of the second pair of pleopods (Nouvel, 1939). The endopodite of the second pair of pleopods is biramous in the males. The inner branch, or appendix masculina, is spinous on one side, while the outer branch resembles the unbranched endopodite of the female and is similarily clothed with long plumose setae. The fully developed appendix masculina possesses 18 strong spines along the side and tip of the ramus. As noted by Nouvel (1939) it is late in developing, and at a length of 35 mm the ramus has only three or four spines (Lloyd and Yonge, 1947).

Kröyer (Ehrenbaum, 1890) found that in animals of the same size the outer (olfactory) branch of the first antenna has more segments and is broader and longer in males than in females. Olfactory hairs normally occur in two transverse rows on the lower side of each segment. In the male, each row is longer, with more hairs, and the number of segments is greater, so that the total number of olfactory hairs is considerably greater than in the female (Tiews, 1954a). The first four to seven segments carry olfactory hairs in the male but not in the female shrimp (Tiews, 1954a). This character permits the separation of sexes down to the size of 30 mm, while the appendix musculina is a valid distinguishing character down to the size of 25 mm, when external sexual dimorphism occurs for the first time.

According to Ehrenbaum (1890) the second antenna is longer than the total body length in males, and shorter in females. Although Tiews (1954a) confirmed that in animals of the same size these antennae are longer in males than in females, he found that in most cases even

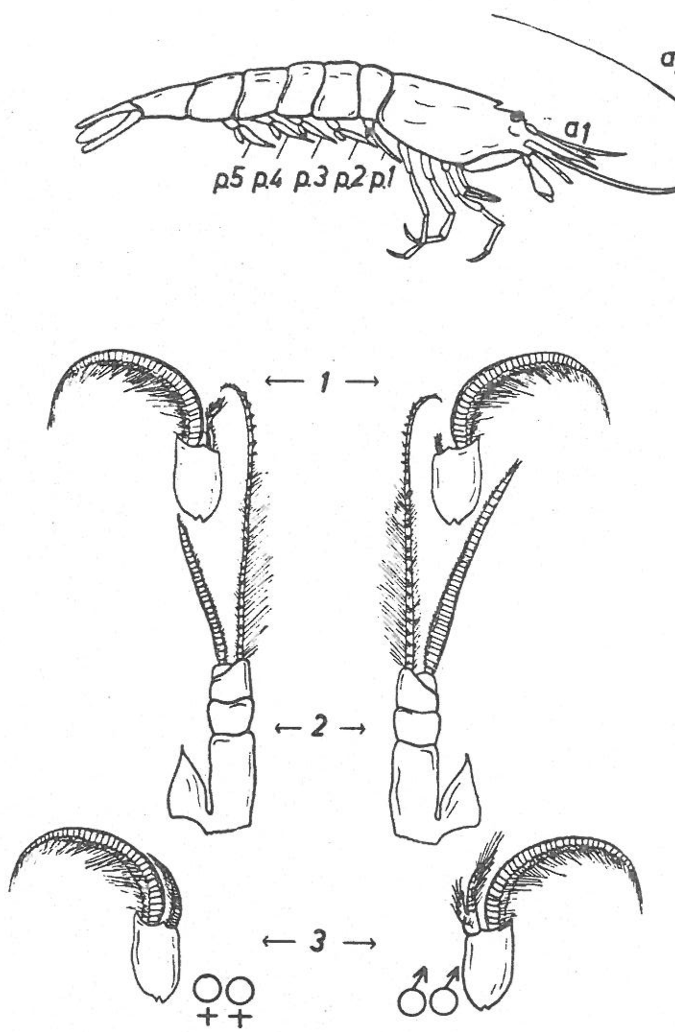


Fig. 1 Sexual differentiation in Crangon crangon (from Meyer-Waarden and Tiews, 1957).

1. 1st pleopods: sexual differences in endopodites;
2. 1st antennae: sexual differences in external (olfactory) branches;
3. 2nd pleopods: sexual differences in endopodites.

a_1 and a_2, 1st and 2nd antennae.
p1 to p5, pleopods.

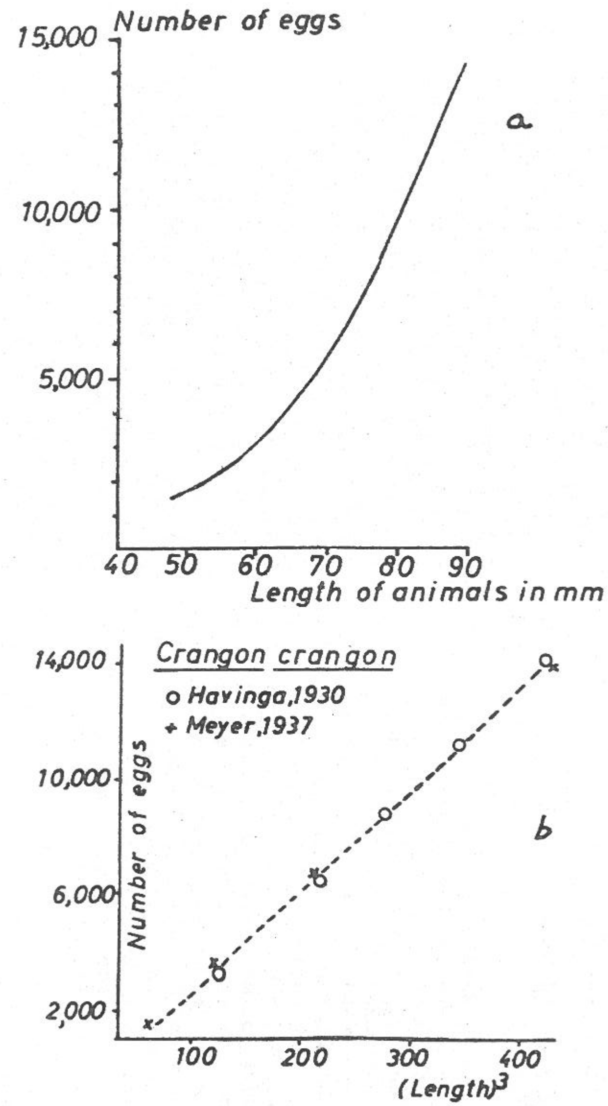


Fig. 2 Number of eggs in Crangon crangon:

a - in relation to length (Havinga, 1930);
b - to $[\text{length}]^3$ (Jensen, 1958).

in males they are shorter than the total body length. This character is not practical for separating the sexes, as in preserved material the antennae often break.

The genital openings in the females and males are on the bases (coxopodites) of the third and fifth pairs of pereiopods respectively (Ehrenbaum, 1890).

Lloyd and Yonge (1947) stated that the female pleopods undergo considerable changes during development and describe these fully.

3.12 Maturity

Age at which sexual maturity is reached and its variations with sex, subpopulations, size and rate of growth

According to Havinga (1930) females become mature at an age of 21 to 22 months; at approximately one year, according to Meyer-Waarden (1935b), and Tiews (1954a); at approximately two years, according to Lloyd and Yonge (1947). According to Tiews (1954a) males also attain maturity at an age of approximately one year.

Meixner (1966a), who reared common shrimps at a constant temperature of 14°C, which is 4°C above the annual average temperature in the German Bight where Crangon has its main centre of distribution, observed that male and female shrimps attained maturity at the same age of approximately 10 months.

Size and weight at sexual maturity

See section 4.13.

3.13 Mating

C. crangon is promiscuous.

See also section 3.16.

3.14 Fertilization

The fertilization of the eggs is external.

See also section 3.16.

3.15 Gonads

The relationship between the number of eggs attached between the swimmerets and the total length measured from the tip of the antennal scale to the tip of the telson is given in Fig. 2a.

Jensen (1958), using the egg counts made by Havinga (1930) and Meyer-Waarden (1937), stated that it seems to be reasonable "to consider the number of eggs per female in Crangon crangon a linear function of the length of the female raised to the 3rd power" (Fig.2b). Lloyd and Yonge (1947) gave a general account of the ovaries and testes "The paired ovaries extend from the dorsal surface of the gizzard ("cardiac" stomach) to the third abdominal segment. Growth in each ovary is slow up to a body length of 40 mm, but increases greatly with the approach of egg laying in the summer of the second year. After spawning the ovary is reduced to about 1/10 of its former mass, but during the summer new eggs are rapidly formed and by the end of the period of egg-carriage the ovary may have regained half of its former size. After the last spawning of the season there is little ovarian activity and the animal passes into the winter resting conditions with the ovaries only slightly exceeding their minimum size."

"The testes are situated in the same region as the ovaries and are also united anteriorly and centrally. They become very active when the males attain lengths of about 40 mm, when all stages of maturation of spermatozoa are present and ripe spermatozoa occur in the vasa deferentia."

"In Crangon the spermatophore is finally extruded as a thin strand-like vermicelli containing masses of sperms at irregular intervals."

Number of eggs or broods produced by an individual

On the assumption that C. crangon spawns thrice a year, 8,000 to 9,000 eggs are produced by an individual during its second year of life and 24,000 to 26,000 eggs during its third year of life, thus a total of at least 32,000 to 35,000 eggs may be produced during its whole life (Meyer-Waarden and Tiews, 1957).

3.16 Spawning

Number of spawnings per year

According to Ehrenbaum (1890) there are two spawnings; according to Havinga (1930), Meyer-Waarden (1953a), and Tiews (1954a) there are three. Meixner (1966a) observed that from five reared females one spawned five times in the aquarium, at water temperatures of 14°C, within five months (April to August), two four times, one thrice, and one twice (average 3.6 spawnings).

Spawning seasons

Wollebaek (1908) mentioned egg bearing females off Bergen from August to December (deep water). Henking (1927) observed the first egg-bearing C. crangon in the Baltic Sea in May. In June and July more than 70 percent of the shrimps were with eggs. No observations could be made by him in August and September, and he did not observe any egg-bearing Crangon during October to December.

Ehrenbaum (1890), Havinga (1930), and Meyer-Waarden (1935a) all observed spawning C. crangon in both summer and winter months along the continental shores of the North Sea. Ehrenbaum and Meyer-Waarden, working at Caroliensiel and the Jade Bay respectively, found two spawning periods, one extending from spring to the end of July and the other from November until February.

Lloyd and Yonge (1947) stated that in the Bristol Channel there are probably spring and summer spawning periods, the two overlapping. The first starts at the end of January or in early February and lasts until mid-April or the beginning of May. Egg-berried shrimps occur in the Severn only during the spring, from March or April to June.

Tiews (1954a) found three spawning periods at Büsum; two extend from April to August, and one from November to March. Very few egg-carrying females were found during September and October. Plett (1965b) recorded the maximum number of larvae along the German coast from June to August.

Spawning time of the day

According to Nouvel (1939) and Tiews (1954a) spawning in the aquarium takes place during dusk.

Sequence of spawning of individuals in a population

Henking (1927) stated that in the Baltic Sea the larger sized shrimps begin to spawn earlier than the smaller ones. During May egg-bearing shrimps were between 50 to 60 mm, and only from June onward small shrimps, down to 30 mm, were with spawn.

At Büsum, Tiews (1954a) observed relatively more small egg-bearing shrimps at the beginning of the summer spawning period than later on.

Shrimps originated from winter eggs are likely to spawn for the first time during the winter, and those from summer eggs during the summer (Havinga, 1930; Tiews, 1954a). The results of both authors differ in that the shrimps are then about two years old according to Havinga (1930), and only one year old according to Tiews (1954a).

Factors influencing spawning time

Low temperatures may delay the spawning period (Lloyd and Yonge, 1947).

Relation of the time of breeding to that of related and/or associated species

Mistakidis (1960) stated that in the Thames estuary where C. crangon are abundant Pandalus montagui spawns from November through winter with the highest peak in January. By the beginning of April the majority of the eggs will be hatched out.

Location and type of spawning ground

According to Tiews (1954a) mating and spawning take place on the fishing grounds along the entire German coast. These grounds may be sandy or muddy, and they are shallower than 20 m. He concludes this from the high percentage of ripe females which had just moulted and were caught by the fishery. (See also section 2.21.)

Nature of mating act

The process of copulation in Crangon has been described by Nouvel (1939) and confirmed by Lloyd and Yonge (1947), and Tiews (1954a). It is essentially similar to that in other Caridea such as Athanas nitescens, Palaemon elegans, and Alpheus dentipes. Some of the details are quoted from Lloyd and Yonge (1947): "After certain preliminary behaviour, described by Nouvel, the male turned the now passive female on to her back and then bent his body in a U-shape transversely across that of the female about the junction of the thorax and abdomen so that the ventral regions of the two animals were in contact." Nouvel (1939) stated that the females sometimes permit a second copulation. This was not observed by Lloyd and Yonge

(1947) and Tiews (1954a). Nouvel (1939) also recorded the copulation of large females up to a length of 58 mm, with males of from 30 to 36 mm.

Tiews (1954a) observed the copulation of a female of 81 mm with a male of 38 mm. The author stated that copulation takes place only after the female has just moulted. He found remnants of spermatophores on the endopodites of the first two pairs of pleopods in 35 out of 89 males which had just copulated. He concluded that these endopodites might sometimes help to attach the spermatophores close to the genital opening of the female.

Variation in mating behaviour

Tiews (1954a) observed that the male might copulate with the female even when swimming.

Nature of egg laying

According to Lloyd and Yonge (1947): "Eggs are laid within two days of moulting into the egg-carrying condition irrespective of copulation. If copulation has occurred, spawning normally follows within 24 h. Nouvel states that small females spawn immediately after copulation, larger ones after 24 h, but very large ones after 48 h. Where copulation has not occurred the eggs fail to develop and drop off. This is apparently due to the very limited amount of secretion produced by the cement glands, the stimulus of copulation being apparently necessary possibly by way of the production of some hormone which affects these glands as suggested by Yonge (1937)". They also stated that: "As the time for spawning approaches, the animal refuses to eat and retires into a sheltered position. The pressure of the ovary on the stomach may prevent normal intake of food. Following moulting and copulation, the female cleans the egg-carrying setae by stroking movements with the tips of the second pair of pereiopods. During spawning the animal lies on one side with the abdomen bent under the thorax and the eggs then pass back in chains from the genital openings assisted by movements of the spoon-like endopodites of the first pair of pleopods."

Further details on egg attachment can be seen in Lloyd and Yonge (1947) and Yonge (1955).

Meyer-Waarden (1935a) stated that towards the end of the egg-carriage, the egg mass is frequently probed and loosened by the second pereiopods which also assist in the final liberation of the larvae. This has been confirmed by Lloyd and Yonge (1947). After hatching, the egg membrance and strands of cement remain attached to the pleopods until the next moult.

Meixner (1967) confirmed that spawning may take place in mature C. crangon without prior mating.

3.17 Spawn

Description of external morphology

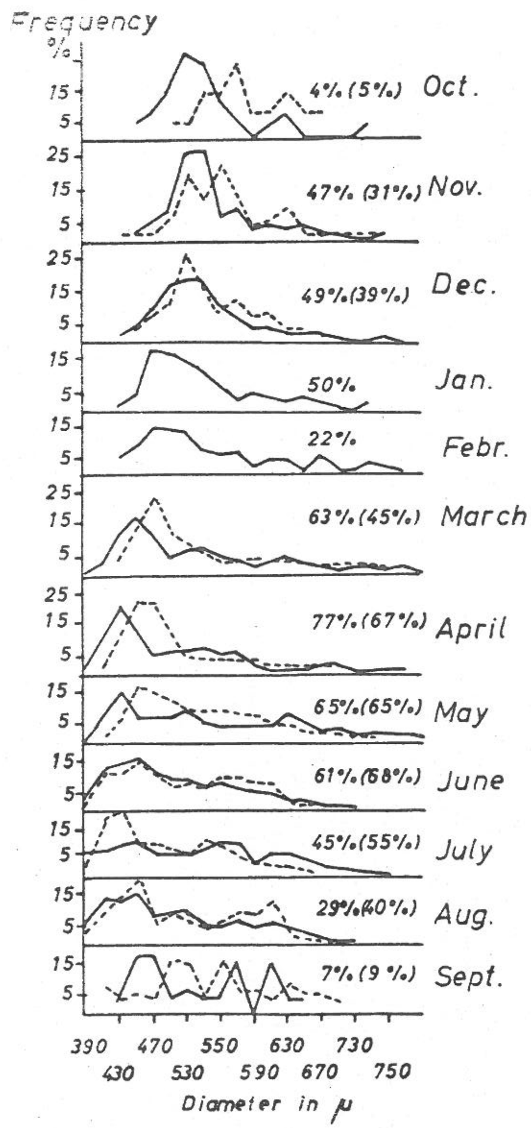
The colour of the fresh egg is a dirty white. The eggs themselves vary slightly in size; some are nearly spherical but the majority are ovoid and have a long axis of 0.024 in (= 0.061 mm) and a short one of 0.018 in (= 0.046 mm) (Kingsley, 1886). Immediately after spawning the egg is round and has a diameter between 0.35 and 0.40 mm. It grows nearly exclusively in one direction and is of elliptical shape shortly before hatching (longitudinal axis = 0.70 mm, short axis = 0.40 mm). During this process the colour changes from white to greenish grey. Shortly before hatching the embryos can be seen through the egg-shell. When boiled the colour of ripe eggs changes to blue violet or nearly black, while unripe eggs remain white. After hatching the empty egg-shells remain attached to the mother animal until the next moulting, which takes place soon after (Ehrenbaum, 1890).

Summer eggs (long axis 0.37 mm) are smaller than the corresponding winter eggs (0.43mm). Eggs in the earliest stages of development are whitish and nearly spherical, while those with embryos ready to hatch are greenish with pigments, much bigger, and shaped like a hen's egg (Thorson, 1946).

The seasonal variation in the size of spawned eggs is given in Fig. 3 after Havinga (1930).

Size and shape of vitellus, vitelline membrane, number of oil globules

"The egg is enveloped in a very thin structureless envelope inside of which were found no traces of an inner or vitelline membrane, nor is there any space between the shell and the yoke. The protoplasm occupies a central position; it is not regular in outline, but gives off pseudopodal prolongations which ramify and pass between the yoke spherules in all directions. The protoplasm is granular, the granules apparently taking a deeper stain than the rest, though



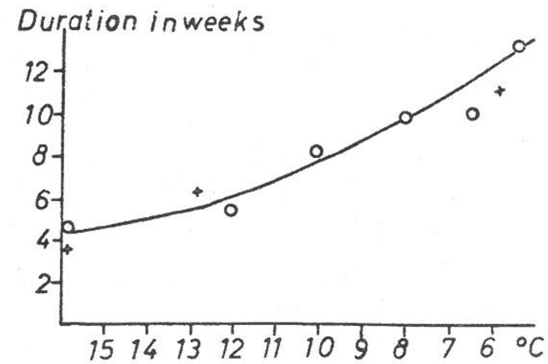


Fig. 4 Development of eggs of Crangon crangon in relation to temperature:

o = calculated by Havinga (1930)
+ = experimental results by Tiews (1954a)

Fig. 3 Seasonal variation of size composition of eggs of Crangon crangon in 1927 (broken line) and 1928. Percent figures refer to percentages of berried females calculated from the total number of females above 50 mm in 1928 and in 1927. (Havinga, 1930) this appearance may be due to a different refractive index. The nucleus is large and vacuolated, and in its interior is a well developed chromatin reticulum, which traverses it in all directions, the fibres uniting on the wall of the nucleus in a thickened layer. The yoke is granular, the yoke globules ranging considerably in size" (Kingsley, 1886).

3.2 Pre-adult phase

3.21 Embryonic phase

General features of development of embryo

"In Crangon the anus occupies the position of the blastopore. In Crangon and many other Crustacea the young germinal area is actually larger than the much older embryo. All the appendages belong to the primitively postoral series and the appendages move forward more rapidly than the corresponding ganglia. There are indications of segmental sense organs in every segment of the embryo. The alimentary tract proper is nearly if not entirely, formed from the proctodeal and stomodeal invaginations, the entoderm giving rise to nothing but the liver. The green gland is mesodermal in origin and belongs to the category of segmental organs. The genital ducts are modified nephridia. The nauplius is an introduced feature and represents no adult ancestral condition in the crustacean phylum". (Kingsley, 1889).

The size increase of the egg during the development of the embryo, as studied by Ehrenbaum (1890) is given in Table I.

Rates and periods of development and survival and factors affecting these, including parental care

Havinga (1930) calculated the duration of the development of the embryo in the eggs in relation to different temperatures using the relative abundance of four different developmental stages of shrimp eggs in catch samples. Tiews (1954a) kept freshly spawned shrimps in a 50-litre aquarium and determined the time of hatching of the larvae under three different conditions. The results of both authors (Fig. 4) are in agreement and demonstrate the relationship between the water temperature and the duration of the embryonic development. Under optimum feeding conditions larvae hatch after three weeks at 18°C and after four weeks at 14°C (Meixner, 1966b).

From observations on berried females of C. crangon on the German North Sea coast, Meixner (1967) estimated the incubation time of eggs as shown in Table II.

TABLE I

Size increase of egg during development of embryo

Stage of development	length, mm	width, mm
Mature eggs, but unfertilized	0.32 - 0.35	0.32 - 0.35
Beginning segmentation	0.35	0.35
Gastrula	0.37 - 0.38	0.33
Embryo without extremities	0.40	0.34 - 0.35
Nauplius stage	0.42 - 0.43	0.37
All extremities laid out	0.47 - 0.48	0.42
First traces of eyes	0.50 - 0.52	0.42 - 0.42
Large eyes and much pigment	0.58 - 0.59	0.40 - 0.41
Shortly before hatching	0.60 - 0.61	0.35 - 0.36

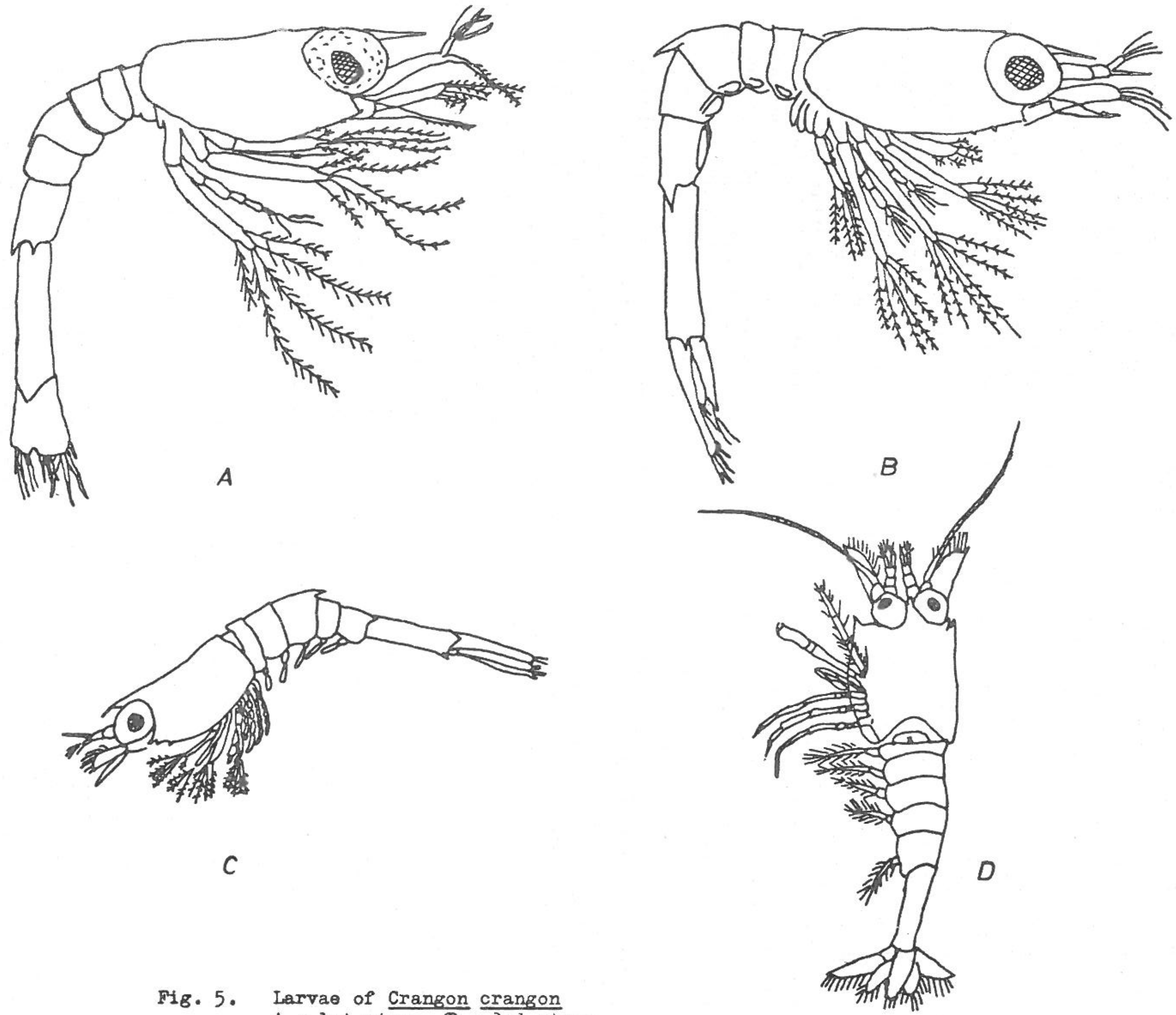


Fig. 5. Larvae of Crangon crangon
A = 1st stage, B = 3rd stage
C = 5th stage (after Williamson, 1915)
D = 1st postlarval stage
(after Havinga, 1929).

TABLE II

Incubation time of Crangon eggs

	April	May	June	July	August	September
Temperature °C	6	9-10	13-14	15-16	16-17	15-16
Incubation time in weeks	10		4.5	3.5	3.5	3.5

3.22 Larvae phase

General features and development

Ehrenbaum (1890) gave the following description for the five larval stages:

The larva, slightly coloured by few chromatophores, hatches as a zoëa-larva, being approximately 2 mm long, excluding the antennae and the setae of the telson. Maxillipedes and telson serve as a locomotor organs, which enable the zoëa to move to the upper water layers. Stage 1 is characterized by 14 setae at the hind edge of the telson and stage 2 by 16. In this stage the appendages of the 6th abdominal segment, enclosed with the telson, are visible through the skin (length of stage 1 = 1.84 mm and of stage 2 = 2.5 to 2.8 mm).

In stage 3, these appendages are liberated and branched into two parts, but have not yet reached the length of the telson. The internal branch is nearly 1/3 shorter than the outer branch. Abdominal segments 6 and 7 are for the first time clearly separated. Above the anal opening an anal spine has been formed. Finally the swimming branch of the first pair of walking legs has developed, so that the zoëa has metamorphosized to a mysis larva (length = 3.2 to 3.4 mm).

Stage 4 is characterized by the length of the appendages of the 6th abdominal segment being the same as of the telson. These appendages are densely covered with setae on their hind and inner edges. On the abdomen the 5 pairs of swimmerets are clearly visible, on which endopodites start to develop. On the last 4 pairs of legs of the thorax the initial segmentation is visible. On the bases of the first 4 pairs of legs the gills start to develop as small buds (length = 3.8 mm).

In stage 5 the thoracic legs are completely developed and five gill buds are present (length = 4.6 to 4.7 mm) (Fig. 5).

The first larval stage is mostly transparent, with yellow pigment on the eye, the sides of the carapace, dorsally and ventrally on the hind region of the abdominal segments, and on the telson. There is also a little brown pigment with the yellow in each chromatophore. The yellow pigment shines and sparkles to give a silvery effect in reflected light. The larva is slightly curved. All animals in this larval stage have the same characteristic coloration, although this may vary in intensity, and they also show the following characters: a sharp, thin keeled rostrum; three teeth on the anterior part of the lateral edge of the carapace; a strong backwardly directed spine on the posterior edge of the third abdominal segment; and two long lateral tooth-like processes on the posterior edge of the fifth abdominal segment (Williamson, 1915).

Ehrenbaum (1890) estimated the duration of total larval development during spring to be approximately five weeks so that each larval stage lasts an average of eight days.

Thorson (1946) confirmed this statement saying that the larvae occur in the plankton from early spring to autumn and the pelagic life will take about five weeks, i.e., there is about one week between two moultings.

Type of feeding

Ehrenbaum (1890) identified in the stomachs of the larvae remnants of different marine diatoms and unidentified zoo-organisms.

Plagmann (1939) investigated twelve zoëa larvae, of which nine had empty stomachs, while fragments of chitin were found in three; in one a piece of Biddulphia was also found.

Meixner (1966a) found that zoëal stages III, IV and V can easily capture the living nauplii of Artemia salina.

3.23 Adolescent phase

General features of development

In the first postlarval stage (stage 6) the second antennae carry long flagella and the pleopods bear long swimming hairs (Fig. 5 D). The rostrum is shorter; the telson has diminished in width towards the back and the number of spines have been reduced from 8 to 5. The next stage (stage 7) measures 6 mm; stage 8, 7.5 mm, stage 9, 10.5 mm (Williamson, 1901).

Tiews (1954a) studied the growth of the outer branch of the first antenna (olfactory branch) from moult to moult. Until the time of sexual dimorphism the number of segments of the olfactory branch increases gradually by one from moult to moult. When the sexes can be separated for the first time by external characters the olfactory branch has 8 segments. The shrimps have then a length of approx. 25 mm. With further development the growth rate of males and females differs and also the number of segments of the olfactory branch. At the time of maturity, both males and females have 24 segments on their olfactory branch, but males measure then approx. 40 mm, the females approx. 54 mm.

Rates and periods of development and survival and factors affecting these including diseases, parasites and predators

The duration of intermoult periods is influenced by various factors. The age of C. crangon and the temperature sea water (Tiews, 1954a) plays an important role in the moulting rhythm (Fig. 9 and also see section 3.43). Having reached maturity the moulting intervals of female C. crangon are shorter than those of the males. If the amount of food is insufficient to cover all metabolic needs, a large increase in the moulting intervals has been observed (Meixner, 1966a). Maturity is generally reached after one year. During the first year of life the shrimp is subject to heavy predation by fish (Tiews, 1965).

Effects of environment, subpopulations, density on rates of development and survival

See section 3.34

Differences from adults in diet, feeding, methods, etc.

Plagmann (1939) found in five specimens of the first postlarval stage spermatophores of copepods, diatoms, and in one case copepods (see also 3.42).

Meixner (1966a) stated that in his breeding experiments the larval stages of C. crangon (zoëa III, IV, and V) and the first postlarval forms easily captured the living nauplii of Artemia. The pubertal and postpubertal Crangon apparently had difficulty in seizing the relatively small brine shrimp larvae with their chelipeds and had to be fed with postlarval Artemia.

3.3 Adult phase

3.31 Longevity

Average life expectancy

According to Nouvel-Van Rysselberge (1937) female shrimps die during their third year of life and males during their second. Tiews (1954a) states that female shrimps rarely reach the end of their third year of life. The males appear to die in the beginning of their third year of life.

See also section 3.43.

Maximum age

Three to five years. (See section 3.43)

3.32 Hardiness

Limits of tolerance to changes in or of environment and feeding

C. crangon can endure great changes of salinity and temperature. It is found during the warm season up river in nearly fresh water (Havinga, 1929). During summer it usually survives water temperatures of 30°C in pools which remain at low water on the tidal flats of the Wadden Sea. Younger shrimps can endure lower salinities than older shrimps. This may explain the occurrence of C. crangon in the middle part of the Baltic Sea where the predominant salinity values are less than 10°/oo. However, the density of such a population is much lower than on the fishing grounds of the North Sea.

Limits of tolerance to handling and life in aquaria or other confined environments

C. crangon died 7 to 8 hr after being placed in fresh water, and one day after being kept in water of 0.15 to 0.16 ‰ NaCl (Mathias, 1938).

C. crangon under aquarium conditions has survived after ice has formed over the surface of the undiluted sea water (Lloyd and Yonge, 1947).

Caudri (1937) found that at a temperature of about 4°C the optimum salinity for survival of young shrimps was 34 ‰, whereas at 18.9°C the lowest mortality was between 20 and 30‰.

Broekema (1942), determining death rates in two-year-old animals kept in different combinations of temperature and salinity, came to the conclusion that the salinity optimum for survival depends on temperature. At a temperature of 20°C the optimum salinity proved to be about 29‰, while at 4°C about 33‰. For one-year-old shrimps the salinity optimum at about 20°C appears to be low, varying between 15 and 20‰. This may be the explanation of the fact that during summer young shrimps penetrate further into the brackish waters than the older specimens.

A combined influence of temperature and salinity could also be demonstrated in newly hatched shrimp larvae. Moreover, the salinity limits for normal development of the eggs proved to be similarly dependent on temperature.

Although generally low temperatures are more favourable than higher ones, an extremely low salinity is relatively better endured when the temperature is high. This is in agreement with the fact that in nature C. crangon is found in low salinities during the warmest months of the year.

The question of possible influence of temperature on the osmoregulation in C. crangon has been treated by Flügel (1960), who critically discussed the results of Broekema (1942). His analyses give the physiological explanation for the fact that "in the northern Baltic Sea Crangon is not capable to live in water of low salinity at temperatures near the freezing point. No difference between males and females was found in the osmoregulation. The osmoregulatory performance of small individuals (2.1 cm) was lower than that of bigger ones (4.9 cm). In newly moulted and in injured individuals the difference of the freezing points of internal and external mediums was always smaller than in normal individuals. Adapted males and females from the North Sea showed the same efficiency as those from the Baltic Sea."

Flügel (1963) stated that the electrical conductivity of the body fluid of C. crangon is higher than the external medium in a range from 3.6‰ to 23-25‰. Between 25‰ and 40‰ the electrical conductivity of the blood is relatively lower. The performance of ionic regulation is always higher in animals adapted to 5°C than in individuals which are adapted to 15°C. The performance of ionic regulation decreases at temperatures below 5° (distinctly at 2°C).

On the basis of preliminary experiments and field observations Lloyd and Yonge (1947) concluded "that males cannot withstand such low salinities as females and that optimal salinity, at a temperature of 15°C, is higher for males than for females. The powers of osmoregulation in the males are not as great as in the females."

Mistakidis (1958) studied mean survival rates of brown shrimps which were exposed up to 30 min at different air temperatures then re-immersed in sea water. The survival rates varied between 75 and 86 per cent. The shrimps did not show any marked difference in survival as a result of varying air temperatures, which were, however, not above 19°C.

Meixner (1967) found that young shrimps taken from water of 2‰ could be transported alive when kept in water of temperatures between 17° and 24°C and salinities between 7.5 and 28‰.

3.33 Competitors

Types and abundance of competitors for spawning area, food, shelter, etc.

Several fish species occurring in the coastal waters, where Crangon is abundant, have to be considered as competitors for food. Carcinus and Macropipus also come under the same category. The relative abundance of the fish and brachyuran fauna of the German shrimp fishing grounds is given by Heidrich (1930), Wulff and Bückmann (1932), and by Meyer-Waarden and Tiews (1965). The degree to which the fishes of this area have to be considered as food competitors can be found in

TABLE III

Estimated total loss of shrimp stock on the German coast through predation by various fish species, in numbers (millions) and weight (tons) (Tiews, 1965)

year	sea snail No.	sea snail t	goby No.	goby t	armed bullhead No.	armed bullhead t	whiting No.	whiting t	smelt No.	smelt t	dab No.	dab t	short spine sea scorpion No.	short spine sea scorpion t	rockling No.	rockling t	eel pout No.	eel pout t	gunell No.	gunell t	total No.	total t
1954	26,200	2,900	37,900	2,600	36,500	2,200	1,500	260	2,200	300	4,300	650	8,400	4,500	1,700	230	380	40	50	5	119,000	13,700
1955	59,900	6,600	61,700	4,300	21,100	1,300	2,000	350	4,200	640	2,500	380	2,000	1,000	860	110	380	40	100	10	154,700	14,700
1956	26,200	2,900	49,900	3,500	30,700	1,800	4,400	780	7,300	110	2,800	420	1,900	1,100	0	0	240	20	100	10	123,500	10,600
1957	46,800	5,100	50,500	3,500	25,900	1,600	12,200	2,200	5,500	820	2,800	420	2,000	1,100	0	0	290	30	50	5	146,000	14,800
1958	86,100	9,500	74,800	5,200	26,900	1,600	4,400	780	6,800	1,000	2,700	400	3,200	1,800	1,700	230	480	50	50	5	207,100	20,600
1959	69,300	7,600	49,400	3,500	21,100	1,300	53,000	9,500	7,800	1,200	3,900	580	2,600	1,400	0	0	340	30	50	5	207,500	25,100
1960	5,600	600	44,700	3,100	40,300	2,400	15,600	2,800	430	60	4,800	720	4,500	2,500	1,700	230	290	30	140	10	118,100	12,400
1961	35,600	3,900	34,600	2,400	28,800	1,700	19,400	3,500	4,500	700	6,900	1,000	4,500	2,500	1,700	230	340	30	190	20	136,500	16,000
1962	16,900	1,900	23,000	1,600	25,900	1,600	5,800	1,100	4,800	720	1,900	290	3,200	1,700	1,700	230	240	20	140	10	83,600	9,200
1963	84,300	9,300	13,200	900	33,600	2,000	10,700	1,900	1,900	290	5,300	800	3,200	1,800	1,700	230	340	30	100	10	154,300	17,300
average 1954/1963	45,900	5,000	44,000	3,100	29,100	1,800	13,000	2,300	4,500	590	3,800	570	3,700	1,900	1,100	150	330	30	100	10	145,100	15,400

Kühl (1956, 1961, 1963, 1964a and 1964b) and Plagmann (1939). Many of the coastal marine animals may compete with the adult and larval stages of Crangon.

3.34 Predators

Types of predators

Herdman (1892), Gilis (1952), Kühl (1956, 1961, 1963, 1964a, 1964b) and others have found that many fish species feed heavily on C. crangon. (See Table III).

On the basis of stomach content investigations carried out by Kühl (1961; 1963, 1964a, 1964b), Tiews (1965) concluded that the main predators of C. crangon on the German North Sea coast, listed in order of relative importance, are: Sea snail (Liparis vulgaris), goby (Pomatoschistus minutus), armed bullhead (Agonus cataphractus), whiting (Merlangus merlangus), smelt (Osmerus eperlanus), dab (Limanda limanda), short-spined sea scorpion (Myoxocephalus scorpius), rockling (Ciliata mustela), eel pout (Zoarces viviparus), gunell (Pholis gunellus) (Table III).

Kühl also found that, on an average, the stomach content of sea snails included Crangon: 7.8; armed bullhead: 4.0; rockling: 3.6; whiting: 2.7; short-spined sea scorpion: 2.7; dab: 0.3; smelt: 0.3; goby: 0.3; eel pout: 0.2 and gunell: 0.2.

In 1949, during the course of his investigations, Kühl noted that at low tide, large numbers of small sized shrimps gathered in the shallow pools of the tidal flats in the Wadden Sea, thus becoming easy prey for all types of sea birds.

On the Belgian coast, according to Gillis (1952), the main predators, in order of importance, are whiting (Merlangus merlangus), thornback ray (Raja clavata), bib (Trisopterus luscus), sole (Solea solea), dab (Limanda limanda), flounder (Platichthys flesus) and plaice (Pleuronectes platessa). Others are conger eel (Conger conger), cod (Gadus morhua), dragonet (Callionymus lyra), gurnard (Trigla spp) and turbot (Scophthalmus maximus).

Predation as controlling factor of size, density, and size composition of population

Tiews (1965) calculating the loss of shrimp stock caused by predatory fish along the German North Sea coast for the years 1965 to 1963, found that on an average, at least 145 x 10^9 shrimps were eaten off annually by predatory fish species. He also found during this research period that at least 1.7 to 4.3 times as many shrimps were taken annually by predatory fish as by the fishery. Under different assumptions the author has estimated that loss through predation is 5.1 to 12.9 times higher than the catch. A negative correlation was found between the loss of shrimp stock caused by predatory fish and the catch of shrimp in the following year (P = 4.9 %), (Fig. 6). The predation on one year's stock influences the catch in the next year in as much as the shrimps caught are usually approximately one year older than the shrimps being removed by predators. This result indicates the inadequacy of protection measures under the given circumstances, as the factors determining the size of stock on the fishing grounds are uncontrollable.

3.35 Parasites, diseases, injuries and abnormalities

Nature and causes

Injuries are rather frequent, especially since freshly moulted specimens are often attacked by Crangon or other animals, as can be observed in the aquarium.

Ability of regeneration

Nouvel —Van Rysselberge (1937) studying the ability of regeneration in various shrimp species found that regeneration in Crangon crangon is completely different from that of Palaemon elegans, Athanas nitescens, Hippolyte varians and Thoralus cranchi. It differs also from that known in brachyurans. In Crangon the regenerated pereiopod resembles, at the next moulting, a complete miniature of the lost part of the pereiopod. In younger shrimps it normally takes three moultings to regenerate the normal walking leg. In older specimens this can last four or more moultings. The process of regeneration of one and the same part can be repeated several times. The ability of regeneration is also not influenced when two, three, or four pereiopods are to be regenerated. The loss of five pereiopods of one side, however, leads to a decrease in the ability of regeneration along the longitudinal axis of the shrimp. Regeneration also takes place when several pairs or all pereiopods are lost but the general rhythm of the regeneration process is disturbed.

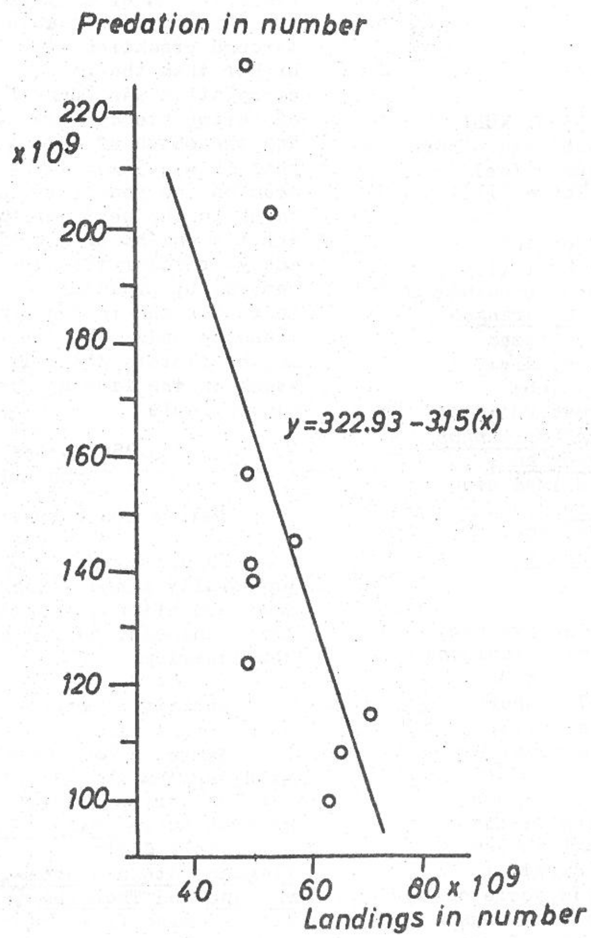


Fig. 6 Relationship between predation and landings of Crangon crangon in the immediate following year on the German coast (Tiews, 1965).

The regeneration of one or two pereiopods leads to a small decrease in the length of the intermoult periods. The regenerating activity of the shrimp decreases when fasting (Nouvel-Van Rysselberge, 1937).

Effect on physiology and survival of individuals

See section 3.53.

3.4 Nutrition and growth

3.41 Feeding

Time of day

Havinga (1929) stated that C. crangon rests quietly, buried in the substratum during the day, and feeds by night. Tiews (1954a, 1954b) observed that C. crangon in aquaria feeds during the day as well as during the night. Nevertheless, it is possible that, since C. crangon has its active phase in the dusk, its main feeding time is during the night.

Place; general area

Feeding takes place throughout the distribution area on the bottom and also above the bottom.

Manner, methods of capture, selection

During feeding, Crangon consumes grains of sand which assist to crush the food in the cardiac part of the stomach. The inner lining of this part of the stomach is composed of relatively soft setae which cannot by themselves crush the food particles. From observation of shrimps with full stomachs put into an aquarium and kept there without food, it has been noted that they emit grains of sand periodically until, after some time, the bottom of the aquarium is covered with a thin layer of sand. After new feeding, grains of sand from the bottom of the aquarium are to be found in the stomach, and this sand obviously serves as a substitute for the stomach mill as described for Potamobius (Plagmann, 1939).

When searching for food, Crangon swims in a zigzag course over the bottom or hunts in higher water layers, bending its carapace. With the aid of its first and second pairs of pereiopods, equipped with strong subchelate pincettes, the shrimp seizes its prey. Aided by the second pair of pereiopods the prey is brought close to the sternum, while the first and second pairs of maxillipeds and both pairs of maxillae make back and forward movements continuously over the prey. While overcoming the prey, the shrimp sinks to the bottom, at the same time attempting to cut it in pieces. Plagmann (1939) observed several young shrimps seizing an 8-cm long worm (Nereis diversicolor) and trying, with some success, to cut it in pieces. Large shrimps are even known to attack an entire worm which they do not eat and digest at once, but after satisfying their hunger, leave the remains protruding from their mouthparts. Snails and mussels are seized directly by the maxillae of the shrimp while schizopods or amphipods are attacked with the walking legs. Plankton prey is captured by generating a water current in the direction of the mouthparts. Crangon can often be grouped among the "gulpers" since whole animals can often be found in the lumen of the stomach.

Plagmann (1939) gave a detailed description of the predigestion stage. The first post-larval forms of Crangon easily capture live nauplii of Artemia salina. The pubertal and post-pubertal Crangon apparently have difficulty in seizing the relatively small brine-shrimp larvae with their chelipeds (Meixner, 1966b).

Frequency

There is little information on the frequency of feeding.

Variation of feeding habits with availability, season, age, size, sex, physiological condition

A comparison between spawning time, migrations, feeding and quality of diet indicates that the months of July, August and September represent a period of increased feeding activity which follows the period of summer spawning activity (Plagmann, 1939).

Plagmann (1939) found that male shrimps eat a large variety of food and many planktonic food items. A lesser variety is eaten by the female shrimps which also eat fewer planktonic items. According to Tiews (1954a) the males are better prepared for hunting activity by their relatively well developed olfactory organs (compare 3.23).

See also section 3.42.

Abstention from feeding

Meyer-Waarden (1934) reported that females which are kept in an aquarium shortly before spawning hide and refuse to take food. After spawning the females resume feeding. Plagmann (1939) found that 62.0% of females with fully developed ovaries had empty stomachs. The respective percentages of females with empty stomachs in the other four stages of ovarian development were between 20.5 and 32.8.

3.42 Food

Food investigations have been carried out by Ehrenbaum (1890), Herdman (1892), Havinga (1930), Kühl (1949), and Plagmann (1939), whose work is the most comprehensive. The brown shrimp is omnivorous. Nevertheless, worms, amphipods, schizopods, copepods, cyprid larvae of Balanus, snails and young mussels constitute the main food items. The variability in the composition of the various food items in the stomach of the common shrimp is very great.

During the course of its life the shrimp slowly changes its diet. For young shrimps below 30 mm the main food item is Corophium; for shrimps of 30 to 45 mm the main food items are worms and amphipods and in larger and older shrimps worms alternate with schizopods. Much cannibalism has been observed among the older shrimps and those between 30 and 45 mm have the widest range of food (Plagmann, 1939).

A food change in the course of a year has been observed by Plagmann (1939) as follows: worms/amphipods/copepods/mussels/cyprid larvae/snails/schizopods. From January to May a crustacean component was observed to be constant in the diet. The copepod diet increased as the worm diet decreased. From June to September a mixed summer diet prevails, and from October to December the summer diet decreases in favour of a malacostracan diet.

Herdman (1892) found in the stomachs of Crangon crustacean remains such as amphipods, small crabs, young shrimps and copepods and also a considerable amount of mollusc remains such as Scrobicularia alba, Cardium edule and Tellina balthica. Annelids must also form a fair proportion of the food, from the number of polychaete setae in the stomachs, and the considerable fragments of Pectinaria tubes and the horny jaws of nereids. Occasionally the stomachs contain Foraminifera, small spines of sea urchins and sometimes green sea-weeds, minute filamentous and microscopic algae and diatoms. After experimenting on shrimps in captivity, the same author found that they will also eat other animal material, such as pieces of dead fish, other shrimps, beef, etc.

In Dutch waters, annelids, especially Nereis succinea and N. diversicolor, form the main diet. Second in abundance as food items are crustaceans among which Corophium is the most important and less abundant are Gammarus, Neomysis and Praunus. Young fish or fish larvae and molluscs, such as Hydrobia and Mya arenaria have seldom been taken. Larger shrimps feed mainly on worms, while the smaller ones feed on Corophium. 38 % of the shrimps investigated had eaten worms only, 31 % crustaceans only, 9 % had fed on worms and crustaceans and 22 % on detritus (Havinga, 1930). The younger shrimps in the Wadden Sea feed on Corophium which occur there in huge quantities up to 40,000 per m^2. The taste of the shrimps is determined largely by the type of food taken. Shrimps which chiefly eat crustacean food have the best taste, while those feeding on worms develop a soaky meat. The so called "green heads" feed on mud, which explains the greenish to blackish color of the "head", and their muddy taste (Kühl, 1949).

Volume of food eaten during a given feeding period

"The average food consumption of Crangon from the time of metamorphosis to the time of reproduction (size of animals 55 mm) amounts to 600 mg dry substance of Artemia for the female and 770 mg for the male. At the same time the average body weight (in mg dry substance) increased by 279 mg and 248 mg, respectively. The conversion factor is approximately 2.2 for the female and 3.1 for the male C. crangon. These results were obtained when shrimps were reared at a salinity of 30‰ and a temperature of 14°C in aquaria" (Meixner, 1966a). The food uptake of Crangon varies according to the type of food, as Meixner (1966a) has demonstrated when feeding Artemia larvae and adults (Table IV).

There is some evidence that the frequency of spawning of females of C. crangon is influenced by their food uptake (Table V) (Meixner, 1966a).

TABLE IV

Food uptake of two *C. crangon* of the same intermoult stage
Temperature: 14°C. Salinity: 30‰
Food: Nauplii and adult forms of *Artemia salina*
Weight in mg dry substance

	Crangon I	*Crangon* II
Length (mm)	15	15
Stage of *Artemia*	larval	adult
Food uptake (mg)	1.0	4.9
Albumin (in dry substance) (‰)	63	38

3.43 Growth rate

Relative and absolute growth patterns and rates

Ehrenbaum (1890) estimated the age of a 60 to 70 mm shrimp to be one and a half years. According to Havinga (1930) female shrimps born in January are 40 mm long at the end of the first year of life, 58 mm at the end of the second year and 74 mm at the end of their third year of life. According to the author, maturity is reached at about the end of the second year of life. Female shrimps born in July reach a length of 33 mm after the first year, and are 58 mm long in the following July. These shrimps spawn for the first time about 21 months after birth.

Meyer-Waarden (1935b) came to the conclusion that female shrimps born in February reach a length of 48 mm after one year and 72 to 78 mm after the second year. The shrimp spawns for the first time at the beginning of its second year of life.

Nouvel-Van Rysselberge (1937) concluded that female shrimps grow from 5 mm to 54.5 mm in their first year of life (June to June) and up 70.5 mm in their second year of life.

Lloyd and Yonge (1947) stated that during the first year of life the growth rate of the two sexes appears to be very similar. Subsequently the females grow more rapidly. Females of 50 to 60 mm are

TABLE V

Influence of food uptake (mg dry substance) on oviposition of four *Crangon crangon*
Before the experiment all females had successfully spawned
Temperature: 18°C. Salinity: 30‰
Food: *Artemia salina*

	♀ I	♀ II	♀ III	♀ IV
Experimental period (weeks)	3	3	3	3
Ration of food (mg)	96.7	82.8	40.2	53.4
Spawning after next moult	+	+	-	-

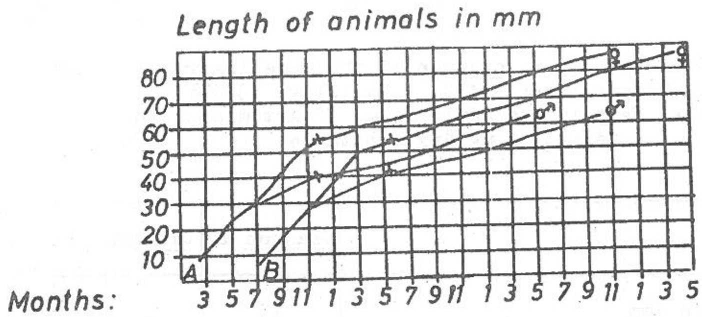


Fig. 7 Growth curves for Crangon crangon as calculated by Tiews (1954a): A= for shrimps which had their 1st post larval stage in February, and B in July. Calculation was based on an average temperature of 10°C x = size at first maturity.

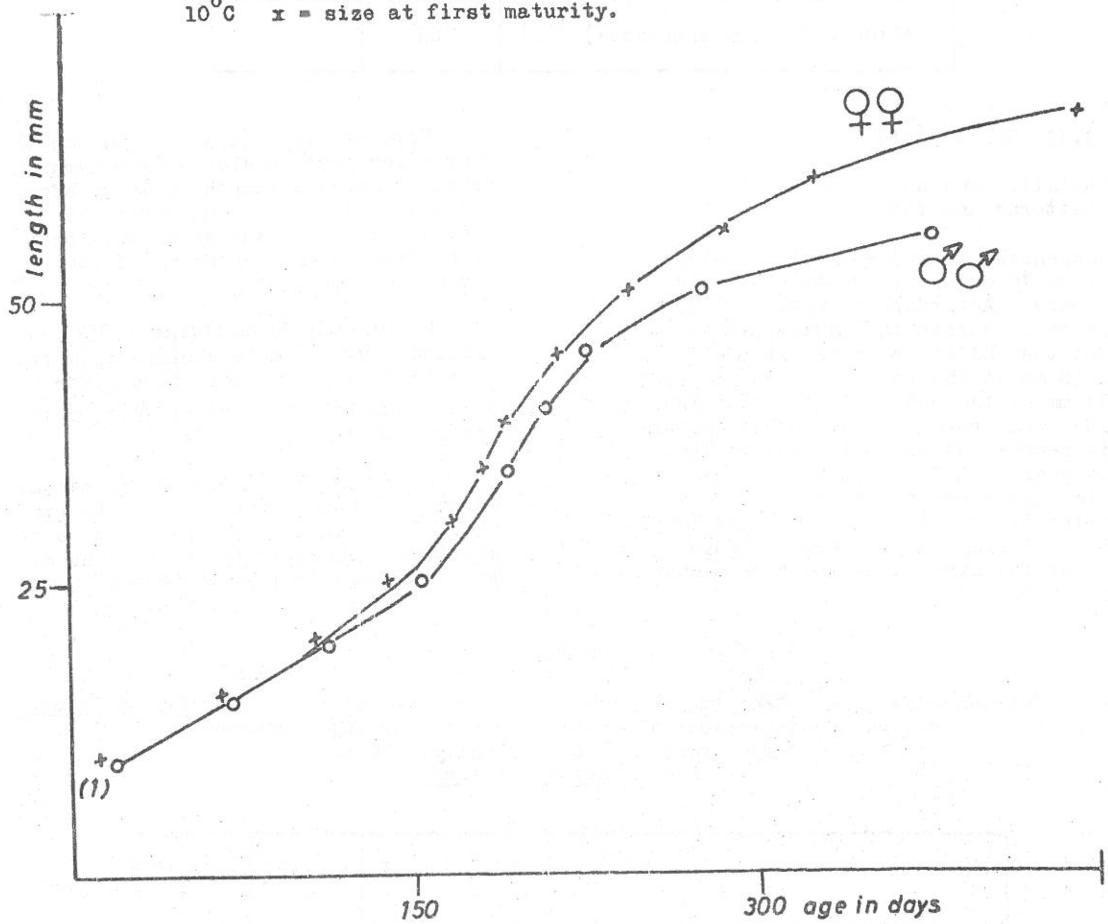


Fig. 8 The total body length (mm) of female and male Crangon crangon from metamorphosis to maturity. Temperature: 14°C, Salinity: 30‰ (Meixner, 1966a).

in the third year, females over 60 mm in their fourth year and those of 80 mm in the fifth year. Males of 40 to 45 mm are in the second year, while those of 70 mm are possibly four years old.

Tiews (1954 a) found when observing shrimps in an aquarium, that the number of segments of the olfactory branch of the first antenna increases after each moult by a definite number, which varies regularly between 1 and 3 according to the age of the shrimp. Knowing the time between two successive moults and the normal average length at each moult (as determined from samples taken at sea), he was able to draw growth curves for males and females. These curves are in agreement with the growth rate as estimated from the displacement of the frequency maxima in series of length measurements taken quarterly from sea samples. His findings were: at the age of six months and at a length of 25 mm, the sexual character can be noted externally. After this time the two sexes grow at different rates. At an age of about one year, when both males and females are mature, the average length of the male is only 40 mm, while the female attains 54 mm, i.e. marketable size. After maturity the growth rate decreases considerably. At the end of the second year of life the length of the female is 70 to 75 mm, that of the male 55 to 60 mm (Fig. 7).

Boddeke (1966a) stated that shrimps born in December and January reach marketable size (52 mm) in 9 months. Shrimp larvae, hatched in the period March to July do not reach marketable size before April of the following year.

The growth-curves for male and female shrimps shown in Fig. 8 were obtained by Meixner (1966a) from rearing experiments at a constant temperature of 14°C, which is approximately 4°C higher than the annual average water temperature on the German coast. Under the experimental conditions, females grew from 6 mm to 62 mm and males from 6 mm to 55 mm in one year. The most intensive growth was between 25 and 50 mm, as postulated by Tiews (1954a).

For mature shrimps within the size-range 40 to 50 mm, the increase in size at each moult is much less in males than in females, and males moult less frequently than females of the same length. This explains why commercial catches of C. crangon of more than 50 mm consist mainly of females (Meixner, 1966a).

Condition factors (ponderal index)

Havinga (1930) found K ($K = \frac{W}{L^3}$) to be approximately 0.007. He measured the length from the tip of the antennal scale to the tip of the telson. The relationship between length, weight and the number per 1 kg of female shrimps at the end of May is as follows:

TABLE VI

Relationship between length, weight and number per 1 kg of female shrimps

Length mm	Weight g	No. per 1 kg
31	0.20	5,000
44	0.57	1,754
55	1.16	862
64	1.90	526
75	3.14	318

Relation of growth to feeding, spawning, other activities and environmental factors (temperature, crowding, etc.)

The time between two successive moults varies with temperature and the age of the shrimp until maturity is reached (Fig. 9) (Tiews, 1954a). Meixner (1967) found that the length of intermoult periods decreases by 1/3 in animals kept at 20°C as compared to those kept at 14°C.

The duration of the intermoult periods depends more on the age than on the length of the animal. This explains why males and females of the same age have more or less the same moulting frequency although they differ greatly in length (Tiews, 1954 a).

Meixner (1966a) reared shrimps and measured the length increase during a 17-days' intermoult period. He distinguished three different phases of the moulting cycle:

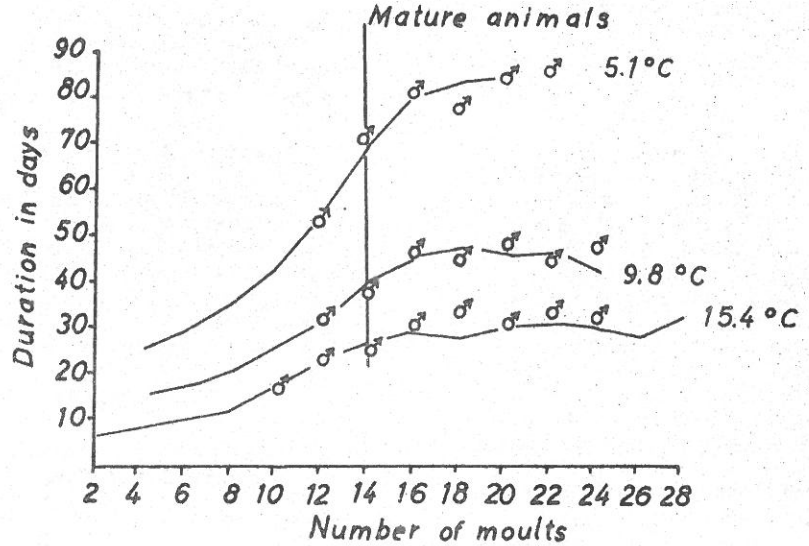


Fig. 9 The duration and number of intermoult periods of female (line) and male (symbols) Crangon crangon at different temperatures (Tiews, 1954a).

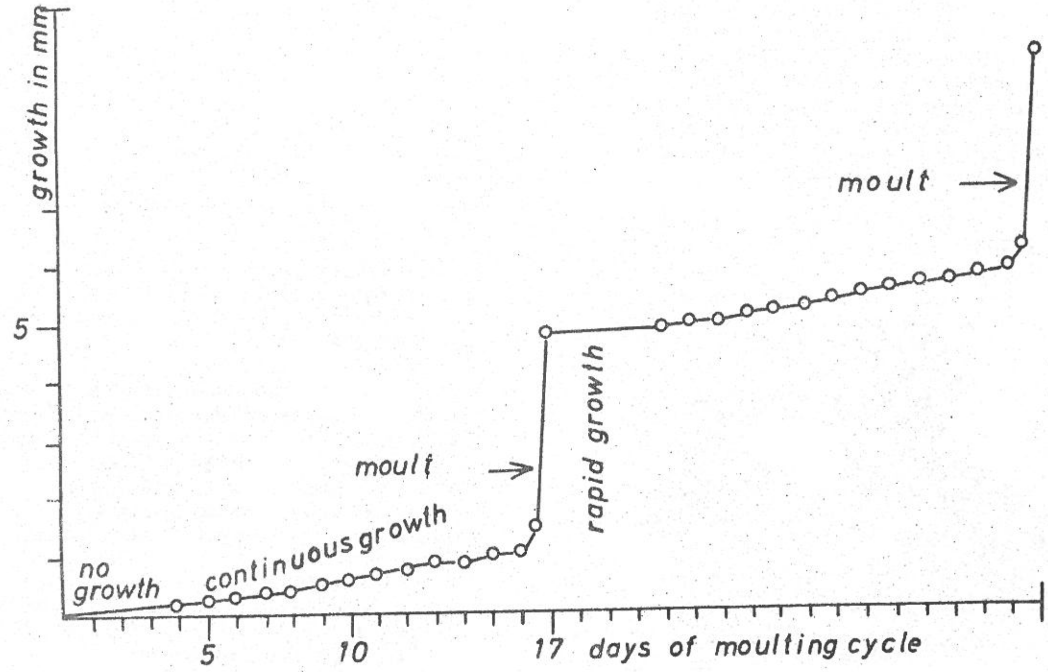


Fig. 10 Daily increase in total body length (mm) of juvenile (36 - 43 mm) Crangon crangon during two moulting cycles. Intermoult period: 17 days. Temperature: 14°C Salinity: 30°/oo (Meixner, 1966a).

Phase I : The first 3 days after ecdysis, no size increase

Phase II : The following 13 days of the intermoult period, a continuous but relatively small growth

Phase III : The day of ecdysis, a rapid growth (Fig. 10).

While the growth at moulting time is a saltatory one caused by water uptake, the increase in length during the relatively long intermoult period (Phase II) is slow and gradual (Fig. 10). The rate of increase is related to the amount of food digested (Meixner, 1966a).

Moulting takes place mainly during darkness (Tiews, 1954a; Meixner, 1967). Plankemann (1935) stated that shrimps moult a few days after being placed into an aquarium. Lack of calcium in the water does not influence moulting. The calcium-concentration of the sea water inhibits moulting. The development of the exuvium is not terminated within a certain time after the moult. Chitin and calcium-carbonate are continuously deposited into the shell. A certain relationship between chitin and calcium-carbonate is maintained. Marine sea water, with decreased pH through HCl, has no influence on the moulting. Moulting, however, is accelerated in sea water enriched with CO_2 or neutralized with NaOH. Both lead also to an increase of shell weight.

Food rich in glycogen accelerates the moulting. This is also the case when the shrimps are kept hungry. Plankemann (1935) assumed that the deposit of chitin in the shell protects the animal against an abnormal increase in blood sugar. The number of moults and shell weight is subject to fluctuation during the course of the year. They are determined on the one hand through the propagation period and through the maturity stage of the gonads, and on the other hand through the resting period during winter. Short-wave light leads to an increase of the metabolic rate and consequently to an increased moulting rate. The carbohydrate metabolism determines the moulting rhythm.

From hatching, a female 86 mm long will have passed through 34 $\pm$ 2 moults, a male of 62 mm through 30 $\pm$ 2 moults (Tiews, 1954a). From metamorphosis until first spawning, a female of 57.5 mm will have moulted 23 to 25 times and a male of 51.5 mm 22 to 25 times (Meixner, 1967).

Food-growth relations

Lack of food decreases or stops the growth or can even lead to a decrease of total length (Nouvel-Van Rysselberge, 1937; Tiews, 1954a; Meixner, 1967).

3.44 Metabolism

Endocrine systems and hormones

Koller (1925, 1927) showed that blood from Crangon adapted to a black background caused melanophore dispersion in animals adapted to a white background; the reverse experiment, transfer of blood from white-adapted to black-adapted Crangon was without effect. Blood from individuals adapted to a yellow background also disperse the xanthophores in white-adapted individuals.

Koller (1928) found a blanching hormone in the eyestalks in Crangon and presented evidence for an additional darkening hormone that originates in the rostral region. Thus two hormones were postulated, a "contractin" and an "expantin".

Goodwin (1960) stated that the pigments in the eyes and in the epidermis of C. crangon are not melanin as reported by Verne (1926) but pigments soluble in cold NaOH which appear to be related to the ommochromes first described by Becker (1941).

The riboflavin content of C. crangon is low (Goodwin, 1960). Unidentified neutral xanthophylls have been found in small amounts in whole animal extracts of Crangon sp. (Goodwin, 1960).

3.5 Behaviour

3.51 Migration and local movements

Extent of movements or migrations

Direct evidence on migration can be provided by marking experiments. Tiews (1953b) tagged C. crangon by wrapping a thin silver wire around the animal between the carapace and the first abdominal segment, the wire being retained up to three successive moults. Münzing (1960, 1962) tested various types of stains to mark shrimps and found that "Gentianna Violet B" (Merck, Darmstadt), gave the best results. In several tagging experiments all recaptures were made within 10 to 15 nautical miles from the point of release.

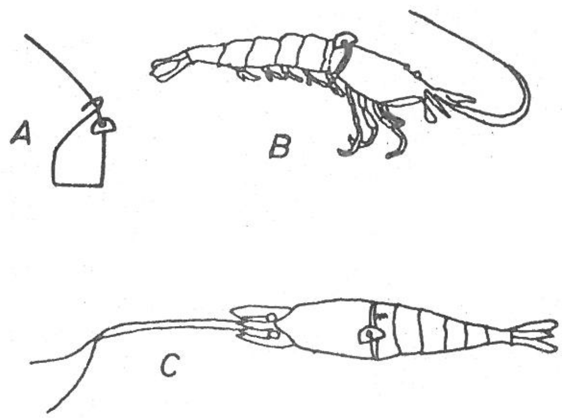


Fig. 11 Tagging method of Crangon crangon

A = prepared tag

B = lateral

C = dorsal view

(Tiews, 1963 a)

Since 1962 more than 50,000 shrimps have been tagged at the Institut für Küsten- und Binnenfischerei, Hamburg, by applying the method described by Tiews (1953b). The silver wire used for these field experiments had a diameter of 0.18 mm and was used with coloured discs of 6 mm (Fig. 11). This method gave larger return rates than the staining method. The best return rates were obtained when using red-white colour combinations (Tiews, 1963a; Kourist, Mauch and Tiews, 1964; Tiews, 1964).

In experiments made during the winter of 1962/63 marked shrimps retained their tags for 3 to 5 months, while in numerous previous experiments tag retention was only up to 2 months. All marked shrimps were recaptured in the spring of 1963 in an area of 15 miles from the point of release. The results indicated that shrimps tagged at the beginning of winter were more or less stationary and did not perform winter migrations, but hibernated close to or on the usual fishing grounds.

Crangon has its most active phase at dusk. During darkness Crangon leaves the bottom of the aquarium where it has been hiding during day time, swims restlessly up and down the walls of the aquarium and buries again at dawn. The animals also swim around during the night even after full feeding, so food search cannot be the reason for their continuous activity. Light intensity was found to be the determining factor (Tiews, 1954a).

Function of migration

Meyer-Waarden and Tiews (1957) distinguished a spawning from a feeding migration. The feeding migration commences with the warming of the coastal waters at the beginning of March, when the shrimp migrate towards the coast to feeding grounds in the brackish waters. From May to July most of the egg bearing females migrate back to offshore waters for hatching the larvae, but return afterwards to areas nearer to the coast. In October, most of the shrimps migrate to their winter quarters in the more saline parts of their coastal distribution area.

Havinga (1930) stated that the availability of food is without any doubt the cause for the irregular smaller migrations of the shrimps. On the other hand he considered that the great seasonal migrations of the shrimps probably depend on changes in temperature, the migrations always being from lower to higher temperatures.

Direction of movements

Münzing (1962) concluded from his tagging experiments that there was not a homogeneous trend of migrations. In May 1961 shrimps had migrated towards the sea as well as towards the shore, but, as was expected, the migration towards the shore predominated. During an October tagging experiment, the larger part of recaptures was obtained in the shallower parts in the Randzel Wadden Sea although, according to the general theory, one would have expected that an off-shore migration of shrimps would have been demonstrated.

Time or season of migration

According to Meyer-Waarden and Tiews (1957) feeding migration into the coastal waters commences in March to April, while C. crangon leaves the brackish coastal waters during the months October to December to occupy its offshore winter quarters. Spawning migrations occur from April to the middle of August. From July to September recruit shrimps occur in large quantities on the fishing grounds.

Changes in pattern of movements or migrations with age, physiological state, season, temperature and environmental conditions

Tiews (1954b) observed that the average catch of shrimps per fishing hour in the Büsum area was higher when the velocity of tidal currents was above the average (spring tides), than during low velocity (neap tides). Tiews assumed that the stronger displacement of water at spring tides carries more shrimps inshore. Moreover, the turbidity of the water is increased. This may have the effect that, at least in shallow waters, the shrimps will swim more actively and therefore be caught more easily by the trawl; whereas at neap tides, in less turbid water, they are more likely to bury in the sand as they generally do in aquaria during daylight.

See also section 4.6.

3.52 Schooling

Extent of schooling habits

No special schooling habits observed.

Composition of stocks by size, age and sex

Age groups and sexes are widely mixed on most of the fishing grounds, but in the most brackish parts of the distribution areas of C. crangon young shrimps and female shrimp predominate.

See section 4.

Mixing of stocks within species at various stages of the life cycle

Mixing of different stocks of C. crangon has not been reported.

Mixing between species

Very little mixing takes place between C. crangon and C. allmanni on the German fishing grounds.

See section 4.6.

Vertical movements

C. crangon has been frequently caught in large numbers as a by-catch of the smelt fishery, pursued by staked bag nets in the Elbe and Weser estuaries. In addition other fishing gear, such as baskets and stow nets, which usually hang free from the bottom successfully catch Crangon (personal observations).

Size, density and behaviour of schools in relation to time of day, geographic location, season, oceanographical factors, physiological conditions

Crangon buries in the sand in the light, and leaves its hiding place in the dark. The light intensity in the water, therefore, may determine the behaviour of individuals and schools.

The schools of C. crangon are densest during late summer and autumn when O-group animals enter the fishing grounds in huge quantities.

3.53 Responses to stimuli

Environmental stimuli

Mechanical (reactions to pressures, currents, sound)

Florkin (1960) reported that laboratory experiments on shallow water shrimps (Palaemon, Crangon, Pandalus) have shown that increased hydrostatic pressures have effects dependent on their magnitude. At 50 atm (about 500 m) increased locomotor activity results. At 150 atm (about 1,500 m) paralytic effects appear after a short time; at 200 atm (about 2,000 m) these are more rapid and complete. Nevertheless, even after brief exposures to pressures equivalent to 5,000 m depths, recovery of normal swimming occurs after about an hour at 1 atm.

Schöne (1952, 1954, 1957, 1959, 1961) studied static position orientation in Decapod Crustacea, including Crangon, and came to the conclusion that the function of the statocyst is basically the same as in fish. He gives a careful analysis of his experimental results to which reference should be made.

C. crangon moves against the current or at least moves its head against the current, as demonstrated in an experimental current channel. Rheotactic orientation ceases immediately after extirpation of the first antenna which indicates the location of the sense for current orientation in the antennules (Luther and Maier, 1963).

Verwey (1960) stated that C. crangon belongs to the area of tidal currents. It moves passively with the tides, but has a firm control over its displacement. During ebb tide when approaching a creek, C. crangon moves diagonally to the current. There are indications that it uses the sun for orientation.

Chemical (olfactory, gustatory, salinity gradients)

Balss (1913) found that chemoreceptors are not only located on the outer branch of the first antennae, but also on the pereiopods and on the mouth extremities.

In Crangon specific chemicals, such as vanillin, acetic acid, quinine, sucrose, NaCl and others were used as stimulating agents. A technique was used whereby the outer flagellum of the antennae alone could be stimulated under water. Under these conditions the animal responds to both sapid and odorous chemicals. The response criterium in this case is an initiation of, or increase in, movements of body parts such as both pairs of antenna, head and chela (Spiegel, 1927a, 1927b).

There are observations which suggest at least partially independent olfactory and gustatory chemo-reception. When the antennules in C. crangon are stimulated under water without affecting any other part of the body, only awakening or alarm reactions result. These contrast with the food-seeking and feeding movements evoked by similar stimulation of other areas of the body. The methods used do not reveal a threshold difference between the antennules and the rest of the body, but this may be due to the existencé of olfactory receptors on other body parts as well. There are, however, wide threshold differences between substances that generally stimulate olfactory receptors and those that normally are considered odorless but are effective stimuli for taste receptors. Thus threshold concentration of cumarin and vanillin is 0.0001 to 0.00005 % while that of acetic acid is 0.01 %; saccharin 0.5 to 0.1 %; NaCl 1.3 to 7.15 %; quinine chloride 0.001 to 0.0005 %. Nevertheless, it has been maintained that taste and smell are not differentiated in Crangon because both odorous and sapid substances stimulate the antennules and because extirpation of the latter does not alter the threshold. Support for this notion is sought in the failure to find more than one morphological type of chemo-receptor on the antennule. However, morphologically indistinguishable receptors may, indeed, have widely different response properties (Spiegel, 1927a, 1927b; Barber, 1961).

Schöne (1961) stated that according to Ubrig (1952) and Buddenbrock (1952) when the CO_2 concentration of the water is increased, Daphnia, Palaemonetes, Crangon and other crustacea swim upward, related to the direction either of the gravitational field or of the light.

Kleinholz (1961) stated that in C. crangon adrenaline and noradrenaline in diluted solutions produce melanophore dispersion; ephedrine, Veritol and Sympatol are effective only in high concentrations. Acetylcholine elicits malanorphore dispersion in Crangon, but the cholinesterase-blocking drugs, physostigmine and prostigmine, do not. The acetylcholine-blocking agents, tubocurarine, atropine, and scopolamine do not prevent melanophore dispersion in response to an illuminate black background (Florey, 1952)

Thermal (temperature)

See section 3.32.

Optical (light)

Colour vision has been found in C. crangon by Koller (1927) using chromatophore responses mediated through the compound eye. Adaption is possible to yellow, orange, and red; yet the specific responses to these colours cannot be evoked by any shade of gray from white to black (Waterman, 1961).

In Crangon the abundance and distribution of the polychromatic chromatophores permit adaptive changes to background colour (Kleinholz, 1961).

4 POPULATION

4.1 Structure

4.11 Sex ratio of the catch

Ehrenbaum (1890), Havinga (1930) and Lloyd and Yonge (1947) found relatively more males in zones of high salinities than in those of low salinities (Table VII).

Tiews (1954a) determined the sex ratio in industrial catches in order to establish the percentage of male shrimps, as males hardly reach edible size. More than 50 percent of the catches of small shrimps (30 to 50 mm in size) made in Büsum during 1951 consisted of males, of which only less than 5 percent would have reached edible size. The relatively high percentage of male shrimps is attributable to the age composition of these catches as shrimps of 30 to 50 mm size are composed of two male age groups (0 and 1-group) but of only one female age group (0-group) (Table VIII).

The catch of edible shrimps above 55 mm in length is almost exclusively composed of female shrimps (Meyer-Waarden and Tiews, 1957).

4.12 Age composition

Age at first capture

In Germany and Netherlands, where small shrimps are fished for utilization in shrimp flour production, the age at first capture is approximately six months. In countries where larger shrimps of over 50 mm size are fished mainly for human consumption, their age at first capture is approximately 1 year.

See section 3.43.

Age at maturity

According to Havinga (1930) and Lloyd and Yonge (1947) maturity is reached at a little less than two years; but according to Ehrenbaum (1890), Meyer-Waarden (1935 b), Nouvel-Van Rysselberge (1937), and Tiews (1954a) at approximately one year.

Maximum age

The maximum age of female C. orangon is given by Havinga (1930) as four years, by Lloyd and Yonge (1947) as five years, and by Tiews (1954a) as three years. Such old shrimps were found to be extremely rare and their percentage in catches was only 0.3 percent (Tiews, 1954a).

The maximum age of male C. orangon is given by Lloyd and Yonge (1947) as four years, and by Tiews (1954a) as a little more than two years.

4.13 Size composition

Length composition of the population as a whole

Havinga (1930), Meyer-Waarden (1935b) Lloyd and Yonge (1947), and Tiews (1954a) have given length frequency distributions of female Crangon populations; while Lloyd and Yonge (1947) also give data on male C. orangon in the Bristol Channel.

Variations with depth, distance off the coast, density, time of day, season

During autumn, when industrial catches of small shrimps are largest, they are obtained mainly from the shallower fishing grounds near the coast.

Size at first capture

Havinga (1930) gives the size at first capture as 20 mm, Meyer-Waarden (1935b) 15 mm, Tiews (1954a) 18 mm, and Kuro, Faure and Laurent (1965) 30 mm.

Size at maturity

The smallest size at maturity according to the different authors is given in Table IX.

According to Havinga (1930), Tiews (1954a), and Kuro, Faure and Laurent (1965a, 1965b) the majority of female C. orangon reach maturity at a length of approximately 52 mm. The size at first maturity, however, appears to be lower in the Baltic than in the North Sea.

Maximum size

The maximum size of female C. orangon was recorded as 91 mm by Havinga (1930) and as 95 mm by Tiews (1954a) while the maximum size of male C. orangon is 75 mm according to Havinga (1930) and 68 mm (Tiews, 1954a) and 60 mm (Boddeke, 1966b).

TABLE VII

Percentage of male shrimps in zones of highest (Z.H.S.) and of lowest salinity (Z.L.S.) in the Dollart and in the Jade (Ehrenbaum, 1890), in Zuidersee and Westerschelde (Havinga, 1930) and in the Bristol Channel and Severn Estuary (Lloyd and Yonge, 1947)

Month	Jade	Dollart	Zuidersee		Westerschelde		Bristol Channel and Severn Estuary Stolford Oldbury	
	Z.H.S.	Z.L.S.	Z.H.S.	Z.L.S.	Z.H.S.	Z.L.S.	Z.H.S.	Z.L.S.
January	-	-	51	-	-	-	25	18
February	-	-	-	-	45	-	-	0
March	-	0	47	-	31	-	31	14
April	-	-	50	0	29	0	12.5	5
May	-	-	19	0	23	0	22	19.5
June	-	0	14	0	27	0	2.5	-
July	4.6	4.1; 11	66	49	24	-	23	38
August	-	-	78	-	39	43	36	34
September	-	-	68	27	29	61	34.5	44
October	20	4.5	53	13	25	-	50	46
November	23	15	73	-	48	-	26	0
December	-	-	56	-	53	-	36	0

TABLE VIII

Percentage of male shrimps in the 30 to 50 mm size group in the catches off Büsum during 1951/52 (Tiews, 1954a)

Months	North of No. 1	Hackfeld	Süder-Piep-Channel	Norder-Piep-Channel	various creeks
1951					
May	60.8	61.4	55.0	66.3	54.3
June	81.3	83.9	79.1	80.8	79.4
July	30.1	22.0	29.3	28.2	40.3
August	61.4	62.8	71.3	63.8	59.3
September	64.3	57.1	69.7	58.4	82.1
October	68.9	73.0	56.8	69.3	69.2
November	58.3	-	-	-	80.2
1952					
March	-	-	-	-	10.7
April	70.3	46.4	65.3	-	66.3
May	59.3	30.8	63.7	35.3	36.8

TABLE IX

Smallest size at maturity

Author	males mm	females mm	locality
Wollebaek (1908)	-	45	Norwegian fjords
Havinga (1930)	-	42 (March)	Dutch coast
Henking (1927)	-	30-34	Pomeranian coast
Meyer-Waarden (1935b)	-	42-48	Outer Jade
Lloyd and Yonge (1947)	-	54	Bristol Channel and Severn
Tiews (1954a)	38	44-52	Büsum area normally
Kurc, Faure, and Laurent (1965)	-	50	French coast normally
"	-	47	Gulf of Gascogne
"	-	37	Bristol Channel
Boddeke (1966b)	22	37-42	Dutch waters

4.2 Abundance and density of population

4.21 Average abundance

Estimates of population size have not yet been made but studies in this field are carried out at the Institut für Küsten- und Binnenfischerei, Hamburg.

4.22 Changes in abundance

Changes caused by hydrographic conditions, food competition, predation, fluctuations and fishing

Tiews (1954b) found a positive correlation between the average catch of shrimps per trip and the water temperature: the higher the temperature (above 16°C) during the fishing season, July to September, the greater the catch per trip. An average difference of 1°C in the temperature resulted in an average increase of 100 kg catch per net per trip. It is the water temperature during late summer that greatly influences the total catch of the year in this area. Unfavourable temperature conditions in summer may have been the cause of the low catches in the Büsum fisheries during the years 1949, 1951, and 1952 (Figs. 12 and 13). The influence of predation on the changes in abundance, as found by Tiews (1965) is described in section 3.34.

4.23 Average density

Annual mean density

According to Tiews (1954b) the annual average shrimp catch (of all groups) per trip of the fishing fleet of Büsum during the years 1930 to 1952 was as follows (each trip corresponds to a fishing time of approximately 5 h):

TABLE X

Annual average shrimp catch/trip of the Büsum fishing fleet

year	kg	year	kg	year	kg
1930	310	1938	379	1946	409
1931	378	1939	412	1947	379
1932	447	1940	505	1948	315
1933	464	1941	616	1949	345
1934	412	1942	353	1950	425+)
1935	301	1943	433	1951	274+)
1936	436	1944	563	1952	248+)
1937	532	1945	170++)		

+) During these years fishing with two nets was introduced in Büsum, while earlier the boats fished with one net only. Figures refer to the catch of one net. The size of nets was then a little smaller than in the previous years.

++) Data incomplete, since catches of small shrimps are not included.

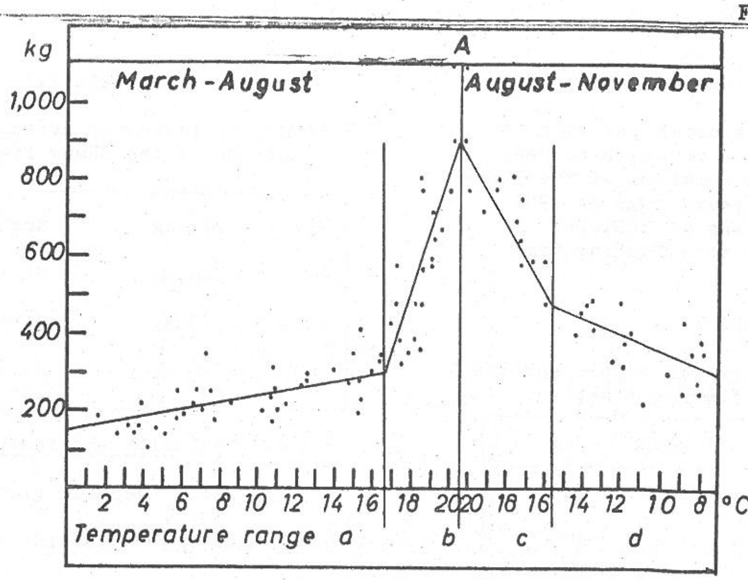


Fig. 12 Relationship between water temperature of 4 temperature ranges (a - d) and average catch of shrimps per trip (1930 to 1939) in the Büsum area (Tiews, 1954b).

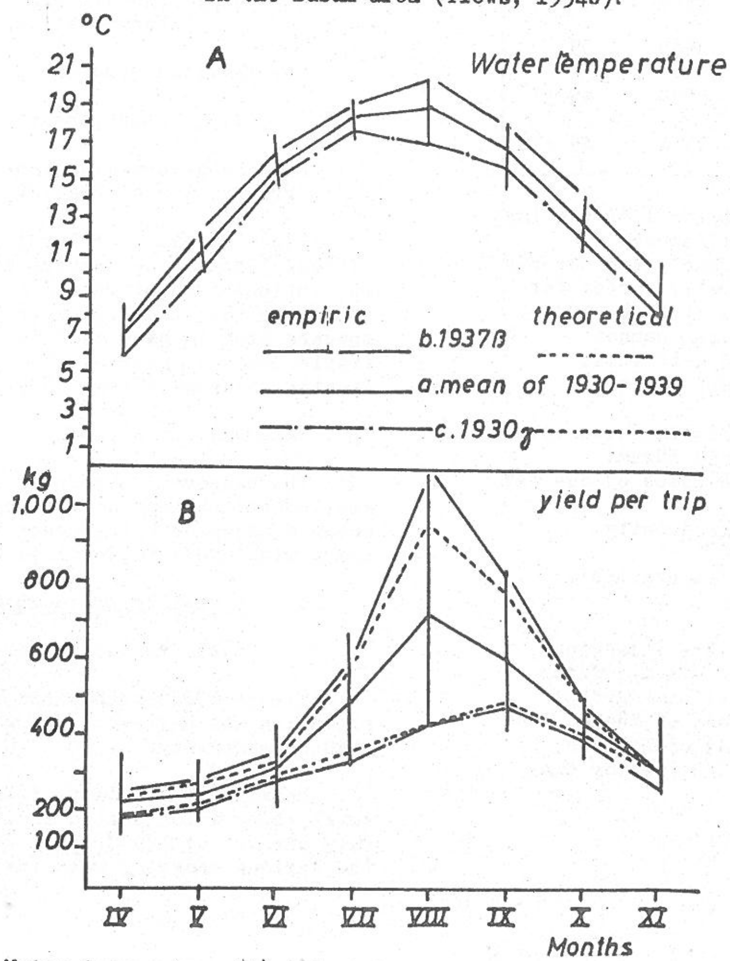


Fig. 13 Water temperature (A) and yield of shrimps per trip (B) given as monthly mean for a = 1930-1939, b= 1937 and c=1930 in the Büsum area. The dotted curves (β = 1937 and γ = 1930) are based on the water temperature - catch relationship found (Tiews, 1954b).

Density of adult females

The annual average catch per trip of edible shrimps (the size of which corresponds to that of adult females) of the Büsum fishing fleet for the years 1936 to 1951 (Tiews, 1953a, 1953b) was as follows (each trip corresponds to a fishing time of approximately 5 h):

TABLE XI

Annual average catch/trip of edible shrimps of the Büsum fishing fleet

year	kg	year	kg
1936	89	1944	249
1937	96	1945	170
1938	96	1946	161
1939	97	1947	123
1940+)	185	1948	116
1941	238	1949	59
1942	194	1950	49 ++)
1943	171	1951	49 ++)

+) During the years 1940 to 1947 fishing effort was very much reduced (1/5 to 1/7) and probably the catches were much more carefully sorted for obtaining all edible shrimps. Consequently these figures cannot directly be compared with those collected in the other years.

++) During these years fishing with two nets was introduced in Büsum. Figures refer to the catch of one net.

4.24 Changes in density

Seasonal variations in available stock

Tiews (1954b) gives the following seasonal variation of the average catch per trip of shrimps of all size groups of the entire fishing fleet of Büsum for the years 1930 to 1939 as follows (each trip corresponds to a fishing time of approximately 5 h).

Table XII

Seasonal variation of average catch/trip of shrimps of the Büsum fishing fleet

April	221 kg	August	717 kg
May	244 kg	September	605 kg
June	313 kg	October	433 kg
July	493 kg	November	316 kg

4.3 Natality and recruitment

4.31 Reproduction rates

Annual egg production rates

See section 3.15.
No calculations for whole population available.

4.32 Factors affecting reproduction

See sections 3.34 and 2.21.

4.33 Recruitment

Factors determining recruitment (growth, transformation, movements)

Since growth is related to temperature (Tiews, 1954a), the temperature conditions may influence the time and magnitude of recruitment to the fishery. Temperature appears also to have some influence on the displacement of year-classes over the fishing grounds (Tiews, 1954b).

Seasonal pattern of recruitment

The seasonal pattern of landings of small-sized shrimps on the German coast shows a major peak in August to September and a minor peak in April to May.

4.4 Mortality and morbidity

4.41 Mortality rates

Tiews (1965) found that loss caused by predation was several times greater than by fishing mortality.

Meixner (1967) found that during a total observation period of 1½ years only one out of 129 Crangon died during the various ecdyses, when individuals were kept separate, i.e. one of 1,028 recorded moultings failed to be successful. This indicates a moulting mortality of less than 1 percent and less than 1 per thousand if referred to the total number of moults.

High mortality due to cannibalism has been observed in C. crangon immediately after moulting, when individuals were kept together in aquaria (Tiews, 1954a).

4.42 Factors causing or affecting mortality

Predators

See section 3.34.

Direct effects of fishing

Intensity of fishing is known to be high, but fishing mortality rates have not been assessed.

4.6 The population in the community and the ecosystem

Species composition of the community and relative sizes of their population

Heidrich (1930), Wulff and Bückmann (1932) as well as Meyer-Waarden and Tiews (1965a, 1965b) have studied the catch composition of the German shrimp fishery. According to Meyer-Waarden and Tiews (1965a, 1965b) the most abundant fish species caught along with shrimps was the goby, with a total average catch amounting to 732 million individuals per annum during the years 1954 to 1960, followed by the plaice with 215 million. Herring, pipe fishes, common sole, smelt and dab were caught in the order of 80 to 50 million individuals; armed bullhead, whiting, sea snails, flounder and sprat in the order of 30 to 10 million, and finally the three-spined stickleback, eel-pout, eel, short-spined sea scorpion, cod, sand-eels, dragonet, solenette, gunell, anchovy, rocklings, gurnards and horse mackerel amounting to less than 10 million. Shore crab and swimming crab were found to range between 120 and 100 million individuals. All the fish and crustaceans caught along with the shrimp show distinct fluctuations in their abundance from year to year.

The industrial catches of the German shrimp fishery during the years under observation contained less than 10 percent of undersized protected fish mentioned in Annex II of the Fisheries Convention (1946).

In the years when the industrial catches were large, as in 1954, 1955 and 1957, the percentage of fish was low (about 5 percent), whereas when the shrimp catches were poor, as in 1960, the percentage of undersized fish was close to 10. In 1959, also the industrial shrimp catches included nearly 10 percent of fish, but this is attributable to the strong 1959 year-class of whiting that had immigrated to the German coastal waters increasing the normal catch of undersized protected fish (some 2,000 tons per annum) by about 50 percent.

Although the fishing effort in the German shrimp fishery has increased 3.5 to 4 times since 1930, no decrease in the density of population of young fish could be observed in the case of plaice and sole (Meyer-Waarden and Tiews, 1965a, 1965b).

Interrelations of the population of the species in the community and ecosystem; place in the food chain; trophic level, etc

C. crangon is the most important food of several fish species in the community (Tiews, 1965).

See section 3.34.

Type of fluctuations (cyclic and non-cyclic)

Fluctuations seem to be non-cyclic (Tiews, 1954b, 1965).

Changes in environmental factors and their effect on the population

See section 3.32 and 3.34.

5 EXPLOITATION

5.1 Fishing equipment

5.11 Gears

Present gear (type and size of twine, webbing, shape, assembly, size, mesh size)

The most common gear now used in the Crangon fishery is a pair of beam trawls.

The German shrimp trawl has been described fully by Meyer-Waarden and Tiews (1957) and von Brandt (1959).

The length of the iron tubular beams varies between 6 and 9 m, and the shoes have a height of 50 to 60 cm. The ground rope is armed with 32 to 36 wooden bobbins. The design of the net varies greatly. The total length of the net is 10 to 12 m, of which the cod end is 2.5 to 3 m.

Von Brandt (1959) described in detail a number of typical nets used in Husum, Tönning, Büsum, Friedrichskoog and Neuharlingersiel.

Formerly the nets were made of cotton, but at present synthetic materials are used. Twin beam trawls were introduced on the coast of Ostfriesland after 1930, and in Schleswig-Holstein in 1948 (Tiews, 1952). At present shrimp fishing in Germany is nearly exclusively carried out with two beam trawls.

The fishermen of Ostfriesland use small trial nets before setting the main gear. A description of a try-net is given by von Brandt (1959).

The Dutch shrimp fishery also used beam trawls of a similar type (Tesch and de Veen, 1938). This was also the case in the French fishery (Belloc, 1938) until recently, but now otter trawls yield the larger part of the catches. Only smaller boats with small engines of 20 to 25 hp are still using beam trawls. In Belgium beam trawls were in use (Verbrugghe, 1932), but were later replaced in most cases by the otter trawl. During recent years, however the Belgian fishermen changed over to beam trawls again, as they consider them more effective in the tidal areas where the shrimp fishery is carried out. The French shrimp otter trawl is described by Kurc, Faure, and Laurent (1965a) (Fig. 14).

Kurc (1964), Kurc, Faure, and Laurent (1965b) described a new otter-trawl developed for shrimp fishing in the Gulf of Gascoyne, the so-called "Devismes modifié" type (Fig.14). The net is divided in two sections and has two cod ends with different mesh sizes. The small mesh of the upper section catches the shrimps which jump through the netting that separates the lower from the upper section. The lower cod end has larger mesh to allow any small fish caught to escape easily. Catches of undersized fish are thus considerably reduced.

The design of the two-section shrimp trawl has been modified and used recently in a Dutch model of a beam-trawl (Boddeke, 1965a, 1965b) (Fig. 15). According to Boddeke (1965a) by-catches can be reduced by one sixth by using this new type of beam trawl. But Tiews (1966), experimenting with the same net, did not obtain the same results when used over the German fishing grounds.

On the east coast of England the beam trawl is exclusively used for fishing brown and pink shrimps (Mistakidis, 1958). In the Thames area the otter trawl has been introduced recently. On the northwest coast in addition to the beam trawl, fishing of brown shrimps is done by push and shank nets, the latter being small trawls pulled by horse carts. In the Bristol Channel small quantities of brown and pink shrimps are taken in salmon putts and stall nets. However, approximately 90 percent, if not more, of the total landings are fished by the beam trawl. The length of the beam varies between 5.5 m and 7.3 m, depending on the overall length of the boat and the length of the shrimp net is usually one and a half times the length of the beam, their mesh size varying from 19 to 25 mm full mesh.

Changes in types of gear during the development of the fishery

On the German coast push nets and the shrimp basket used to be the common gear for catching shrimps, but today the latter has all but completely disappeared (Meyer-Waarden and Tiews, 1957).

A description of the shrimp basket and of another primitive shrimp fishing gear, the fyke net with wings (Fig. 16), is given by Meyer-Waarden (1931).

A more modern, but also disappearing gear in the German shrimp fishery is the shrimp stow net. While the shrimp basket is a fishing gear for the shallow and more sheltered fishing waters, the shrimp stow net is for the deeper creeks with more rapid currents. This net has been described by Meyer-Waarden (1931) and von Brandt (1959).

These stow nets can fish only either in the ebb or flood tide.

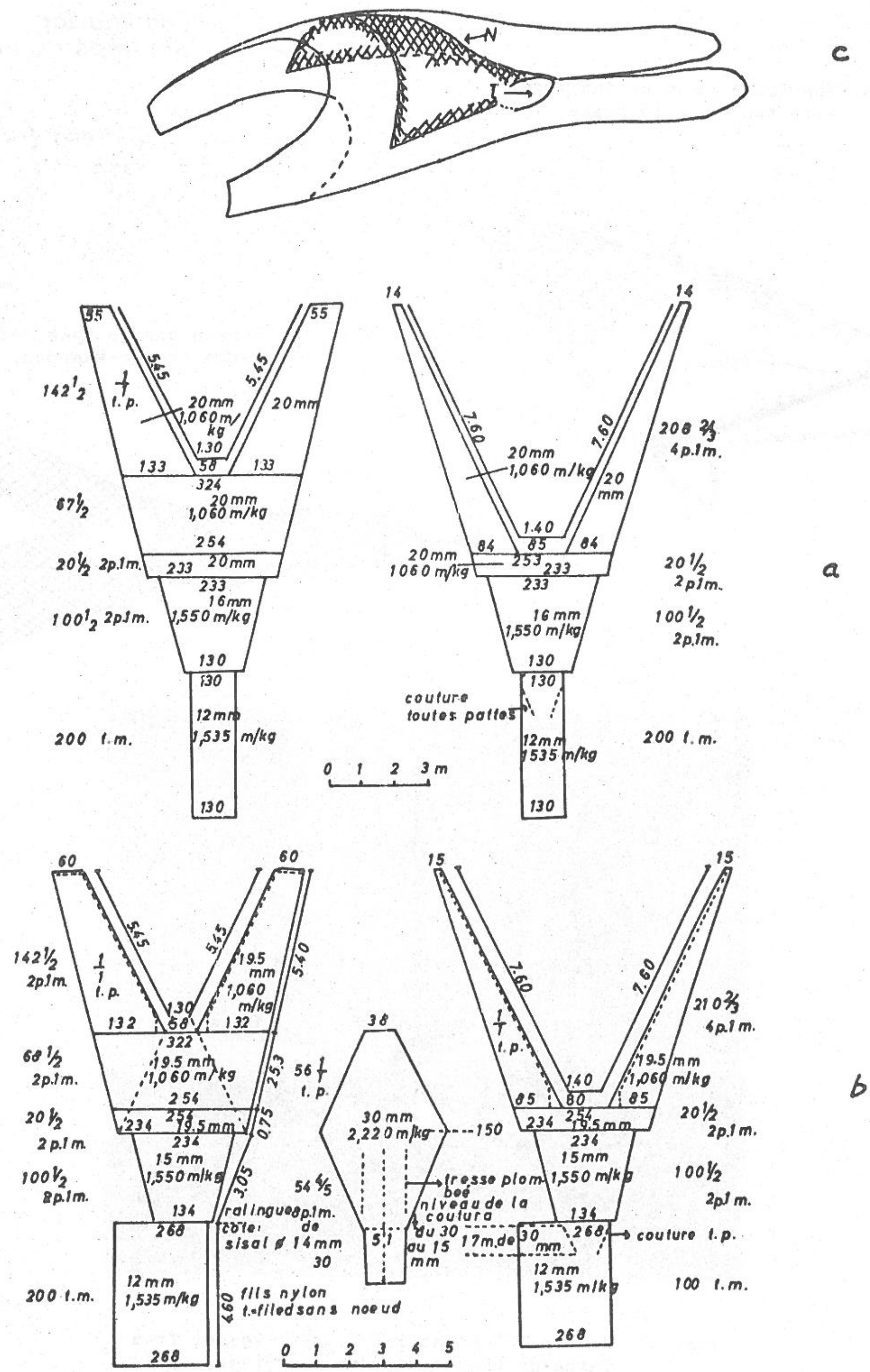


Fig. 14 French otter board shrimp trawl made of nylon, knotless, as used in Vendée, 12.20/16.60 m: (a) = classical type, (b) = the same net, but with second selection bag of the "Devismes"-type, as demonstrated on top (c) (Kurc, Faure and Laurent 1965b).

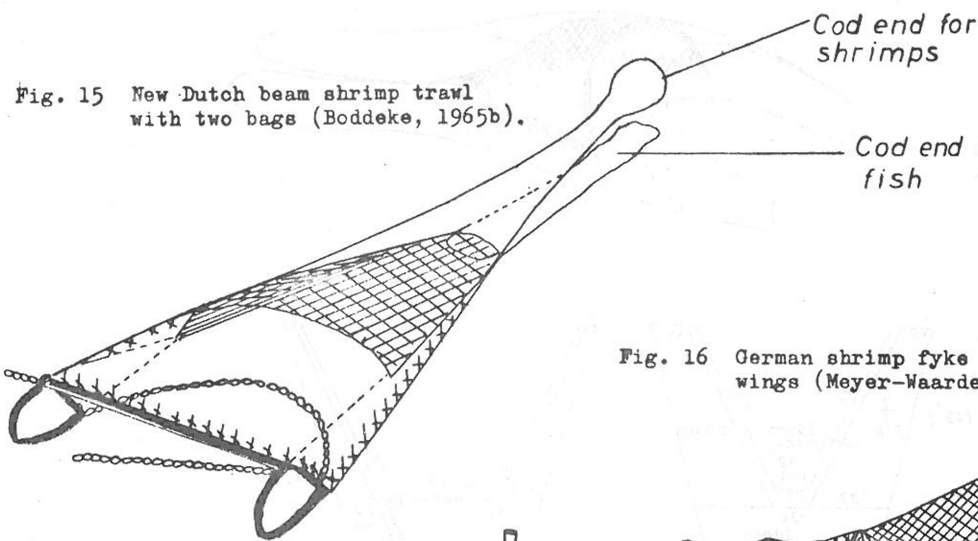


Fig. 15 New Dutch beam shrimp trawl with two bags (Boddeke, 1965b).

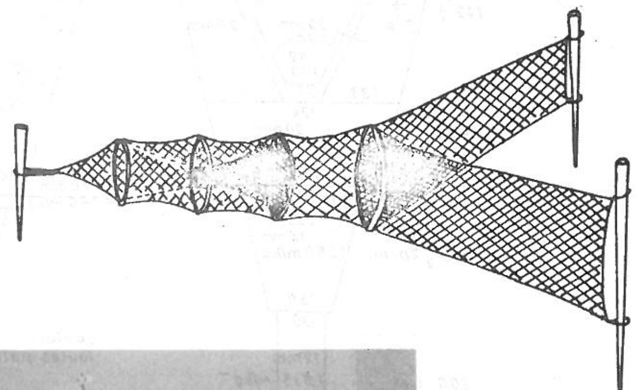


Fig. 16 German shrimp fyke net with wings (Meyer-Waarden, 1931).

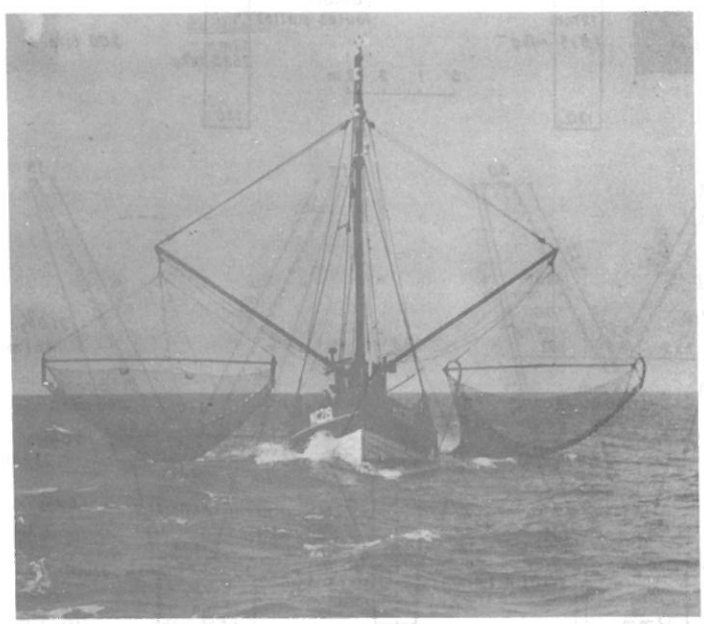


Fig. 17 Modern German shrimp fishing vessel from Cuxhaven (Meyer-Waarden and Tiews, 1957). (Photo: Dr. Nolte)

This type of stow net has been modified to facilitate operation during both the tides, with a special hanging design that permits considerable increase of catching power. Nevertheless the modified gear is not widely used for shrimp fishing (Meyer-Waarden, 1931).

Henking (1927) described some beam trawls which are used in the Baltic Sea for fishing C. orangon. Shrimps are caught there only as bait for the cod fishery, since large shrimps are not abundant enough to sustain a large-scale shrimp fishery.

A description of the original "shrimp net" used in the neighbourhood of the Thames Estuary, prior to 1830-40, its modification in early 1850, and the introduction of the "four beam trawl" at the same period is given by Mistakidis (1960).

In early days horses were used for towing shrimp nets in Belgium (Verbrugghe, 1932) and England (Davis, cited by Schnakenbek, 1942). The Belgian shrimp trawl was kept open by a ground beam in the middle of which a stick was attached to keep the mouth of the net open.

Use of echosounding or fish detectors

Echosounding is used now in the German shrimp fishery, but Crangon cannot be detected on fish finders (sonar).

5.12 Boats

Type, Size, Power, Changes in types of boats during the development of the fishery

In the early days in Germany small wooden, open or covered, sailing boats were used for shrimp fishing. Motorization started around 1900 and by 1927 all shrimp fishing boats were powered (Tiews, 1953a).

Today the type of boat remains the same except in size, the length varying from 12 to 17 m and equipped with engines between 50 and 75 hp (Tiews 1965) (Fig. 17).

All boats are equipped with 50 litre oil-fired boilers to cook the catch of edible shrimp immediately after hauling, sorting and cleaning the catch. Nearly all vessels are equipped with mechanical sieves for sieving the catches. Most of the vessels do not possess fish rooms. Only the larger ones have refrigerated fish rooms.

In the Netherlands shrimp vessels are larger than in Germany, up to 21 m long and having engines up to 150 hp. These boats fish shrimps during the winter also and much farther away from their home ports than the German fishing boats do. The average engine power has steadily increased from 45 hp in 1951 to 93 hp in 1962 (Boddeke, 1962a, 1962b, 1966a).

In France, small fishing vessels having engines from 40 to 80 hp are used for shrimp fishing (Kuro, Faure, and Laurent, 1965a).

5.2 Fishing areas

5.21 General geographic distribution

Geographic distribution

Crangon fishing, on commercial scale, is carried out along the entire coasts of Germany (North Sea coast), the Netherlands and Belgium, as well as on the east and west coasts of England, and in several areas on the French coast. There appears to be some prospects for Crangon fishing on the Danish North Sea coast, at least in the southern area. However, this is not exploited by the Danish fishing industry.

5.22 Geographic ranges

Distances from coast

Crangon fishing is pursued close to the coast, the fishing areas varying in distance from half to 20 n mi (37 km), depending on their location.

Drainage basins

The fishing areas are usually within or close to estuaries.

Areas of greatest abundance (political or geographical designations or degrees of latitude and longitude)

Areas of greatest abundance are the entire coasts of Germany and the Netherlands.

Meyer-Waarden and Tiews (1957) state that the brown shrimp is caught along the entire German North Sea coast. The fishing grounds are in the estuaries and in the region of the large and small creek systems of the Wadden Sea. They are limited, in the sea, by the 15 to 20 m line which runs along the coast of Schleswig-Holstein, in the Elbe/Weser estuary up to 20 to 25 n mi (46 km), off the coast and along the coast of East Friesland up to 10 to 15 nautical miles. During spring and late autumn the fishing is carried out more seaward than during the months July to October, when fishing is almost exclusively confined to areas close to the coast. There are good shrimp fishing grounds near the estuaries of the rivers Eider, Elbe, Weser and Ems. Hydrographically the entire fishing area is characterized by strong tidal currents of strength up to 3 m/sec, and by continuous discharge of fresh water into this area by the rivers mentioned. Because of the marked annual and seasonal fluctuations in the quantity of fresh water discharges, the salinity on the fishing grounds is subject to great fluctuations.

Mistakidis (1960) stated that in England the three main centres of the shrimp fishery are the Wash, the Thames estuary, and the Lancashire coast. Landings of pink and brown shrimps in these areas amount approximately to 80 percent of the total landings.

Kurc, Faure and Laurent (1965b) stated that along the French coast there are areas in the Atlantic as well as on the Channel, which are rich in sand shrimps, especially those close to the estuaries of the rivers Gironde, Loire, and in the Bight of the Seine (Fig. 18). In each of these areas about one third of the total annual production (which is between 1,400 and 1,800 t) is produced. There is also a small shrimp fishery along the coast of Vendée, in the Bight of Mont Saint Michel and on the east coast of Contentin.

Differential abundance associated with hydrographical features

See section 4.11

Changes in ranges during development of the fishery

When only push nets, baskets and stow nets were used, the fishery was fairly close to the shore. When trawling was introduced, the range depended on the action radius of the boat. Sailing boats operated along the coast, while powered boats could fish further out to sea.

5.23 Depth ranges

Bathymetric contour

The fishery along the German coast is limited by the 15 to 20 m depth line (Meyer-Waarden and Tiews, 1957).

Variations of density with depth

During spring and late autumn the density of shrimp stocks is greater in the deeper areas than in the shallow. The contrary is the case during the months of July to October (Tiews, 1953a, 1953b).

5.24 Conditions of the grounds

The fishing grounds have sandy or muddy bottoms with usually rich food supply.

5.3 Fishing seasons

5.31 General pattern of seasons(s)

The main fishing season extends from spring to late autumn depending on the migration of *Crangon* in the fishing grounds (see section 3.51).

In the Netherlands there is a regular winter fishery. In the other countries the shrimp fishing boats are too small to permit a winter fishery. In Germany a winter fishery is of no interest to the fishermen, since prices are fixed upon agreement between the fishermen and the industry for the whole year, and so the lower winter catches do not yield a profit.

For small fishing boats bad weather prevailing during winter would greatly hamper fishing operation. Another factor hampering the conduct of a successful winter fishery in the German waters is that heavy winter storms usually destroy the markings of the numerous creeks making navigation extremely difficult (Meyer-Waarden and Tiews, 1963b).

5.32 Dates of beginning, peak and end of season(s)

Approximate dates in various fishing areas

The German shrimp fishery usually starts at the end of March or the beginning of April when water temperatures are generally above 5 °C, and terminates at the end of November. Maximum catches of small sized shrimps are obtained during July to October, when 70 to 80 percent of the annual catches are taken. The catches of large sized shrimps, i.e. those for human consumption, are much more balanced with peaks in April to May and in October (Fig. 19) (Meyer-Waarden and Tiews, 1957, 1965a). Also the Belgian shrimp fishery lasts from March to November (Gilis, 1952).

The Dutch fishery for large sized shrimps operates through the year.

In 1963 and 1965 maximum production was recorded during September to October (Boddeke, 1966b).

5.33 Variation in date or duration of season

Severe and prolonged winters retard the beginning of the fishery, just as early win-

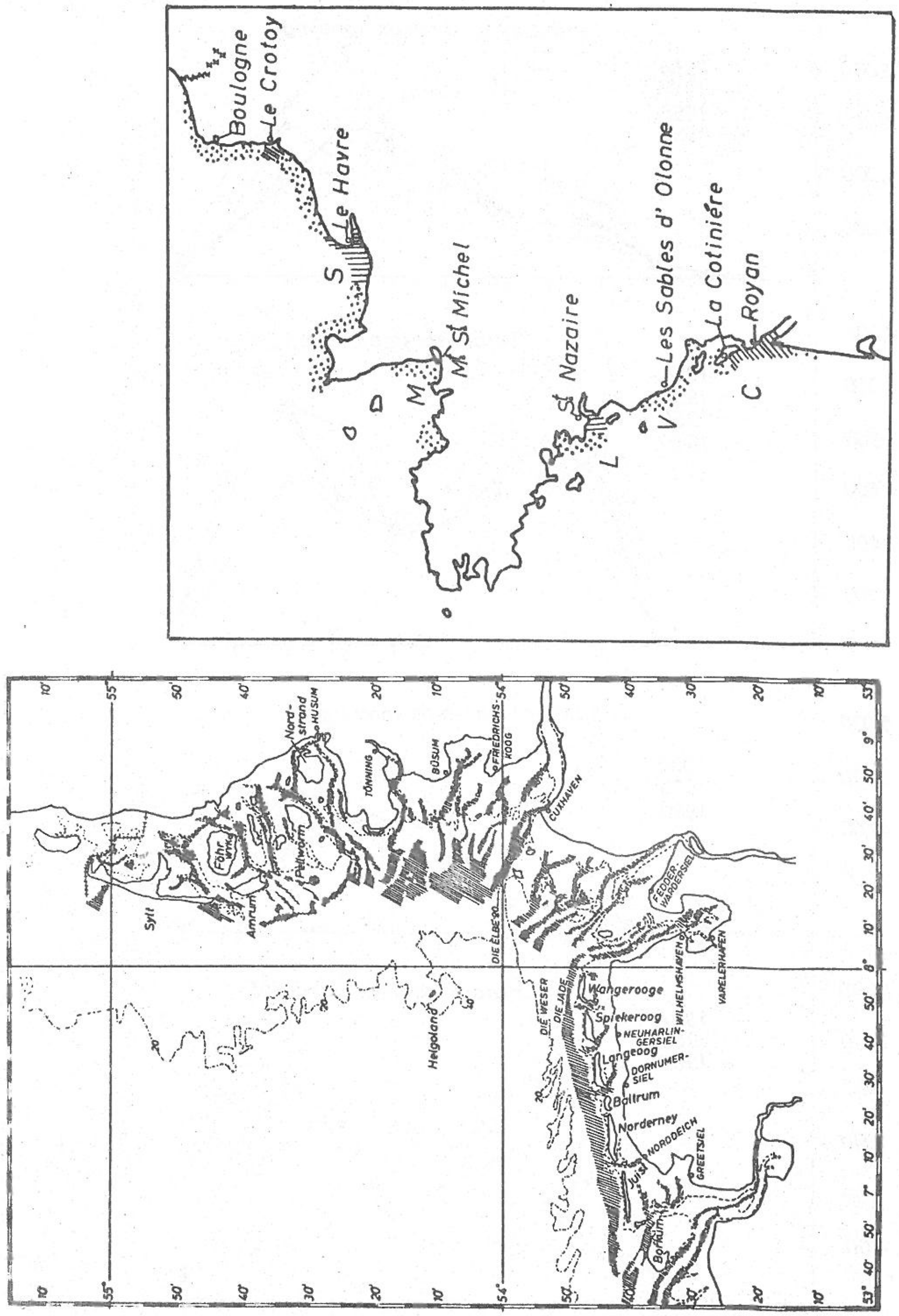


Fig. 18 German (Meyer-Waarden and Tiews, 1965a) and French shrimp fishing areas (Kurc, Faure and Laurent, 1965b)

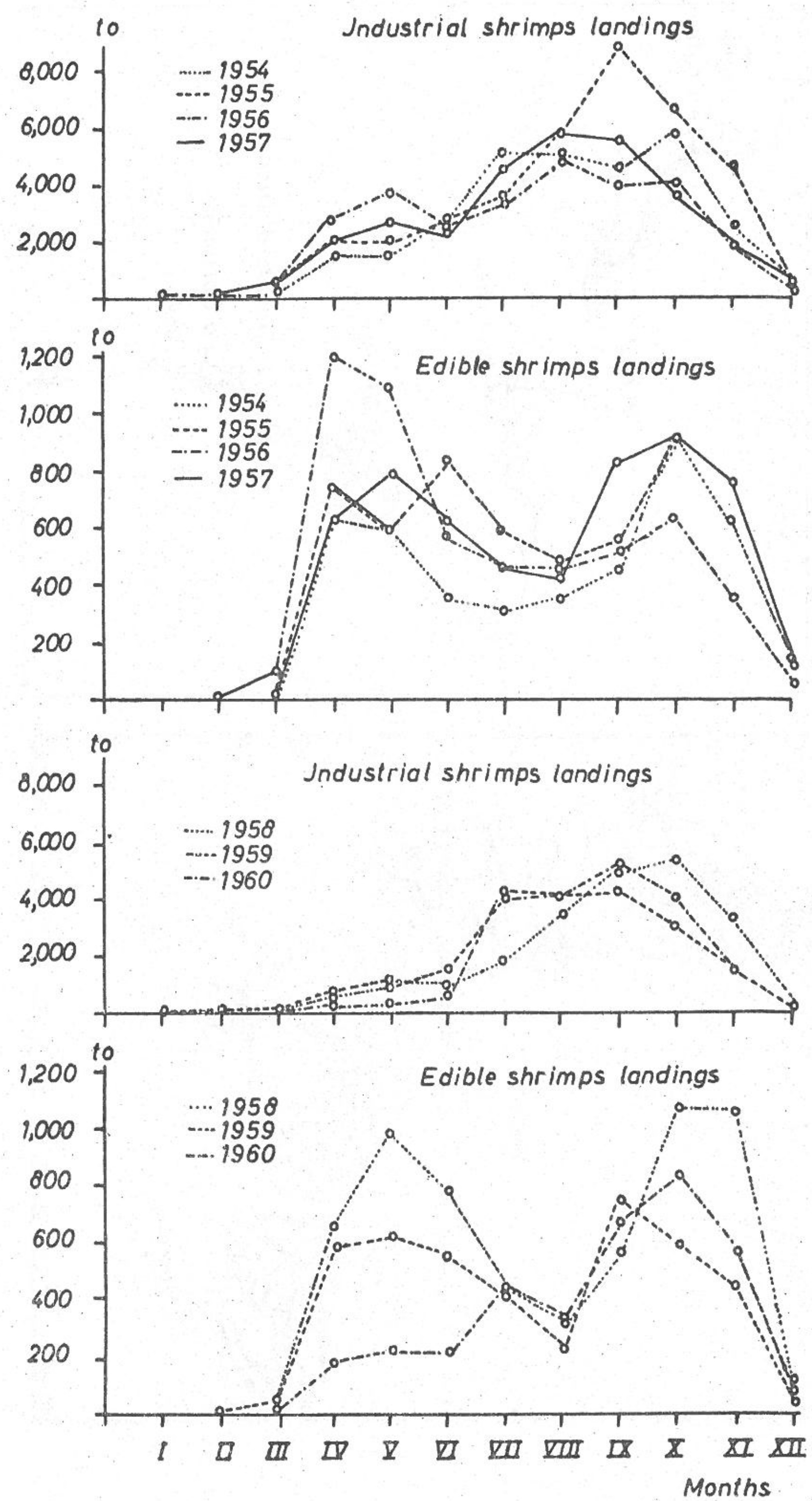


Fig. 19 Seasonal distribution of German shrimp landings 1954-1960 (Meyer-Waarden and Tiews, 1965a).

ters cause its earlier termination. In warm years German fishermen may extend the fishing season until Christmas.

During the years 1930 to 1939 the peak of the fishing season was usually in August. Since 1949, quite likely due to climatological changes and consequent cooler August temperatures, the peak has shifted to September/October (Tiews, 1954b).

5.4 Fishing operations and results

5.41 Effort and intensity

Type of unit of effort

Since most of the fishing trips in the German shrimp fishery do not exceed 16 h, one fishing trip can be considered a unit of effort. Since 1958 nearly all shrimp cutters fish with two nets, while before 1930 they fished with one net only. Two-net fishing was introduced on the coast of Niedersachsen during the years 1930 to 1939, and on the coast of Schleswig-Holstein from 1948 to 1958.

Tiews (1954b) designated catch per unit effort for the fishing fleet of Büsum, as the catch per net per 10 h trip taking into consideration the seasonal variations in fishing time.

The fishing trips of the large Dutch shrimp fishing vessels last five days. The catch per trip of these boats cannot, therefore, be compared with that of the smaller boats which go fishing, as the German boats do, from early morning until the afternoon (Boddeke, 1962a, 1962b). Gilis (1960) expressed the catch per unit of effort of the Belgian fleet, as the catch per 100 h fishing, multiplied by the hp of the engine.

Landings per unit of fishing effort

Tiews (1954b) has given the average landings of small and edible shrimps per trip for the period 1930 to 1952 for the shrimp fishing vessels stationed in Büsum.

Bartling (1964, 1965) found that a fishing boat of 14 to 16 m length fished nearly twice as many shrimps as one of 10 to 12 m length.

The fluctuations in landings per unit of fishing effort of the Belgian shrimp fishery for the period 1935 to 1959 are given by Gilis (1960)(Table XIII).

Catches per unit of fishing effort

In the Thames estuary the catch per hour is usually 32 to 68 kg, the quantity depending on the fishing ground and on the season of the year. Catches of 225 to 270 kg are not unusual. However, there are also records of only 9 or 13 kg of shrimps caught in two hours trawling (Mistakidis, 1960).

French shrimp catches during winter generally do not exceed 3 kg of edible shrimps per h. During June to July the catches per h are between 2 and 15 kg while in December they are often below 1 kg (Kurc, Faure and Laurent, 1965b).

Fishing effort per unit area

No information.

Total fishing intensity

The German shrimp fishery carried out 51,715 fishing trips (of less than one day each) in 1964. Of these, 30,587 were on the coast of Niedersachsen. This showed a decline in fishing effort as compared to the period 1958-63, when on an average 32,958 fishing trips were made. The changes in fishing effort on the German coast during 1954 to 1964 have been traced by Tiews (1965).

The number of Belgian shrimp fishing boats has declined steadily since before the second World War. In 1936 it was 285 and in 1959 only 149. However, the size of engine has increased from 33.2 hp during the years 1935 to 1939, to 62.7 hp during 1956 to 1959 (Table XIII) (Gilis, 1960).

The sizes of the Dutch shrimp fishing fleet in the years 1951, 1954, 1957, 1960 and 1961 are given by Boddeke (1962b).

Causes of variation in fishing effort and intensity

The German shrimp fishing fleet amounting to 690 fishing boats in 1937, decreased to 674 boats in 1955 (Meyer-Waarden and Tiews, 1957). In 1964 only 489 boats were operating as a result of a special scheme sponsored by the government under which certain fees were paid to the fishermen upon retirement on condition that their old boats were destroyed for thinning out the fleet in order to make it more profitable (Tiews, 1965).

5.42 Selectivity

The cod end, as well as the anterior parts of the net contribute to selective fishing (Bohl, 1963a, 1963b).

The absolute catches of edible shrimps are largest when mesh sizes of 11 to 12 mm (from knot to knot) in the cod end are used. Smaller mesh sizes yield smaller catches of

TABLE XIII

Fishing effort and shrimp landings in Belgium from 1935 to 1959 (Gilis, 1960)

Year	Number of cutters	Mean Horse Power	Number of Fishing Hours (FH) x Horse Power (HP)	Total Yields	Mean Yield per 100 FH x HP (kg)
1935	264	30.2	7 440 025	2 670 969	35.9
1936	285	29.6	7 666 817	3 496 069	45.6
1937	256	33.6	8 135 032	4 059 381	49.9
1938	236	35.6	8 452 478	2 949 915	34.9
1939	201	38.8	8 368 266	2 728 055	32.6
Average	248	33.2	8 012 523	3 180 878	39.7
1946	250	39.7	4 172 168	1 289 200	30.9
1947	226	40.0	5 729 473	2 033 963	35.5
1948	210	49.4	5 541 345	1 651 321	29.8
1949	191	49.4	6 346 759	1 796 133	28.3
1950	211	51.1	6 790 653	1 548 269	22.8
Average	218	45.5	5 716 079	1 663 777	29.1
1951	195	54.6	8 081 989	2 068 299	25.5
1952	188	54.5	7 888 720	2 608 057	33.1
1953	187	54.7	7 455 812	1 961 880	26.3
1954	189	57.0	6 692 910	1 514 175	22.6
1955	181	58.2	7 123 992	2 100 346	29.5
Average	188	55.8	7 448 684	2 050 555	27.5
1956	186	62.9	8 495 949	3 193 010	37.6
1957	176	62.6	6 524 808	1 004 414	15.4
1958	154	61.5	4 749 476	764 988	16.1
1959	149	63.3	5 784 426	1 072 776	18.5
Average	166	62.7	6 388 664	1 508 797	23.6
Total average	207	47.0	6 917 952	2 132 171	30.8

edible shrimps but considerably larger catches of smaller shrimps (Gilis, 1952; Mistakidis, 1958; Bohl and Koura, 1962; Kurc, Faure and Laurent, 1965b). The relation between the 50 percent retention length and the value of catch sizes times selection factor is given by Bohl and Koura (1962) (Fig. 20).

According to Bohl (1963a, 1963b), since the anterior parts of the net have selective properties, the following mesh sizes obtain the best catches of edible shrimps:

TABLE XIV

Mesh sizes

Part of the (trawl)	Mesh bar (mm)	Number of meshes (depth)
Anterior	14	ca 125
Medium	12	ca 145
Posterior	10 - 11	ca 155 - 175
Cod end	10 - 11	

The change in mesh sizes is claimed to yield the following advantages:

(i) A larger quantity of edible shrimps is caught for no extra expenditure or work.

(ii) Because of the large mesh size the quantity of small shrimps caught is reduced and better and larger catches of large-sized edible shrimps are obtained.

(iii) The larger mesh of the cod end (10 to 11 mm) allows an immense number of juvenile shrimps to escape, thus helping in the protection of shrimp stocks.

In the German shrimp fishery the mesh sizes of the cod ends have been increased since 1962 because of the difficulty in marketing small sized shrimps consequent to the abolition of the law that guaranteed the selling of small sized shrimps (Meyer-Waarden and Tiews, 1957).

5.43 Catches

Total annual yields

The Yearbook of Fishery Statistics published by FAO gives the total annual yields in various countries (FAO, 1965)(Table XV).

Total annual yields from different fishing grounds

Mistakidis (1960) reported that the landings of pink and common shrimps in England and Wales during the past 48 years showed fluctuations between 890 t and 3,700 t. Certain distinct falls in landings may have been due to the reduced effort during the war years and immediately after, and to the severe winters of 1928 to 1929, 1939 to 1940, and 1946 to 1947. Even if these exceptionally poor years are not taken into consideration, on the whole, landings during the past 25 years were smaller than for the period 1910 to 1930. Whether reductions in landings was the result of a decline in the stock, or of reduced fishing effort, it is difficult to determine as there are no available data with regard to the number of boats and men engaged in the shrimp fishery.

Meyer-Waarden and Tiews (1965a) have described the development of the German shrimp fishery during 1928 to 1960 and furnished the yearly landing figures (Table XVI). The yields showed considerable fluctuations during this period. The German shrimp landings by areas as given in Table XVII indicate however that the development was different from area to area. During the period 1949 to 1959 catches of edible shrimps increased in Oldenburg, Ostfriesland and Schleswig-Holstein, and decreased in the Elbe/Weser area. During the same period catches of small industrial shrimps decreased in Oldenburg and Elbe/Weser, but showed an increase in Ostfriesland and in Schleswig-Holstein.

Catch statistics of the Belgian shrimp fishery have been collected since 1935. During the years 1935 to 1939 the annual catches fluctuated between 2,671 and 4,059 t and amounted, on an average, to 3,181 t. From 1946 to 1950 the catches varied between 1,289 and 2,034 t and were on an average 1,664 t. During 1951 to 1953 the annual average catch amounted to 2,051 t and decreased during the period 1956 to 1959 to 1,509 t (Table XIII) (Gilis, 1960). In Belgium there is no fishery for small shrimps for industrial use, as is also the case in France (Personal communications).

The Dutch landings of edible and small shrimps for 1951 to 1961 are given by Boddeke (1962a, 1962b, 1966).

Maximum equilibrium yield

No information.

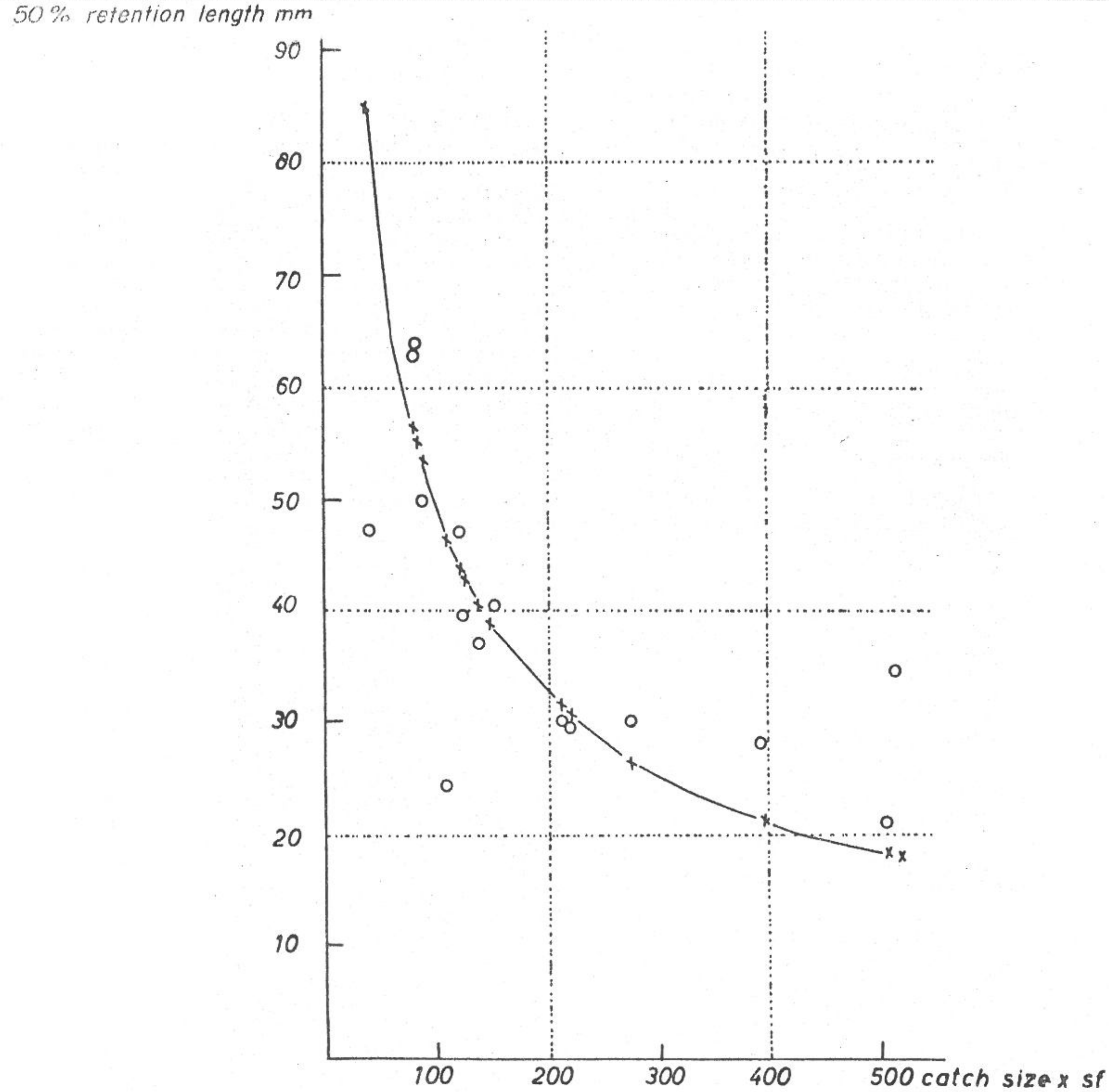


Fig. 20 Relation between the 50% retention length and the value of catch size times selection factor (Bohl and Koura, 1962).

TABLE XV

Landings (in t) of common shrimp by countries according to Yearbook of Fishery Statistics

	1938	1948	1958	1961	1962	1963	1964
Total	<u>46.0</u>	<u>31.0</u>	<u>48.0</u>	<u>47.0</u>	<u>45.0</u>	<u>72.0</u>	<u>57.0</u>
Algeria 1/	0.3	–	0.7	–	–	0.4	0.2
Belgium	3.0	1.7	1.1	1.4	0.9	1.3	1.4
Denmark	0.2	0.4	0.2	0.3	0.2	0.1	0.1
France	2.4	1.7	1.9	1.7	2.1	2.4	2.8
Germany, Federal Republic	34.2 3/	15.1 3/	29.4	27.6	24.8	42.4	28.7
Netherlands	–	9.2	13.3	14.9	16.4	24.7	21.9
Sweden	ø	ø	ø	ø	ø	–	–
U.K. (England and Wales) 2/	2.4	2.6	2.1	1.0	1.1	1.4	1.6
U.K. (Scotland)	–	–	–	–	0.1	0.1	0.1

1/ The landings given for Algeria are considered doubtful by the author
2/ Figures include also landings of pink shrimp (<u>Pandalus montagui</u>)
3/ FAO estimate

TABLE XVI

German common shrimp landings in tons

Years	Edible Shrimps	Small Shrimps	Total
1928	3066	9 176	12 424
1929	3077	15 114	18 191
1930	3784	16 476	20 260
1931	3304	21 962	25 266
1932	3003	19 837	22 840
1933	3100	24 000	27 100
1934	3414	26 686	30 100
1935	3887	19 753	23 640
1936	4698	34 991	39 689
1937	6060	44 540	50 600
1938	5755	33 620	39 375
1939	5404	29 406	34 810
1940	5131	18 092	23 223
1941	7392	16 366	23 758
1942	4207	6 334	10 541
1943	1957	2 651	4 608
1944	1650	2 741	4 391
1945	1689	541	2 230
1946	2858	3 748	6 606
1947	3928	7 261	11 189
1948	5962	8 212	14 174
1949	3437	15 685	19 122
1950	2637	30 165	32 802
1951	3302	23 311	26 613
1952	3286	21 078	24 364
1953	4295	35 656	39 951
1954	4456	28 738	33 194
1955	5641	37 281	42 922
1956	5412	27 476	32 888
1957	5689	29 158	34 847
1958	6051	22 301	28 352
1959	4413	21 278	25 691
1960	3603	20 276	23 879

TABLE XVII

German mean landings on common edible shrimps (a) and small shrimps (b) by districts in tons

Years	Elbe - Weser		Oldenburg		Ostfriesland		Schleswig-Holstein		Total landings	
	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)
1928/30	881	3 142	89	1 733	224	5 387	2 115	3 337	3 309	13 589
1931/39	1 079	6 162	200	3 512	312	8 624	2 700	10 021	4 292	28 311
1949/59	786	3 945	250	2744	565	9 499	2 820	10 369	4 420	26 557

6 PROTECTION AND MANAGEMENT

6.1 Regulatory (legislative) measures

6.11 Limitation or reduction of total catch

Limitation on the efficiency of fishing units

There are no limitations at all in the Belgian shrimp fishery. The Dutch "Produktschap voor Vis en Visprodukten" has prescribed that fishing boats landing shrimps are not allowed to have a dragging power above 2,000 kg.

In England the different Fisheries Districts have exercised various legislative restrictions on the sizes of fishing boats, length of beam of trawls and push nets, diameter of nets, duration of operation of trawls and obligatory release of undersized fish.

Limitation on the number of fishing units, fishermen

In Germany credit facilities for replacement of old shrimp fishing boats are given only on condition that the old boats are destroyed in order to limit the number of fishing boats. However, so far a number has not been fixed by the law.

Limitation on total catches (quota): daily, seasonal, annual

When catches are large the processing firms in Germany that have contracts with fishermen for supply of edible shrimps for processing fix a ceiling for the daily quota to be delivered. Such restrictions do not normally exist for small sized fodder shrimps.

According to the Fisheries Convention for the NE Atlantic (24 June 1959), the industrial by-catches of the shrimp fishery are not allowed to contain more than 10 percent of undersized protected fish. Meyer-Waarden and Tiews (1965a) have calculated that the industrial catches of the German shrimp fishery during the years 1954 to 1960 contained less than 10 percent of undersized protected fish.

6.12 Protection of portions of population

Closed areas such as spawning or nursery grounds

In France the shrimp fishery is prohibited in certain areas, mostly in bays, in order to prevent catches of undersized commercial fish.

Closed seasons

In England, a closed season for shrimps and prawns (December through April), is imposed in the Lancashire and Western Sea Fisheries District.

Limitations on size or efficiency of gear or craft

The State of Schleswig-Holstein in Germany has regulations prohibiting mesh sizes below 7 mm (from knot to knot). There are no other governmental limitations in the German shrimp fishery, except some marketing ordinances (Meyer-Waarden and Tiews, 1957).

In France the minimum mesh size in the cod end of nets made of synthetic fibres has been fixed at 21 mm (stretched).

In the Netherlands coastal fishery the lower limit of mesh size of shrimp trawls is fixed at 17 mm.

In England, the Dee Fishery District, the Kent and Essex Sea Fisheries District, the Cumberland Sea Fisheries District, the South Wales Sea Fisheries District and the Lancashire and Western Sea Fisheries Joint Committee, all exercise limits on mesh size of shrimp and prawn nets. The last two agencies also impose obligatory release of undersized shrimps. The Cumberland Sea Fisheries District have restrictions on the size of fishing boats as well.

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