SYNOPSIS OF BIOLOGICAL DATA ON THE NORWAY LOBSTER

Nephrops norvegicus (Linnaeus, 1758)

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

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MFS	Provisional editions of "FAO Manuals in Fisheries Science"	MFS	Editions provisoires des «Manuels FAO de science halieutique»	MFS	Ediciones provisionales de los «Manuales de la FAO de Ciencias Pesqueras»
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SYNOPSIS OF BIOLOGICAL DATA ON THE NORWAY LOBSTER

Nephrops norvegicus (Linnaeus, 1758)

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PREPARATION OF THIS SYNOPSIS

The purpose of this synopsis is to bring together the current information on the natural history and fishery of the Norway lobster, Nephrops norvegicus, and to draw attention to the major gaps in the information available on this species.

CONTENTS

* 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

Nephrops norvegicus (Linnaeus, 1758)

1.12   Objective synonymy

Cancer norvegicus Linnaeus, 1758
Astacus norvegicus (Linnaeus, 1758)
    Fabricius, 1775
Astacus norvegicus (Linnaeus, 1758)
    Pennant, 1777
Homarus norvegicus (Linnaeus, 1758) Weber,
    1795
Nephrops norvegicus (Linnaeus, 1758) Leach,
    1814
Nephrops norvegicus meridionalis (Linnaeus,
    1758) Zariquiey Cenarro, 1935

1.2   Taxonomy

1.21   Affinities

- Suprageneric

Kingdom Animalia
    Subkingdom Metazoa
        Phylum Arthropoda
            Class Crustacea
                Subclass Malacostraca
                    Series Eumalocostraca
                        Superorder Eucarida
                            Order Decapoda
                                Suborder Reptantia
                                    Section Macrura
                                        Superfamily Nephropoidea
                                            Family Nephropidae

- Generic

Nephrops Leach, 1814
gender: masculine (Hemming, 1955, 1955a;
Holthuis, 1945; International Commission on
Zoological Nomenclature, 1928, 1958)

Monotypic, since Leach (1814) described the
genus from a single species. All the extant
species ascribed to this genus, with the excep-
tion of N. norvegicus, have been removed by
Jenkins (1972) to the genus Metanephrops Jenkins,
1972. Nephrops differs from Metanephrops in the
following features: the rostrum has three pairs
of lateral spines instead of one and the dorso-
lateral margins of the rostrum are not continued
back on to the carapace as more or less parallel
ridges; the antennal spine is small; only five
longitudinal ridges are present on the carapace
posterior to the postcervical groove; the scapho-
cerite is narrow and lanceolate and the first
pair of pereiopods is distinctly heterochelous
(Jenkins, 1972).

- Specific

- Identity of type specimens

The type material of Cancer norvegicus
almost certainly no longer exists.

- Type locality

The type locality is: in Mari Norvegico.
Although Linnaeus may have collected N. norvegicus
during his travels in the province of Skane on
15 July 1749 (Kullen Peninsula, South Sweden,
$56°18'N$ $12°28'E$), the possible selection of this
as the type locality should be considered invalid.

- Diagnosis

N. norvegicus differs from other members of
the Nephropidae in the following characteristics:
the rostrum has three pairs of lateral spines;
the dorsolateral margins of the rostrum are not
continued back on to the carapace as more or less
parallel ridges; the eyes are large and kidney-
shaped; the antennal spine is small; only five
longitudinal ridges are present on the carapace
posterior to the post-cervical groove; the scapho-
cerite is narrow and lanceolate; the first pair
of pereiopods are large, slim and distinctly
heterochelous, bearing rows of protuberances along
the edges and upper and lower surfaces of the
propodites, and the dorsal surfaces of the abdo-
minal segments·are sculptured.

- Subjective synonymy

Astacus rugosus Rafinesque, 1814
Nephropsis cornubiensis Bate and Rowe, 1880

The description of Nephropsis cornubiensis
almost certainly refers to a juvenile N. norvegicus,
and therefore must be considered invalid until
additional evidence is provided.

1.22   Taxonomic status

N. norvegicus is a morpho-species.

N. norvegicus is the type species of the
genus, the only other species is Nephrops reedi
Carter, 1898, from the Pliocene (probably Boytonian)
at Boyton, Suffolk, England. According to Carter
(1898) this species differs from N. norvegicus, by
the larger size of its chelae, by the form and size
of the tubercles and their arrangement in rows on
the dorsal and palmar surfaces of the chelae. In
N. norvegicus the rows of tubercles are placed
approximately opposite each other and about equi-
distant from the inner and outer borders, whereas
in N. reedi the palmar row is nearer the inner
and the dorsal nearer the outer borders of the
chelae (Carter, 1898; Woods, 1925-1931).
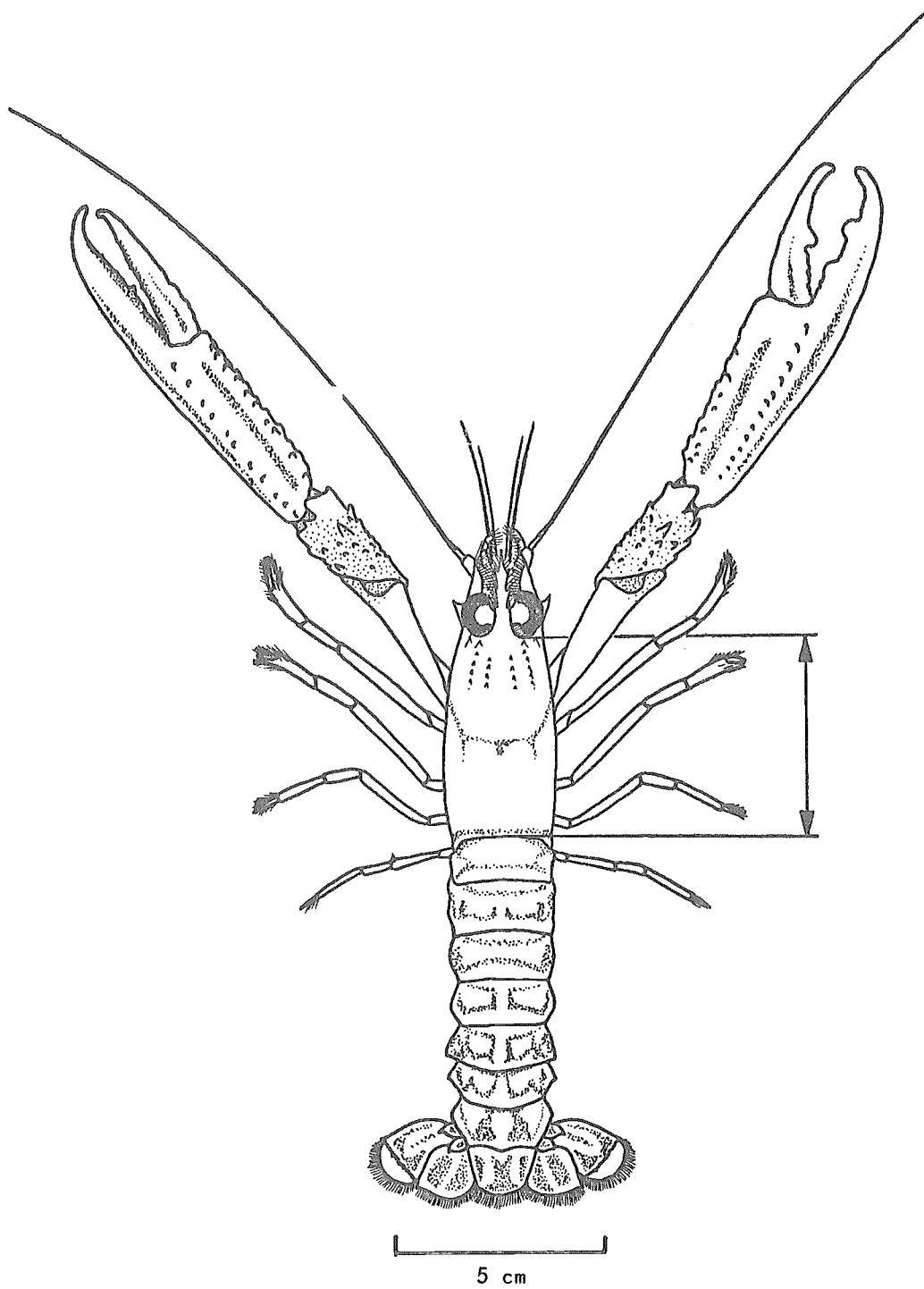
Fig. 1 Adult male Norway lobster, _Nephrops norvegicus_, (Linnaeus, 1758) from the Irish Sea,
arrows mark the standard measurement of carapace length. (After Farmer, 1972a)

1.23 Subspecies

<u>Nephrops</u> <u>norvegicus</u> <u>meridionalis</u> Zariquiey Cenarro = <u>N.</u> <u>norvegicus</u> (Linnaeus, 1758) var. <u>meridionalis</u> Zariquiey Cenarro, 1935.

Type locality: Golfe du Lion. It has also been reported from the Catalonian coast, east of Alicante, from Melilla (Spanish Morocco), from San Sebastian and Coruña (north coast of Spain) and from Huelva (southwest Spain) (Zariquiey Cenarro, 1935), and from the Côtes de Vinaroz (Vives and Suau, 1963).

This subspecies was based on the presence of a podobranch on the second maxilliped, although Holthuis (1945) has since shown this to be inconstant.

<u>N.</u> <u>norvegicus</u> <u>meridionalis</u> should therefore be considered invalid.

1.24 Standard common names, vernacular names

In scientific literature, Norway lobster, Dublin Bay prawn, langoustine, scampo, lagostim and Kaisergranat are usually used as the common names for <u>N.</u> <u>norvegicus</u>. The names given in the list below are used for <u>N.</u> <u>norvegicus</u> in different areas (Davidson, 1963, 1972; Figueiredo and Thomas, 1967; Forest, 1973; Havinga, 1929), however it should be noted that some of these names may occasionally be used to refer to other species of Decapoda.

Country	Names
Algeria	Làngûstina
Belgium	Langoustine, Noorse Kreeft, Langoestin
Cyprus	Astakos
Denmark	Jomfruhummer, Dybvandshummer, Bogstavhummer, Gul Hummer
Eire	Dublin Bay Prawn
Faeroe Islands	Hummary
Federal Republic of Germany	Kaisergranat, Buchstabenhummer, norwegischer Hummer
Finland	Keisarin, Krevetti
France	Langoustine, Cacahouét, Arganelle
Greece	Karavída
Iceland	Humar, Leturhumar
Italy	Scampo, Scampolo, Astracio
Malta	Ksampu
Monaco	Lengustina
Morocco	Langoustine
Netherlands	Noorsche Kreeft, Letterkreeft
Norway	Sjøkreps, Bokstavhummer, Sandhummer, Trollhummer, Jomfruhummer

Country	Names
Portugal	Lagostim
Spain	Langostino, Camaron, Cigala, Maganto, Escarmarlanch, Escamarlà
Sweden	Havskräfta, Kejsarhummer
Tunisia	Jarradh el Bahr
United Kingdom	Prawn, Beardog, North Shields Prawn, Dublin Bay Prawn, Scampi, Norway Lobster
Yugoslavia	Skämp

1.3 Morphology (Fig. 1)

1.31 External Morphology

Detailed descriptions of the external morphology have been given by Boone (1938) and Holthuis (1950). The following description is taken mainly from Holthuis (1950):

"The rostrum is fairly long and slender, ending in a sharp point that is curved slightly upwards. Each side bears 2-4 sharp teeth fringed with setae. The upper surface of the rostrum bears two longitudinal rows of small tubercles, the underside 1-2 median spines. The carapace has a small, but distinct, antennal spine. The dorsolateral margins of the rostrum are not continued back on to the carapace, but are replaced by two longitudinal rows of spines which decrease in size posteriorly. The cervical groove is distinct and at its rear edge bears 4 small spines. The eyes are large, broad and kidney-shaped (hence the name <u>Nephrops</u> = kidney-eye). There is no stylocerite. The antennular peduncle is short and does not reach the end of the rostrum, the first segment being larger than the remaining two. The antennae, which each bear a single flagellum, are longer than the biramous antennules. The scaphocerite is well developed, being narrow, lanceolate and terminating in a sharp spine, which nearly reaches the end of the rostrum. The pereiopods are without exopodites, although the first 4 pairs bear epipodites. The branchial complement is given in Table I. The first pair of pereiopods is strong and slim, the chela being four times as long as broad. The propodus is twice the length of the dactylus. Along each side of the chela runs a median ridge, which on the upperside bears a single row of large tubercles, and on the underside a double row. There are also rows of tubercles along the edges of the chelae, which are larger on the inside edge. The areas between the tubercles are filled with a felt-like layer of short setae. The carpus is approximately one third of the length of the propodus, and carries a few strong spines. The merus is almost half the length of the propodus, flattened and

TABLE I

Branchial complement of N. norvegicus

Gill types	Maxillipeds			Pereipods				
	1	2	3	1	2	3	4	5
Pleurobranchs	–	–	–	–	1	1	1	1
Arthrobranchs	–	–	2	2	2	2	2	–
Podobranchs	–	1*	1	1	1	1	1	–
Epipodites (mastigobranchs)	1	1	1	1	1	1	1	–

* This gill may be small or rudimentary

bearing on both the upper and lower surfaces one row of spines which increase in size distally. The ischium is short. The chelae are usually distinctly heterochelous – one chela being shorter and stouter than the other and bearing quite coarse blunt teeth along its cutting edges, whereas the other chela bears only small fine teeth. The remaining pairs of pereiopods are very much shorter and slimmer than the first pair. The second and third pairs are similar in structure, although the third pair is slightly shorter. The second and third pereiopods are chelate, the dactylus being shorter than the propodus which in turn is slightly longer than the carpus. The merus is almost the same length as the carpus and propodus together. The ischium is the same length as the carpus. The fourth and fifth pereiopods are similar in structure, but are non-chelate, the fifth being slightly shorter and slimmer. The dactylus is shorter than the propodus, whereas the carpus is slightly more than half the length of the propodus. The merus is twice as long as the carpus, which is also approximately the same length as the ischium. The first abdominal segment bears an uninterrupted transverse groove dorsally, whereas the second abdominal segment bears an anterior groove which is usually uninterrupted, and a posterior groove which is discontinuous. The posterior abdominal segments have anterior and posterior transverse grooves, which are joined by a short median connexion. The ends of the transverse grooves extend on to the sides of the segments and end in complicated sculpturing. All the grooves are filled with a layer of felt-like short setae. The epimeres of the abdominal segments are furnished with sharp points which are directed posteriorly. The abdominal segments carry pleopods which are biramous, with the exception of the first. In the male the first two pairs and in the female the first pair of pleopods are modified. The telson is short,

although rather longer than broad, and tapering slightly towards the rear, which is in the form of a semicircle. The telson bears a spine at each corner and setae along its posterior edge. The uropods are short, broad and triangular in outline. The posterior margin is semicircular. The exopodite has an obvious diaeresis. The colour of the animal when alive is generally pink/orange with darker markings on the carpopodites."

The morphology of the secondary sexual characters has been described by Brocchi (1875) and Lüling (1958), and their development up to sexual maturity has been covered by Farmer (in press c). (See also sections 3.11 and 3.12.)

A description of the functional morphology of the mouthparts and pereiopods has been given by Farmer (1974). (See also section 3.41.)

The development of the chelae of the first pair of pereiopods has been covered briefly by Farmer (in press a) in relation to allometric growth associated with sexual maturity (see also section 1.32). Initially the dentition of the two chelae is similar, the heterochelous state appearing at a carapace length of approximately 5–6 mm (Fig. 2). Andersen (1962) examined the number of tubercles present on the large chelae to check whether there were any racial differences. Significant differences were found in the numbers of tubercles on the chelae of different animals, but the variation was unexplained. Both Andersen (1962) and Farmer (1973) found that there was a slight bias for the crusher claw to be on the right side of the body. Individuals with two similar claws are rare, particularly those with two crusher claws. According to Farmer (1973), the cutter claw is generally longer than the crusher (in 82 percent of males and 89 percent of females).
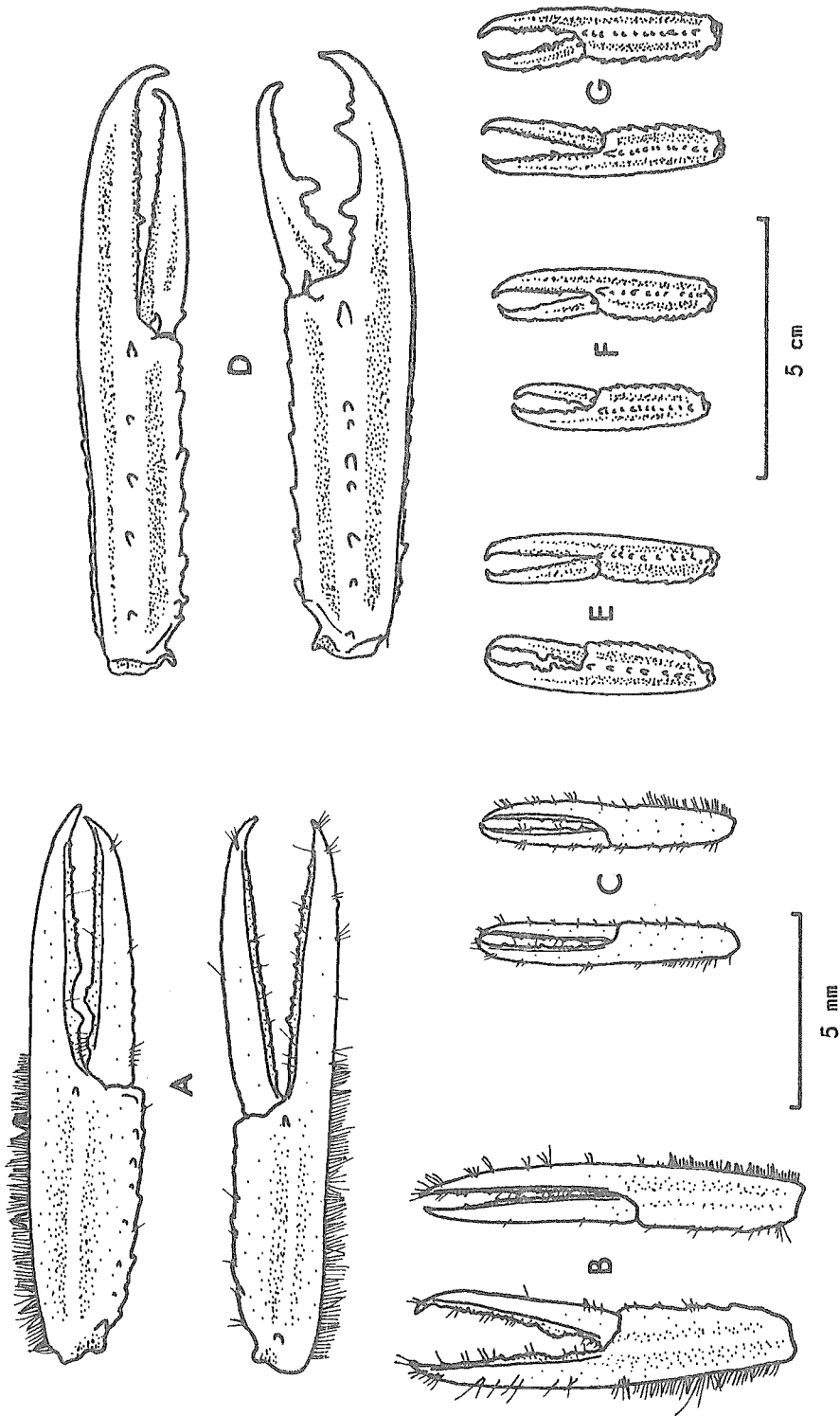
Fig. 2 N. norvegicus. Chelae of (A) immature male, carapace length 10.2 mm; (B) immature female, carapace length 7.5 mm; (C) immature male, carapace length 4.8 mm; (D) mature male, carapace length 53.6 mm; (E) mature male, carapace length 28.3 mm; (F) immature male, carapace length 27.3 mm; (G) mature female, carapace length 31.1 mm, showing differentiation into crusher and cutter chelae. (C) shows the symmetrical stage. (From Farmer, in press. a)

TABLE II

Regression values of total length plotted against carapace length (all measurements in mm)
where $y = \alpha x + \beta$

Authority	Area	Sex	α	β
(1) Matta, 1959 "	N. Tyrrhenian Sea "	males females	3.2170 3.4300	4.140 - 1.830
(2) Figueiredo and Barraca, 1963	Portugal	males and females	3.0890	11.100
(3) O'Riordan, 1964	Irish waters	males and females	3.2500	- 1.000
(4) Gibson, 1967	South coast Ireland	males and females	3.068	5.080
(5) Pope and Thomas, 1967 "	Moray Firth Minch	males and females males and females	3.063 2.993	7.200 10.600
(6) Fontaine and Warluzel, 1969	Gascogne	males and females	3.363	- 1.050
(7) Symonds, 1972a "	Northeast England "	males females	3.020 3.100	10.700 8.350
(8) Farmer, in press a " "	Irish Sea " "	males females males and females	3.3166 3.4170 3.3182	- 0.183 - 1.825 - 0.258

TABLE III

Regression values of abdominal width (2nd segment) plotted against carapace length
where $y = \alpha x + \beta$ (all measurements in mm), from Farmer (in press a)

Authority	Area	Sex	α	β
(1) Pope and Thomas, 1967 " " "	Moray Firth " Minch "	males females males females	0.4883* 0.5834* 0.4861* 0.5830*	0.3290* - 1.2860* 0.4160* - 1.4900*
(2) Symonds, 1972a	Northeast England	males and females	0.5019*	- 0.2229*
(3) Farmer, in press a " "	Irish Sea " "	immature males and females mature males mature females	0.4787 0.5272 0.5911	- 0.2790 - 0.7850 - 1.4810

* Recalculated values since these were originally in the form of carapace length
on abdominal width and therefore required inversion for comparison

TABLE IV

Regression values of other body proportions where $y = \alpha x + \beta$

Authority	Area	Sex	α	β
A: Carapace length (mm) against width first abdominal segment (mm)				
Symonds, 1972a	Northeast England	males and females	1.9810	1.4700000
B: Carapace length (mm) against length second abdominal segment (mm)				
Symonds, 1972a	Northeast England	males and females	3.3690	1.1900000
C: Carapace length (mm) against telson length (mm)				
Symonds, 1972a	Northeast England	males and females	2.6120	- 0.9600000
D: Total weight (g) against tail weight (g)				
(1) Symonds, 1972a	Northeast England	males	2.7880	15.5000000
"	"	females	2.8820	1.9200000
(2) Pope and Thomas, 1967	Moray Firth and Minch	males	3.2310	- 0.9000000
"	Moray Firth	females	2.7270	1.6000000
"	Minch	females	2.9900	0.2000000
(3) Gibson, 1967	Irish Waters	males	3.3400	- 4.3350000
"	"	females	2.0900	0.8130000
E: Tail weight (g) against meat weight (g)				
Gibson, 1967	Irish Waters	males	1.4500	0.3270000
"	"	females	1.2600	0.0340000
F: Total weight (g) against carapace length (mm)				
(1) Pope and Thomas, 1967	Moray Firth	males	3.3210	0.0002188
"	Minch	males	3.2040	0.0003221
"	Moray Firth and Minch	females	2.9630	0.0006840
(2) Symonds, 1972a	Northeast England	males	3.1170	0.0004523
"	"	females	2.8490	0.0010760
(3) Farmer, in press a	Irish Sea	males and females	3.3345	0.0002245

The exopodite of the antennule bears a number of aesthetascs. Farmer (1973) has shown it is not possible to age N. norvegicus by counting the number of aesthetasc-bearing segments, unlike certain other Crustacea. (See also section 3.43.)

1.32 Morphometrics

The generally recognized standard measurement for N. norvegicus is carapace length, and this is defined as the distance from the posterior margin of the orbit to the mid hind edge of the carapace (Fig. 1). Total length, when used, is measured from the tip of the rostrum to the posterior edge of the telson, excluding the fringe of setae, with the animal lying on its back so that the abdominal segments are not flexed. Other measurements which have been used include total wet weight, propodus length and abdominal width.

There have been a number of investigations on the relationships of different body proportions. Andersen (1962) plotted carapace length against total length and obtained an arithmetic relationship; total weight plotted against total length gave a geometric relationship. Andersen did not, however, calculate regression values for these. Thomas (1954) also plotted total length against carapace length, but did not calculate regression values. According to Poulsen (1946), who also investigated the relationship of total weight to carapace length, berried females were always slightly heavier than males, which were in turn heavier than non-berried females. Poulsen calculated an expression for the state of nutrition (K), which he expressed by the formula:

$$K = \frac{100 \, g}{L^3}$$

where g is the total wet weight in grammes and
L the total length in centimetres. It was found
that males generally showed a better state of
nutrition than females. There was also a distinct
change in the state of nutrition throughout the
year, this being higher in both males and females
in the autumn than in spring.

The available data on the relationship
between total length and carapace length are
provided in Table II. There is quite considerable
variation between the data from different areas,
although according to Farmer (in press a) this may
be the result of slight variation in the method
of measurement rather than indicative of racial
differences.

Available data on the relationship between
abdominal width and carapace length are given in
Table III. Obvious differences exist in the
relationship between males and females, and it
has been shown by Farmer (in press a) that there
are distinct differences between immature and
mature animals, as well as between mature males
and females (Fig. 3). The difference between
males and females reflects the increased width of
the abdomen in females for carrying eggs (Pope and
Thomas, 1967; Farmer, in press a). Symonds (1972a)

suggested that his figures showed no significant
difference between males and females because his
measurements of abdominal width did not include
the pleura.

Farmer (in press a) has shown that the
relationship between propodus length (first
pereiopod) and carapace length changes in males
at sexual maturity (Fig. 4) to give positive
allometric growth. This results in mature males
having large chelae which are used in agonistic
behaviour; such males frequently spar with one
another using a lateral merus display. Hillis
(1972d) examined the relationship between propodus
length and carapace length with a view to deter-
mining the age of individual $\underline{N}$. norvegicus (see
section 3.43), but did not calculate a specific
expression to describe it.

Other relationships described in $\underline{N}$. norvegicus
refer to additional abdominal measurements and
weight relationships. These are included in
Table IV. O'Riordan (1967) working on similar
relationships produced the following expression
to calculate the percentage tail weight for a
given size of animal:

$$P = 45.85 - 0.3667C$$
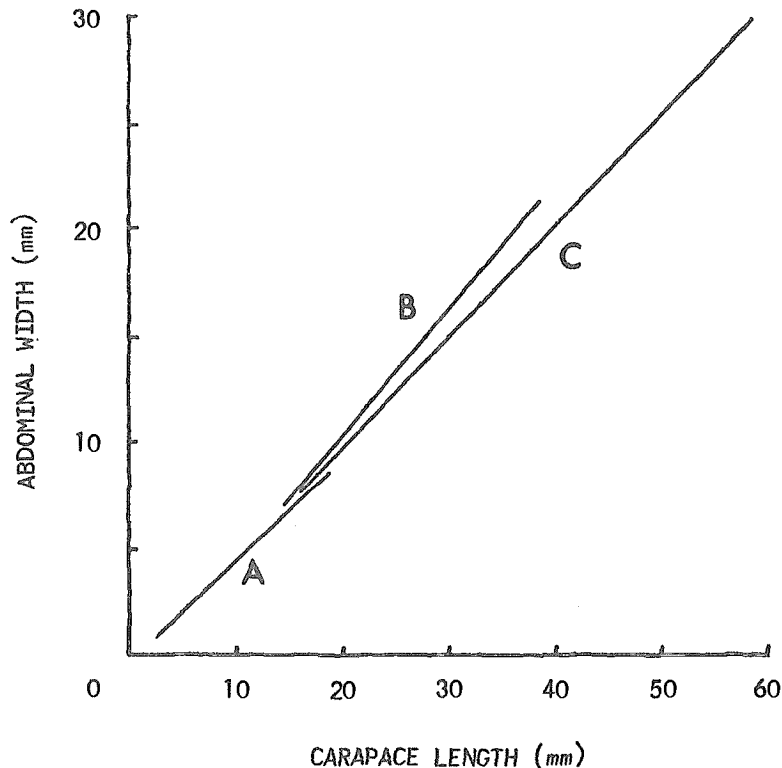
Fig. 3 $\underline{N}$. norvegicus. Abdominal width (second segment) plotted against carapace length.
(A) immature males and females ($y = 0.4787x - 0.279$);
(B) mature females ($y = 0.5911x - 1.481$);
(C) mature males ($y = 0.5272x - 0.785$). (After Farmer, in press a)
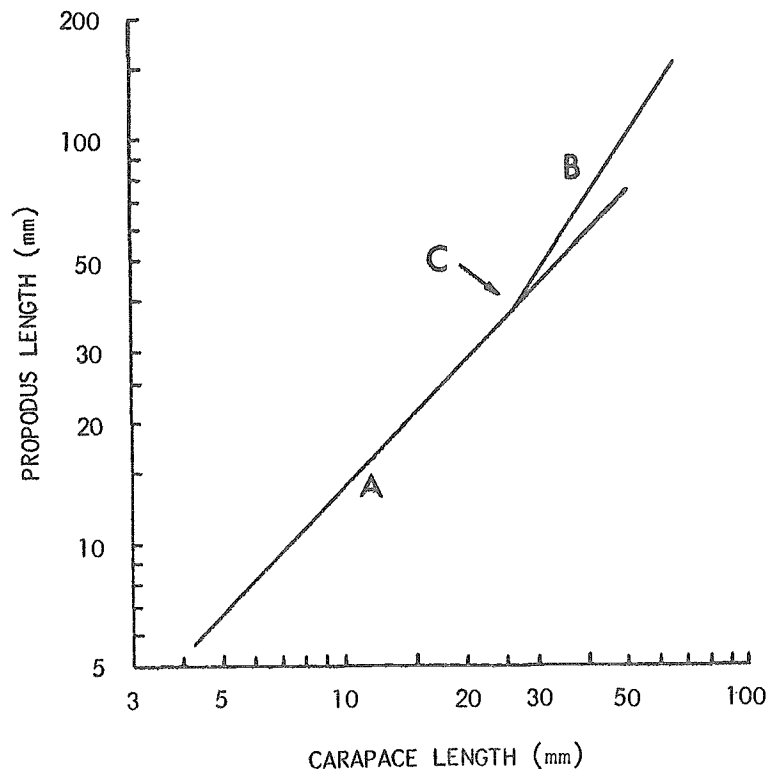
Fig. 4 N. norvegicus. Propodus length (first pair of pereiopods) plotted against carapace length. (A) females and immature males ($y = 1.282x^{1.0299}$); (B) mature males ($y = 286x^{1.5080}$); (C) indicates attainment of sexual maturity in males. (After Farmer, in press a)

where P is the percentage tail weight and C is the carapace length in millimetres.

1.33   Internal Morphology

The morphology of the internal reproductive organs is covered in sections 3.11, 3.12 and 3.15.

The cerebral ganglion of N. norvegicus has been described by Bazin (1970). There is a pair of organelles ("deutocerebral organs") within the deutocerebrum, consisting of symmetrical groupings of cells around a central cavity and protruding under the ganglion. Each organelle is connected by tracts to the groups of olfactory neurons.

Yonge (1924) has given a detailed description of the complete alimentary canal of N. norvegicus. The mouth lies immediately behind the mandibles, and is partially occluded by the labrum. It leads into a short thick oesophagus which opens into the cardiac fore-gut, a large sac-shaped structure occupying most of the cephalothoracic cavity. The cardiac fore-gut has a thick chitinous lining which is calcified in certain regions to give rise to a series of ossicles which form the gastric mill (Fig. 5). Leading from the cardiac fore-gut is the pyloric fore-gut which has a single dorsal caecum and a pair of lateral ampullary or gland filters. The paired hepatopancreas opens via a pair of small ducts into the anterior region of the mid-gut which leads from the pyloric fore-gut. The mid-gut, which is narrow and thin-walled, passes through the posterior region of the cephalothorax and the abdomen until it meets the hind-gut a short distance from the anus. The mid-gut bears two dorsal diverticula. The hind-gut is a short stout tube opening at the anus on the ventral surface of the telson. Yonge (1924) also described the innervation of the hind-gut.

The proprioceptors of the basi-ischio-meropodite region of the walking leg of N. norvegicus has been described by Clarac and Masson (1969). There is a myochordotonal organ in the meropodite which is connected to the dorsal bundle of the proximal head of the accessory flexor muscle. In the ischiopodite there are two
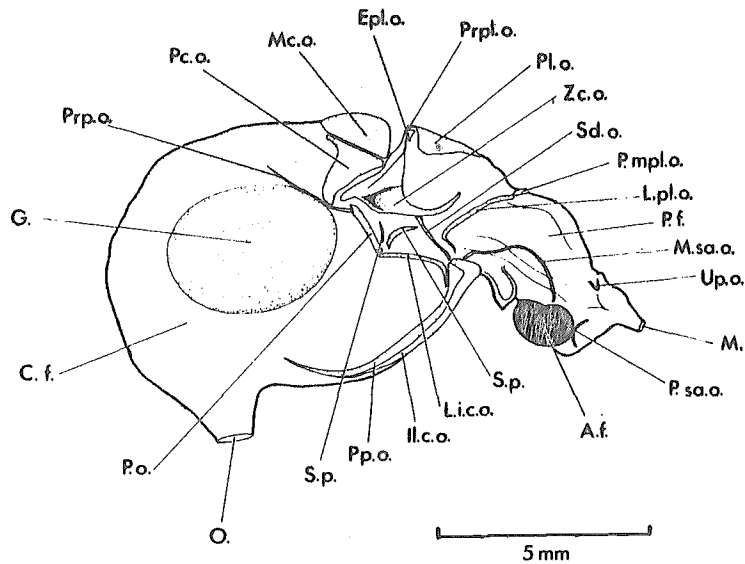
Fig. 5 N. norvegicus. Lateral (left) view of stomach showing position of gastrolith
and ossicles (stippled). A.f.: ampullary filter; C.f.: cardiac fore-gut;
Epl.o.: exopyloric ossicle; G.: gastrolith; Il.c.o.: inferolateral cardiac
ossicle; L.i.c.o.: lateral intermediate cardiac ossicle; L.pl.o.: lateral
pyloric ossicle; Mc.o.: mesocardiac ossicle; M.: mid-gut; M.sa.o.: median
supra-ampullary ossicle; O.: oesophagus; Pc.o.: pterocardiac ossicle;
P.f.: pyloric foregut; Pl.o.: pyloric ossicle; P.mpl.o.: posterior mesopyloric
ossicle; P.o.: pectineal ossicle; Pp.o.: postpectineal ossicle; Prpl.o.:
prepyloric ossicle; Prp.o.: prepectineal ossicle; P.sa.o.: posterior supra-
ampullary ossicle; Sd.o.: subdentary ossicle; S.p.: setose pads; Up.o.: uro-
pyloric ossicle; Zc.o.: zygocardiac ossicle. (From Farmer, 1973)

chordotonal receptors, the first near the post-
axial wall is sheet-like and attached to the
inferior retractor of the meropodite, the second
in the anterior part is a thin strand. There is
also a receptor in the basipodite, except in the
first pair of pereiopods where the ischiopodite/
basipodite joint is fused. According to Wales
et al. (1970), in general the receptors of the
walking legs of N. norvegicus closely resemble
those of Homarus gammarus, the European lobster.

The mouthpart receptors of the labrum,
paragnaths and the opening into the oesophagus
have been described in detail by Moulins, Dando
and Laverack (1970). There are three bilateral
groups of proprioceptors (MPRs) arranged around
the mouth. The anatomy and physiological res-
ponses of the MPRs were found to be very similar
to those reported in H. gammarus.

1.34 Cytomorphology

According to Farmer (in press b) N. norvegicus
has a haploid chromosome number of 75, although
there may be some karyotypic variation. Farmer
suggested that a satellite present in approxi-
mately one third of the meiotic cells examined
might represent a sex chromosome (Fig. 6).

The fine structure of the spermatozoa has
been described by Chevaillier and Maillet (1965,
1965a). The spermatozoon is composed of three
parts: the nucleus which extends into the three
nuclear arms which contain complex lamellar
structures; the two centrioles and degenerated
mitochondria above the nucleus, and the anterior
part or capsule, which is composed of two layers
and ends in an apical granule. The capsule when
fully developed is 2μm in diameter and 17μm in
length. The development and maturation of the
spermatozoa is covered by Chevaillier (1965),
Farmer (in press) and Figueiredo and Barraca
(1963).

The ovarian germinal cells of N. norvegicus
are present at all stages of ovary development,
in a fine strand passing along the axis of each
half of the ovary. Throughout the process of
maturation each oocyte is surrounded by a uni-
cellular layer of follicular cells, which remain
within the ovary on release of the ova (Farmer,
in press; Figueiredo and Barraca, 1963). Matura-
tion of the gross morphology of the ovary is
covered in section 3.15.

Yonge (1924) described the histology of the
alimentary canal and hepatopancreas, in relation
to function.
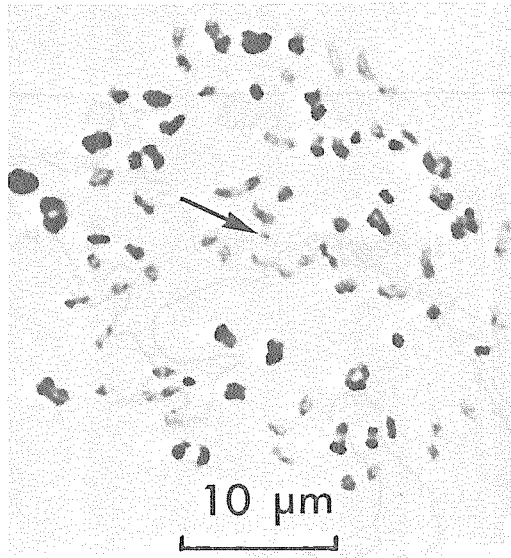
Fig. 6 *N. norvegicus*. Photomicrograph of the chromosomes of a primary spermatocyte (arrow marks the satellite). (From Farmer, in press b, reproduced by kind permission of the Editors of *Crustaceana*)

1.35 Protein Specificity

No data are available on protein specificity in *N. norvegicus*.

2 DISTRIBUTION

2.1 Total area

– Land areas[1]:

100 AFRICA, 111 Tunisia (Davidson, 1963), GFCM, 1970); 112 Algeria (GFCM, 1970; Heldt and Heldt, 1931; Holthuis, 1945); 113 Morocco (Boone, 1938; Bouvier, 1917; de Buen, 1916; GFCM, 1970; Havinga, 1929; Heldt and Heldt, 1931; Vilela, 1970); 121 Libya (Forest, 1973); 122 United Arab Republic (Holthuis, 1945).

200 NORTH AMERICA, 250 Greenland (Heldt and Heldt, 1931; Thomas, 1961a).

500 EUROPE, 511 Denmark (Aker and Tiews, 1965; Boone, 1938; de Buen, 1916; Poulsen, 1946); 512 Faeroe Islands (Andersen, 1962; Poulsen, 1946); 513 Iceland (Boone, 1938; de Buen, 1916;

Havinga, 1929; Heldt and Heldt, 1931; Sigurdsson, 1965; Skuladottir, 1967); 514 Norway (Boone, 1938; de Buen, 1916; Havinga, 1929; Heldt and Heldt, 1931; Poulsen, 1946; Sars, 1884); 515 Bear Island (Thomas, 1961a); 516 Sweden (Aker and Tiews, 1965; de Buen, 1916; Poulsen, 1946); 521 Netherlands (Holthuis, 1945, 1950); 522 Belgium (Boone, 1938); 524 France (Boone, 1938; Bourdon, 1965; Fontaine, 1967; GFCM, 1970; Heldt and Heldt, 1931; Le Gall, 1935, 1937; Legendre, 1924); 525 Monaco (GFCM, 1970); 531 Ireland (Boone, 1938; Cole, 1965; DAFD, 1965a; Heldt and Heldt, 1931; Hillis, 1972d; O'Riordan, 1961, 1961a, 1962a, 1964, 1965; Selbie, 1914); 533 England, Wales (Boone, 1938; de Buen, 1916; Cole, 1965; Farmer, 1972a; Heldt and Heldt, 1931; Storrow, 1912; Symonds, 1971, 1972a; Thurston, 1970); 534 Scotland (Allen, 1967; Boone, 1938; de Buen, 1916; Cole, 1965; Heldt and Heldt, 1931; Holthuis, 1945; Marine Laboratory, Aberdeen, 1971; Thomas, 1954, 1959, 1960a, 1961a, 1965b, 1970a); 535 Northern Ireland (Cole, 1965; O'Riordan, 1961a, 1964); 537 Isle of Man (Bruce, Colman and Jones, 1963; Cole, 1965; Farmer, 1972a; O'Riordan, 1962a); 541 Portugal (Heldt and Heldt, 1931; Holthuis, 1945; Nobre, 1931; Zariquiey Alvarez, 1968); 542 Spain, Balearic Islands (Boone, 1938; de Buen, 1916; GFCM, 1970; Heldt and Heldt, 1931; Holthuis, 1945; Massuti, 1970, 1971; Stephensen, 1923; Vives and Suau, 1963; Zariquiey Alvarez, 1968); 543 Italy (Alfirevic, 1968; Boone, 1938; Froglia, 1972; GFCM, 1970; Heldt and Heldt, 1931; Issel, 1930; Matta, 1959); 546 Corsica (Forest, 1973); 547 Malta (Forest, 1973); 548 Gibraltar (Forest, 1973); 551 Yugoslavia (Alfirević, 1968; Jukić, 1971; Karlovac, 1953, 1955a; Zupanovic, 1968); 552 Albania (Forest, 1973); 553 Greece (Forest, 1973; Heldt and Heldt, 1931); 561 Federal Republic of Germany (Aker and Tiews, 1965; Heldt and Heldt, 1931).

– Sea areas[1]:

ANE (Atlantic, N.E.) Northern limits: Greenland, Iceland, Bear Island and Nordkapp of Norway. Western limits: west coast of Ireland. *N. norvegicus* does not occur in the Baltic Sea.

ASE (Atlantic, S.E.) Southern limits: Morocco, off Rabat. Eastern limits: Egypt (A.R.E.). *N. norvegicus* occurs commonly in the western Mediterranean Sea, becoming less widespread eastward.

– Biogeographical and natural characteristics

N. norvegicus is a marine boreal species, inhabiting the Mediterranean Sea and the continental shelves of the northeastern Atlantic Ocean, where suitable substrates exist. It has been recorded at depths to 800 m (see sections 2.3 and 5.23).

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[1] Land/sea areas taken from Rosa (1965)
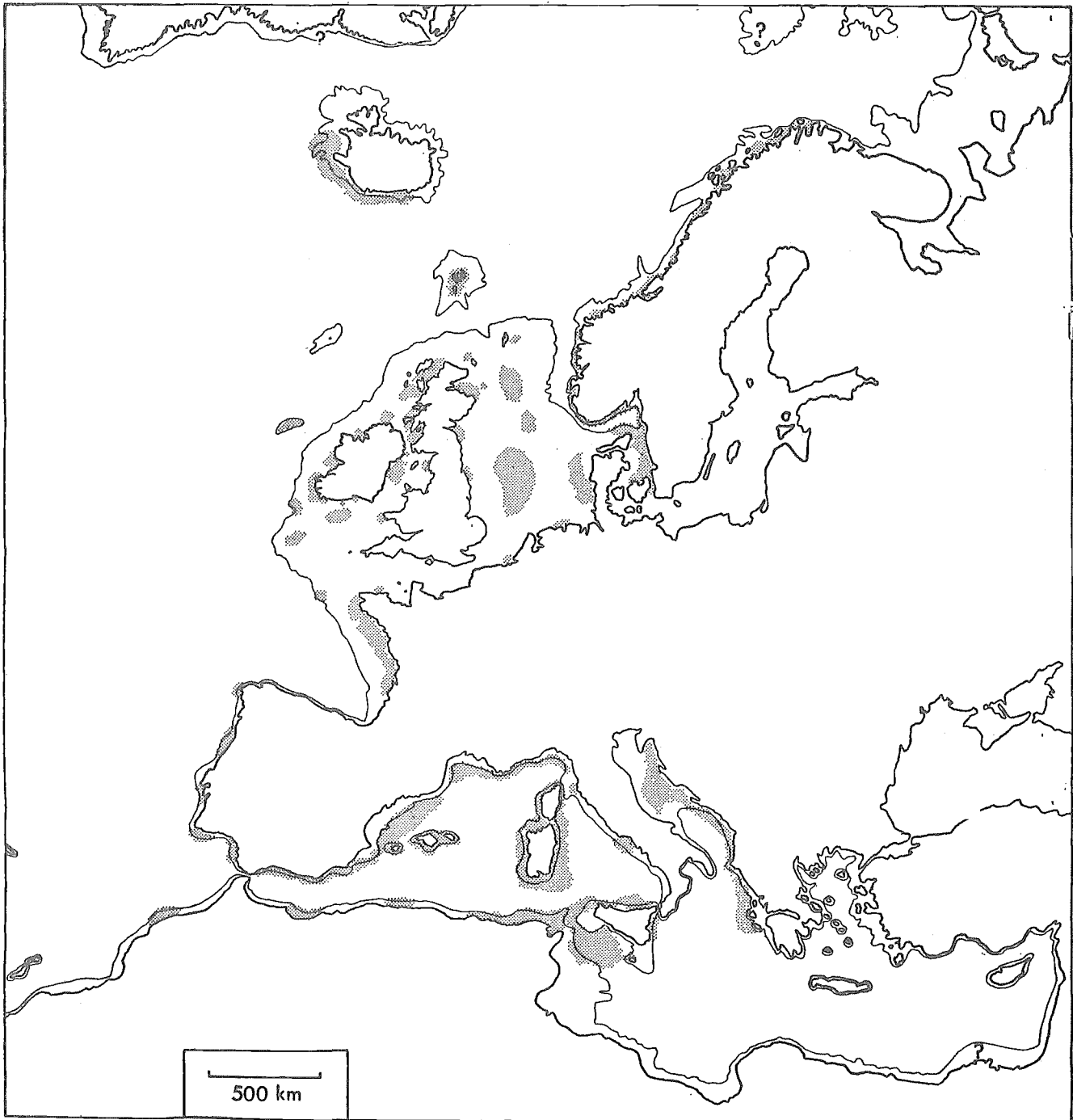
Fig. 7   Known geographical distribution of <u>N. norvegicus</u>. The 200 m isobath is
indicated, corresponding roughly with the edge of the continental shelf.
The precise positions of the areas marked thus: ? are not known.

The distribution of N. norvegicus is shown in Fig. 7.

2.2 Differential distribution

2.21 Larvae

The larvae of N. norvegicus are planktonic and free-swimming. As a result the larval distribution is usually more widespread than that of the juveniles and adults. According to Jorgensen (1925) larvae found off the Northumberland coast (England) are derived from three sources: the local population; the area in the Firth of Forth, and an even more northerly population. It was suggested that the larvae drift southward along the coast for some weeks. The occurrence of larvae as reported by Jorgensen (1925) and other authorities is given in Table V.

Thomas (1954) gives the relative distribution of the adults and larvae in Scottish waters, from which it is apparent that dispersal is passive. At depths down to 50 fath (90 m) there appeared to be no variation in density with increasing depth. Jorgensen (1925) reported that larvae were rarely taken near the surface, at least during the day. Fraser (1965) gives the distribution of larvae in Scottish waters throughout the period 1935-1964. Most larvae were taken well below the surface, although there was a slight increase in numbers in the surface waters during the period dusk to dawn. Fraser concludes that the N. norvegicus populations of the Firth of Forth area and the Fladen ground are probably self-contained, although there was evidence of considerable dispersal of larvae away from the parent stock, due to currents.

Kurian (1956) considered N. norvegicus larvae to be rare in the Adriatic Sea in comparison with other decapod species. However, Karlovac (1953) collected sufficient larvae in the Adriatic to determine the main hatching period. It was again suggested that the dispersal of the larvae occurs passively by means of currents.

Hillis (1968, 1972, 1972d) has carried out detailed studies of larval distribution in the Irish Sea (see also DAFD, 1970). It was found that generally the larvae occupied the same areas as the adults, although there was some evidence that tidal currents in the south-eastern part of their range affected the distribution (Hillis, 1972). It was noticeable that the older larvae tended to be caught in the southern and eastern parts of the area sampled. Hillis (1972d) suggested that this might be due to either differential periods of hatching and growth

rates, or irregular waves of hatching. Larvae were found to be most abundant at a depth of 10-20 fath (20-40 m) and 40 fath (80 m) during daytime sampling. According to Williamson (1956) N. norvegicus larvae normally occur at depths greater than 17 m. Santucci (1926b) has reported larvae from 25-150 m in the Tyrrhenian Sea.

2.22 Juveniles and adults

Juvenile and adult N. norvegicus are benthic, and construct burrows in the soft substrate on which they live. The distribution of adult N. norvegicus is shown in Fig. 7. It is now certain that the discontinuous distribution is related to the availability of suitable substrates for burrow construction rather than other environmental variables. (See section 2.3.)

The distribution of N. norvegicus off the east coast of Ireland tends to have two main centres, one inshore of Clogherhead, the other in the Lambay-Rockabill area (Hillis, 1972d), each of which has a discrete nursery ground in shallower water than that occupied by the adults.

Differential distribution of juveniles and adults has not been recorded in other populations of N. norvegicus.

2.3 Determinants of distribution changes

2.31 Temperature

It has been suggested that N. norvegicus is a glacial relict, and that its isolated occurrence in the Adriatic Sea is a result of Quaternary glaciation and the supposed need for low temperatures and salinities (Lorenz, 1863, and later quoted by Brehm, 1952). Gauss-Garady (1912) found that in fact N. norvegicus was more widely distributed in the Adriatic than Lorenz had supposed. Lorenz's view was questioned by Pesta (1914, 1918) and Schellenberg (1928), since there was no evidence that depth, temperature or salinity rather than substrate limited its distribution. Furthermore, there was the possibility that N. norvegicus might in fact be a Mediterranean species, which had extended its range to the north under the influence of the Gulf Stream, as suggested by Heldt and Heldt (1931).

The maximum and minimum temperatures limiting the distribution of N. norvegicus in its natural environment are not known, although recorded bottom temperatures from the areas inhabited range from 7-13°C in the Irish Sea (Farmer, 1972a) and 10-15°C in the Adriatic (Karlovac, 1953).

TABLE V

Egg-laying and egg-hatching periods and occurrence of N. norvegicus larvae in different areas

Authority	Area	Egg laying	Egg hatching	Period of larval occurrence	Average period of incubation (days)
Andersen, 1962	Faeroes	June-Aug.	May[1]	May-Aug.	9 months (270)
Thomas, 1954	Scottish waters	-	-	Mar.-Oct.	-
Thomas and Figueiredo, 1964, 1965	Scottish waters	Aug.-Nov.	May-Aug.	-	9 months (270)
Fraser, 1965	Scottish waters	-	-	Mar.-June[2]	-
Havinga, 1929	North Sea	-	-	Summer	-
Jorgensen, 1925	Northeast England	-	-	May-Aug.	-
Symonds, 1972a	Northeast England	Aug.-Sep.	May-Aug.	-	10 months (300)
Bruce, Colman and Jones, 1963	Irish Sea	-	-	Apr.-June	-
O'Riordan, 1964	Irish Sea	Sep.	Apr.-May	-	9 months (270)
Hillis, 1968, 1972, 1972d	Irish Sea	-	Apr.-June[3]	Apr.-June	-
Farmer, in press	Irish Sea	Aug.-Sep.	Apr.-June	-	8 months (240)
Figueiredo and Barraca, 1963	Portugal	Aug.-Sep.[4]	Feb.-Mar.	-	6 months (180)
Stephensen, 1923	Mediterranean Sea Bay of Cadiz	- / -	- / -	Winter / Winter	- / -
Vives and Suau, 1963	East coast of Spain	July-Oct.	-	-	-
Santucci, 1926	Tyrrhenian Sea	-	-	Jan.-Mar.	-
Karlovac, 1953, 1955	Adriatic Sea	June-July	Jan.-Feb.	Jan.-Apr.	7 months (210)

1/ August exceptionally
2/ A few up to and including October
3/ A few up to and including September
4/ Occasional specimens in February and March

2.32 Salinity

Salinity does not appear to be an important factor in the distribution of N. norvegicus, although it is suggested by Höglund (1942) that the absence of this species in the Baltic Sea is due to its being unable to tolerate very low salinities. The lowest salinities recorded in regions inhabited by N. norvegicus are 29-30°/oo from the Kattegat (Poulsen, 1946). Maximum salinities recorded throughout its range are 35.86-38.77°/oo in the Adriatic (Karlovac, 1953).

2.33 Depth

N. norvegicus occurs at depths from 15 m to more than 800 m. Although depth does not appear to be a limiting factor, this species has not been recorded off the northeastern Atlantic continental shelf (except in the Mediterranean). This may be related to a lack of suitable bottom deposits rather than depth (see section 2.34).

It has been suggested by Chapman, Priestley and Robertson (1972) that the maximum depth distribution may be related to light intensity, in that it may be the depth at which there is sufficient light for feeding and activity around the middle of the day (see section 3.53).

See also section 5.23.

2.34 Substrate

Havinga (1929), in a comparison of the habitats of H. gammarus and N. norvegicus, pointed out that the latter preferred muddy substrates. The recent work of Karlovac (1953, 1955) and Alfirević (1968) in the Adriatic has shown that there is a close correlation between the distribution and density of N. norvegicus and the nature of the bottom deposit. A similar study by Farmer (1972a) in the Irish Sea has indicated similar results.
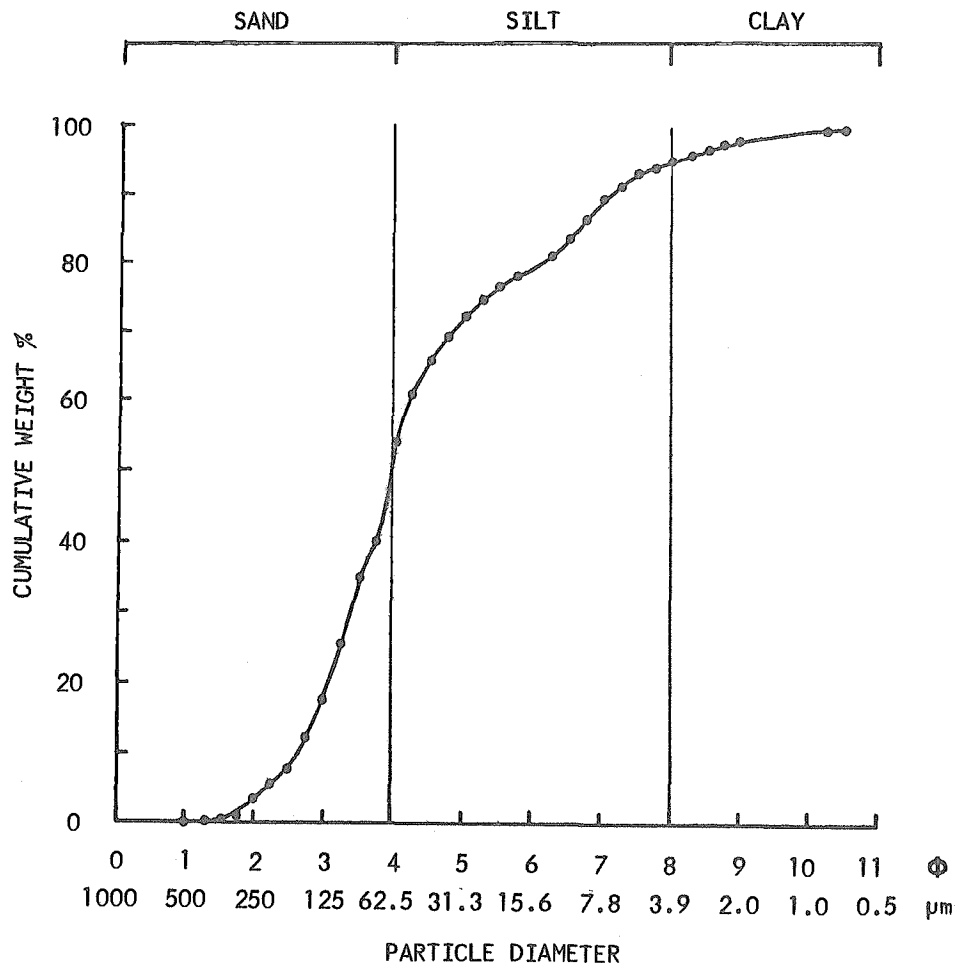
Fig. 8 Sediment analysis of the bottom deposit from the N. norvegicus grounds in the Irish Sea (off the west coast of the Isle of Man). (After Farmer, 1972a)

According to Belderson (1964) the bottom
deposits inhabited by N. norvegicus in the
Irish Sea are residual reworked glacial clays
from the late Holocene. It is likely that many
of the sediments where N. norvegicus are found
are of a similar origin. The sediment analysis
of the main N. norvegicus grounds in the Irish
Sea is given in Fig. 8.

2.35 Food

Although N. norvegicus is largely omnivorous
(see section 3.42) it is likely that the availa-
bility of food affects its distribution. Simpson
(pers. comm. quoted by Chapman and Rice, 1971)
was of the opinion that the growth rate in the
Irish Sea was low because of the high density of
animals present there. Chapman and·Rice (1971)
suggested that the same may be true in the Sound
of Jura, where the density is also high and the
animals are small.

2.4 Hybridization

2.41 Hybrids

There are no recorded instances of hybridi-
zation in this species. Metanephrops spp.,
which might be expected to produce hybrids with
N. norvegicus, have not been recorded from the
known geographical range of N. norvegicus.

3   BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

– Hermaphroditism, heterosexuality,
  intersexuality

N. norvegicus is dioecious and heterosexual.

A number of intersex specimens of
N. norvegicus have been recorded (Andersen, 1962;
Cole, 1901; McIntosh, 1904, 1908, 1911; Marshall,
1902) which show variation in the number and
position of the genital apertures. In all cases,
with the single exception of a female quoted by
Marshall (1902), the individuals have been des-
cribed as males. Presumably determination of the
sex was based on the external genitalia, since
only Marshall (1902) appears to have examined the
internal anatomy of his specimens. Variation in
the number and position of the genital apertures
is recorded as being not uncommon in samples from
the Firth of Forth, Firth of Clyde and Moray Firth
(Scotland) by McIntosh (1904, 1908, 1911),
although it appears to be rare in those from the
Irish Sea (Farmer, 1972; Marshall, 1902).

Four bilateral gynandromorphs have been
recorded by Farmer (1972) from the Irish Sea and
Irish coasts. One specimen has been dissected,
and has been shown to have a perfect bilateral
asymmetry, one side of the animal being totally
male, the other female. It was suggested that
the bilateral asymmetry may be due to a chromo-
somal abnormality in the first cleavage division
of the embryo, and that subsequent cleavage is
determinate.

– Nature and extent of hermaphroditism

Hermaphroditism has not been recorded in
N. norvegicus.

– Sexual dimorphism

The sexes of N. norvegicus can be easily
separated on the basis of the setation and
morphology of the first two pairs of pleopods,
the position of the genital apertures or the
presence of a thelycum in females. The external
genitalia of the adults have been described in
detail by Brocchi (1875) and Lüling (1951, 1958),
as shown in Fig. 9. Farmer (in press c) has
described the development of the external sexual
characters from the early post–larval instars
through to sexual maturity. The first pair of
pleopods in mature males is uniramous and rigid,
and each has a groove on its inner surface. The
second pair of pleopods is biramous with the
exopodite bearing an appendix masculina. In
mature females the first pair of pleopods is
uniramous, but slender and flexible. The second
pair is similar to those of the males, except
that there is no appendix masculina. All five
pairs of pleopods of mature females carry
ovigerous setae, at all times of the year.
Ovigerous setae are also present on the sternal
ridges of the abdomen.

After copulation mature females carry· the
spermatophore in the thelycum (or receptaculum
seminalis), which is essentially an invagination
of the sternites of the last two thoracic segments.
The thelycum of a mature female is shown in Fig. 9.

The internal reproductive system of
N. norvegicus is basically similar to that of
other decapods. The ovaries and testes are
elongate paired organs, the two halves being
joined at approximately the mid–point to form
an H-shaped structure (see Fig. 10). The two
anterior lobes extend into the cephalic region
around the fore-gut, while the posterior lobes
continue into the abdominal segments lying along-
side the mid-gut. Details of the development and
maturity of the gonads are given in section 3.15.
The vasa deferentia open on the coxopodites of
the fifth pair of pereiopods, whereas the oviducts
open on the coxopodites of the third pair. The
androgenic gland, present in males only, is

O.s.

A

C

F.a.

E

O.s.

A.m.

B

D

5 mm
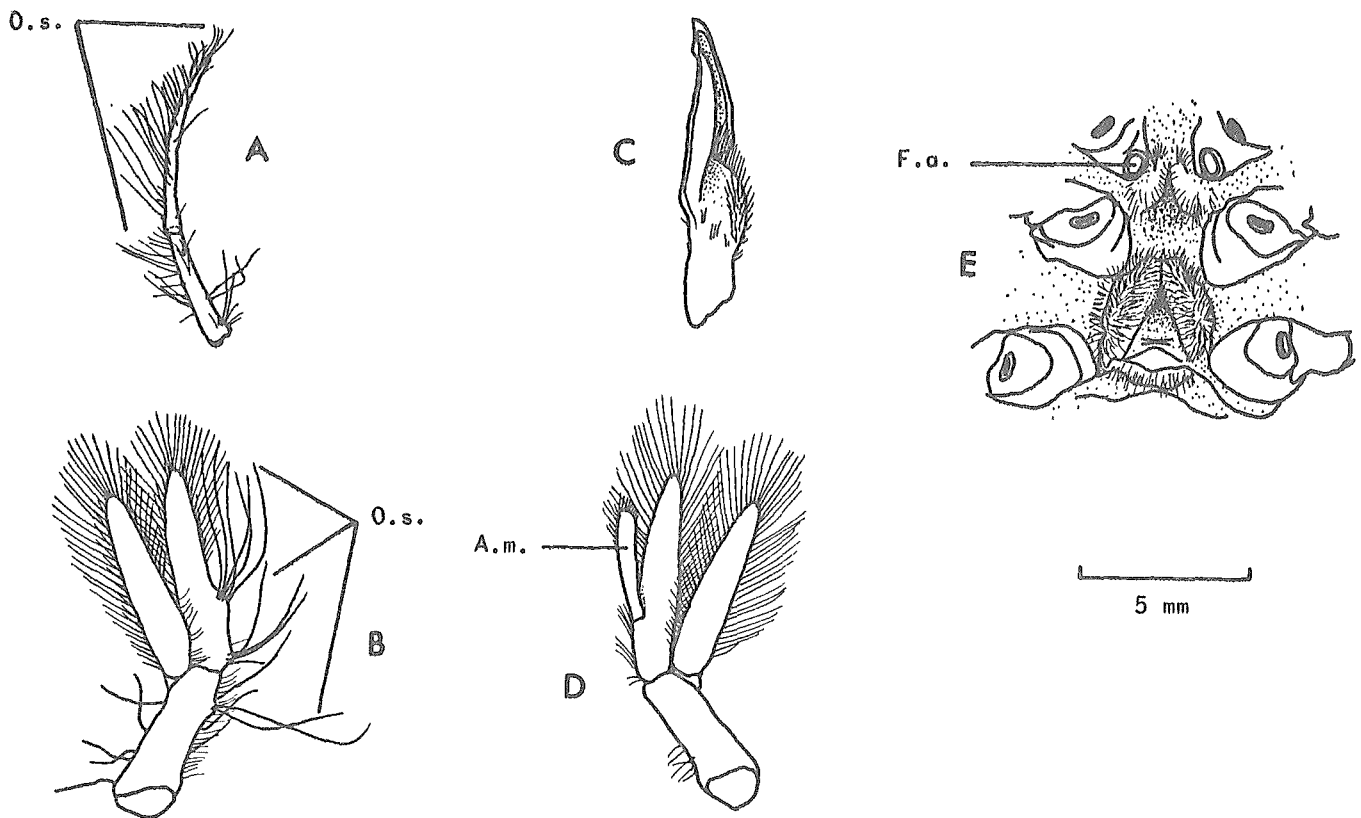
Fig. 9 N. norvegicus. Pleopods of mature female: (A) first left pleopod; (B) second left pleopod; and mature male: (C) first right pleopod; (D) second right pleopod. (E) thelycum of mature female. A.m.: appendix masculina; F.a.: female genital aperture; O.s.: ovigerous setae.

situated at the distal end of the vas deferens (Charniaux-Cotton, Zerbib and Meusy, 1966). The gland is very sinuous and convoluted (diameter of the tubule is 40μm). There is no evidence of an homologous organ in females.

There is a very pronounced sexual dimorphism in the size of the chelae of adult N. norvegicus. From sexual maturity onwards the chelae of males grow much more rapidly than those of females (see section 1.32). Similarly there is a significant difference in the abdominal width of males and females of similar size. In females the pleura of the abdominal segments are splayed outward, presumably to provide more space to accommodate the eggs whilst carried on the pleopods (see section 1.32).

3.12 Maturity

– Size at which sexual maturity is reached and its variations with sex, sub-populations, age and rate of growth

Size at sexual maturity has rarely been recorded for male N. norvegicus. Storrow (1912) observed a number of large males "with spermatophores leaving the deferent ducts or in the

penes". The smallest of these had a total length of 100 mm (carapace length 30 mm) and Storrow assumed this to be the size at which males become sexually mature. Figueiredo and Barraca (1963) described various stages in the development of the testes, but gave no indication of the size at which spermatogenesis commences. Hillis (1972d) attempted to estimate the proportion of mature males in samples from the Irish Sea by subtracting the number of immature females from the total number of males. Hillis did not however give details of the size division of immature and mature individuals.

By using morphological characters (relative growth of the chelae, and the development of the external sexual characters) Farmer (in press a) concluded that sexual maturity in male N. norvegicus occurs at a carapace length of approximately 26 mm.

The attainment of sexual maturity in females has usually been estimated on the basis of the smallest ovigerous individuals, or more rarely on the development of the ovary and the presence of a spermatophore in the thelycum. The results of various authors are summarized in Table VI. The more recent estimates tend to agree on a carapace length of approximately 20 mm for female maturity.
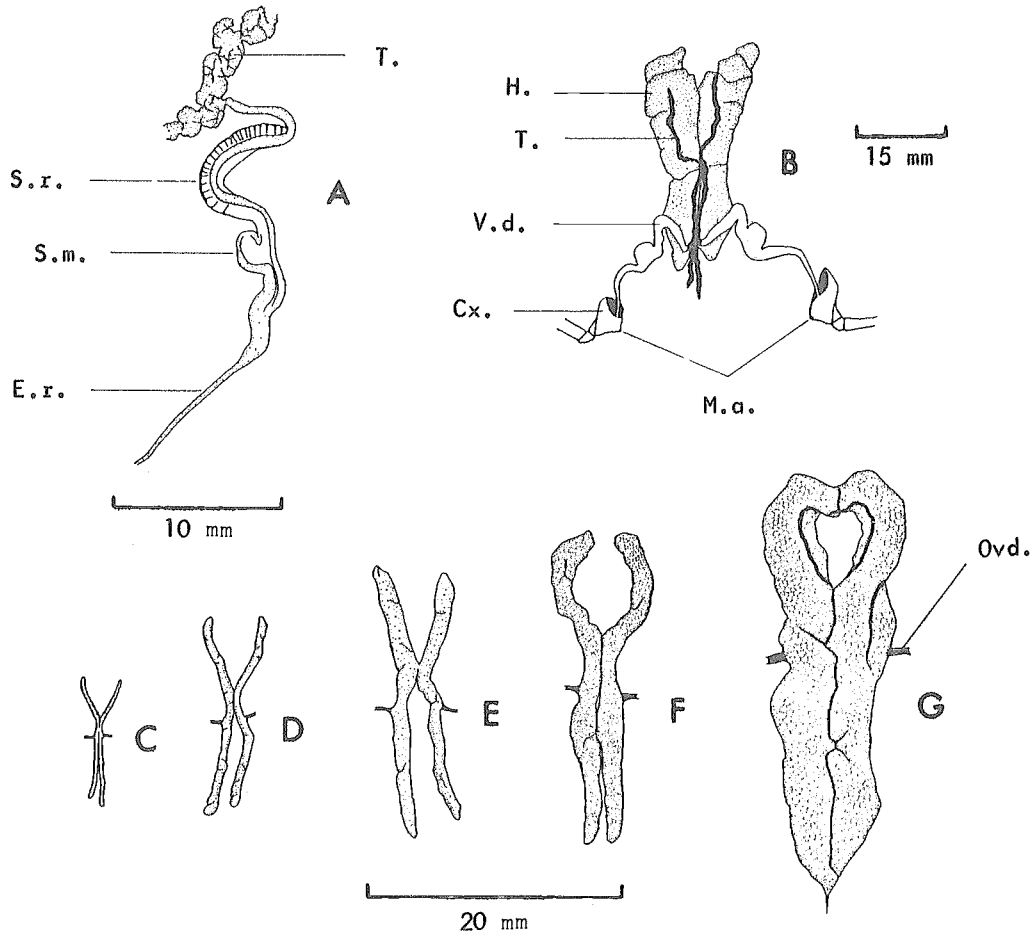
Fig. 10 N. norvegicus. Reproductive system. (A) left vas deferens from adult male,
androgenic gland omitted (carapace length 42.6 mm); (B) general view of male
reproductive system showing position relative to hepatopancreas and the
coxopodites of fifth pereiopods; (C) ovary stage 1 (immature female);
(D) ovary stage 1 (mature female); (E) ovary stage 2; (F) ovary stage 3;
(G) ovary stage 4. Cx.: coxopodite; E.r.: ejaculatory region; H.: hepatopancreas;
M.a.: male genital aperture; Ovd.: oviduct; S.m.: muscular sphincter;
S.r.: secretory region; T.: testis; V.d.: vas deferens. (After Farmer, in press a)

Farmer (1973) provides details of growth rates
and estimates of mean sizes for animals of different
age groups from the Irish Sea. From his data it
appears that females reach maturity after two years,
and males after three. No data are available on
the age at which sexual maturity is reached in other
areas.

3.13 Mating

Mating is promiscuous.

The mechanics of copulation in N. norvegicus
have been described by Lüling (1968) based on the
morphology of the pleopods and the thelycum,
although already figured by Höglund (1942) without

precise details. The details of copulation have
been confirmed by Farmer (in press). Copulation
only occurs between males and newly-moulted
females. It is suggested that recently-moulted
mature females produce a pheromone, which attracts
males and may also inhibit feeding. After
stroking the female with the antennae, the male
straddles the female and turns her over onto her
back with the third maxillipeds and second pair
of pereiopods. The first pair of pleopods is
thrust into the thelycum. The abdomen is flexed
rapidly two or three times, forcing a sperma-
tophore into the thelycum by sliding the
appendices masculinae of the second pleopods
along the grooves on the inside of the first
pleopods. The pair separates, and no further

TABLE VI

Onset of sexual maturity in female N. norvegicus

Authority	Area	Carapace length (mm)	Method of estimation
Andersen, 1962	Faeroes	27 (90)	smallest ovigerous female
Poulsen, 1946	Skagerrak and Kattegat	36 (120)	smallest ovigerous female
Thomas and Figueiredo, 1964, 1965	Moray Firth	21	smallest ovigerous female
Bagenal, 1952	Clyde area	20 (70)	smallest ovigerous female
Thomas, 1962, 1964	Scottish waters	22-29	gonads/spermatophores
Thomas, 1954	Firth of Clyde	20 (70)	smallest ovigerous female
DAFD, 1966	Scottish waters	22	50% females ovigerous
Figueiredo and Thomas, 1967a	Moray Firth	22	50% females ovigerous
Storrow, 1912	Northeast England	24 (80)	smallest ovigerous female
Farmer, in press	Irish Sea	19-22	gonads/spermatophores
O'Riordan, 1964	Irish - general	20	smallest ovigerous female
Gibson, 1967	South coast of Ireland	20	smallest ovigerous female
Fontaine and Warluzel, 1969	Coast of Gascogne	20	gonads/spermatophores
Figueiredo and Barraca, 1963	West Portugal	26	smallest ovigerous female
Vives and Suau, 1963	East coast of Spain	27-30 (90-100)	gonads
Karlovac, 1953 "	North Adriatic High Adriatic	24 (80) 18 (60)	smallest ovigerous female "
Matta, 1959	Tyrrhenian Sea	30	smallest ovigerous female

(Figures in parentheses are the original total lengths quoted by the authors before conversion to carapace length)

TABLE VII

Stages of oocyte/ovarian maturation (Farmer, in press) compared with the equivalents of other authors. (Stages I-IV represent increasing stages of maturity, stage V represents resorption after egg-laying)

Stage and duration	Mean[1] diameter oocytes	Colour		Equivalent Stages				
		Fresh	Preserved[2]	Thomas, 1960	Thomas, 1962, 1964 and Fontaine and Warluzel, 1969	Figueiredo and Barraca, 1963	Symonds, 1972a	Hillis, 1972d
I (3 months)[3]	0.19 mm	white	white	0-I	0-I	I-II	0-I	pale
II (3 months)	0.37 mm	cream	buff	I	I	II	II	-
III (3 months)	0.63 mm	pale green	pink	II-III	II-III	III-IV	III	medium
IV (2 months)	0.93 mm	dark green	orange	III-V	III-V	IV-VI	IV-V	dark
V (3-4 weeks)	0.19-0.93 mm	mottled green/cream	mottled white/pink	VR[4]	-	-	VR[4]	-

1/ Developing oocytes only (except stage I, excluding terminal strand passing through the centre of each half of the ovary)
2/ In alcohol, formalin or ethylene glycol
3/ Except immature individuals
4/ Stage V showing resorption

interest in the female is shown by the male.
Penetration lasts only a few seconds. According
to Farmer (in press) only one spermatophore is
transferred during copulation. In the laboratory
copulation occurred at dusk or at night, agreeing
with the results of Gauss-Garady (1912). Since
mature females moult once per year in most cases,
after the previous year's eggs have hatched,
copulation occurs (in the Irish Sea) during May-
August, when moulting is taking place.

Thomas (1962, 1964) and Farmer (in press)
have found that most mature females carry sperma-
tophores (up to 100 percent), although the minimum
size of the females carrying the spermatophores
differs in the two respective areas, viz. 22 mm
carapace length from Scottish waters, and
17-18 mm in the Irish Sea. Immature females are
occasionally found to carry spermatophores.

3.14 Fertilization

It has been generally assumed that fertili-
zation of the eggs occurs as they pass over the
opening of the thelycum from the oviducts (e.g.,
Figueiredo and Thomas, 1967), although this has
never been proved. Farmer (in press) has dis-
cussed the various possible methods of fertili-
zation that could take place, and concluded that
fertilization is extremely unlikely to occur as
the eggs pass over the thelycum. Instead he
suggested that fertilization may in fact be
internal, since from histological studies of
spermatophores in situ, there is no evidence of
the release of spermatozoa from the opening of
the thelycum.

3.15 Gonads

The morphology of the gonads is covered in
section 3.11 and shown in Fig. 10.

– Development

The structure and development of the sperma-
tozoa have been studied by Chevaillier (1965,
1967a) and Chevaillier and Maillet (1965, 1965a).
See also section 1.34.

In Portuguese stocks of N. norvegicus,
spermatogenesis occurs throughout the year,
although spermatozoa accumulate in the tubules of
the testis from July onwards (Figueiredo and
Barraca, 1963). Similar studies in the Irish Sea
(Farmer, in press) also indicate that spermato-
genesis occurs throughout the year, but that
spermatophores are carried in the vasa deferentia
at all times. Photographs of relevant stages of
spermatogenesis have been published by Chevaillier
(1965, 1967a), Farmer (in press) and Figueiredo
and Barraca (1963).

The development of the oocytes has been
described by Farmer (in press), Figueiredo and
Barraca (1963), Fontaine and Warluzel (1969),
Symonds (1972a) and Thomas (1960a, 1962, 1964)
who assigned roughly similar stages to the
development and maturation of the ovaries and
oocytes. The equivalent stages of oocyte/ovarian
maturation for different authors are given in
Table VII.

The mean weights of oocytes at various
stages of development are given by Thomas (1962,
1964). According to Farmer (in press) ovarian
germinal cells take 11-12 months to develop into
mature oocytes ready for egg-laying in N. norvegicus
in the Irish Sea.

Changes in the weight of ovaries through
the year and in different size ranges of females
from the east coast of Spain have been given by
Vives and Suau (1963). Maximum ovary weight was
6.485 g from a specimen in June with a total
length of 15 cm. Immature females and those with
undeveloped ovaries gave corresponding weights of
0.007-0.09 g.

– Relation of egg number to body length

Estimates of the fecundity of N. norvegicus
have been carried out by Thomas (1962, 1964),
Figueiredo and Nunes (1965), Fontaine and
Warluzel (1969) and Farmer (in press). The
results are summarized in Fig. 11. The data
given by Farmer refer to numbers of eggs
attached to the pleopods of newly-berried
females; the other estimates were based on the
number of oocytes in the ovary of mature indivi-
duals. According to Farmer (in press) the lower
estimates he obtained were due to the following
factors:

(i)   not all the oocytes in the ovary are
      released at egg-laying: some remain
      and are resorbed, others constitute
      the germinal strand which is present
      at all times and is retained after
      egg-laying;

(ii) there is a progressive loss of eggs
      from the pleopods during incubation,
      due to predation and abrasion.

Figueiredo and Nunes (1965) found that about
10 percent of the eggs carried on the pleopods
are lost per month during incubation, and that
not all the eggs attach to the pleopods during
egg-laying.

According to Storrow (1912) (also quoted by
Havinga, 1929) the number of eggs carried by
N. norvegicus ranges from 1 400 to 4 100.
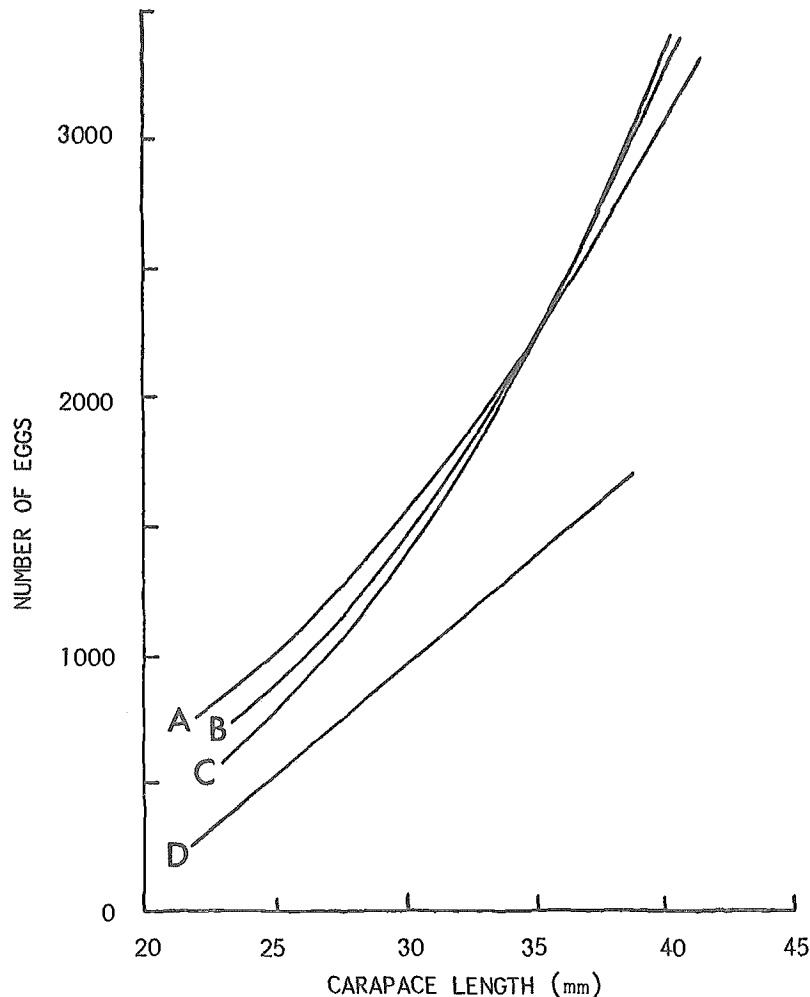
Fig. 11 N. norvegicus. Estimates of the fecundity of females of different sizes.
Numbers of ovarian oocytes (A) from Scottish waters (Thomas, 1962, 1964);
(B) from the coast of Gascogne (Fontaine and Warluzel, 1969); (C) from
the coast of Portugal (Figueiredo and Nunes, 1965); (D) numbers of eggs
on the pleopods of newly-berried females from the Irish Sea (Farmer,
in press a)

Gauss-Garady (1912) and Poulsen (1946) also give
ranges of the number of eggs carried by females
on the pleopods, viz. 800-1 200 and 1 000-5 000
respectively, but not a specific relationship
between size and the number of eggs carried. The
average female carries about 2 000 eggs (DAFS,
1963a).

- Number of broods

See section 3.16 (number of spawnings per
year.

- Correlation between the number of eggs
  and the nature of the environment

No data are available.

3.16 Spawning

- Number of spawnings per year

According to Andersen (1962) for the Faeroes,
and Höglund (1942) for Scandinavian waters, egg-
laying occurs in alternate years. Similarly
Storrow (1912) reported that females from the
Northumberland coast (England) did not lay eggs
annually. The results of Symonds (1972a) from
the same area are inconclusive. In Scottish
waters and the Irish Sea the majority of females
lay eggs every year (Thomas, 1962, 1964; Thomas
and Figueiredo, 1964, 1965; Farmer, in press a).
Figueiredo and Barraca (1963) working on stocks
off the coast of Portugal concluded that eggs are
laid annually, based on ovary maturity and stock

composition. According to Karlovac (1953) the majority·of females in the Adriatic Sea lay eggs every year.

Accurate estimates of the proportion of females laying eggs each year are difficult to obtain. Karlovac (1955) based his tentative estimate of 84 percent on the ratio between the number of ovigerous (berried) females and the total number of mature females, assuming that the numbers caught are representative of the actual number in the population. Thomas (1964) based his estimate for Scottish waters on the percentage in June of mature females with ovaries sufficiently developed to indicate that eggs will be laid in that year. His estimate was 90 percent. The comparable figure given by Farmer (in press a) for the Irish Sea stock is 91.5 percent. Farmer found that in a sample containing a particularly large number of berried individuals, obtained in May, 100 percent of the females carried spermatophores and had ovaries sufficiently advanced to indicate that egg-laying would occur the same year.

– Spawning seasons

Details of the periods of egg-laying in different localities are given in Table V. There is a general trend for egg-laying to occur later in the year in more northern latitudes, and earlier in the Mediterranean Sea.

– Spawning time of day

According to Ehrenbaum (1916), Gauss–Garady (1912) and Farmer (in press a) spawning takes place at night.

– Factors influencing spawning time

Variation in the time of spawning appears to be related to the latitude of the population involved. It would appear therefore that temperature may be concerned with the timing of the spawning season (Farmer, in press a).

– Location and type of spawning ground

The spawning grounds of N. norvegicus correspond to their normal geographical distribution, since migration in this species does not occur to any major extent (see section 3.51). Although N. norvegicus is a fossorial species, it is not known whether egg-laying takes place in the burrow.

– Ratio and distribution of sexes on spawning grounds

Studies on the sex ratio in N. norvegicus in different areas have shown that throughout most of the year there is a strong preponderance of males in the catches, although during the period from egg-hatching to egg-laying the proportion of females generally increases to approximately 50 percent. The percentages of females in the catches obtained from different stocks are given in Table VIII. A more detailed treatment of the sex ratio is given in section 4.11.

Closely associated with the change in the sex ratio in samples taken throughout the year is the relative abundance of ovigerous females. Although it seems likely that the majority of mature females lay eggs every year, berried females are notably scarce in trawl samples. Details of the relative abundance of berried females throughout the year are given in Table IX. Generally there is an increase in the proportion of berried females caught during the period when the female sex ratio reaches 50 percent or more (see Table VIII). This corresponds to the period when females are hatching eggs, are moulting and are laying eggs again for the following year. The general absence of berried females throughout most of the year is explained by their tendency to remain within their burrows when incubating eggs. This is covered in more detail in section 3.53.

– Nature of spawning act

Egg-laying has been observed in the laboratory and briefly described by Gauss–Garady (1912) and Ehrenbaum (1916). The female lies on her back, resting on the abdominal segments and the tips of the outstretched chelipeds, with antennae resting on the substrate. The eggs are extruded from the genital apertures on the coxopodites of the third pair of pereiopods, and pass over the sternal plates into the channel on the underside of the abdomen formed by the pleura. Here egg attachment takes place. In view of the position assumed during egg-laying, it is unlikely that it occurs in the burrow.

According to Farmer (1974) the female cleans the setae on the pleopods with the fifth pair of pereiopods before egg-laying.

Ovigerous setae are present on the pleopods of mature females at all times of the year (Farmer, in press c). The eggs attach to the setules present at the tips of the ovigerous setae on the pleopods and sternal ridges of the abdominal segments by a funiculus formed from the outer egg membrane (Farmer, 1972a, in press a and c). According to Cheung (1966), there are four layers surrounding the eggs of N. norvegicus, viz. the trichromatic membrane (which is composed of three distinct layers) and an inner chitinous membrane. Cheung gives details of the staining and histochemical properties of the various layers, and suggests that the "glue", which cements the eggs to the setae, originates within the egg and not in the pleopodal glands.

TABLE VIII

Percentage female N. norvegicus in monthly samples in different localities

Authority	Area	Percentage females in samples											
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Thomas and Figueiredo, 1964, 1965	Scottish waters	-	-	12.2	-	20.4	43.2	39.8	46.7	45.6	40.6	15.1	23.7
Storrow, 1912	Northeast England	21	47	-	43	22	6	8	15	20	42	43	50
Symonds, 1972a*	Northeast England (a) laboratory samples 1962-68	14	27	24	23	29	10	4	8	15	42	34	30
	(b) commercial samples 1962-67	33	27	36	54	17	17	12	14	27	44	50	48
O'Riordan, 1964	Irish Sea	9	11	8	16	24	45	52	32	35	20	20	18
Hillis, 1972d*	Irish Sea	25	21	34	28	42	69	59	54	44	37	36	34
Farmer, MS	Irish Sea	19	23	35	20	28	33	37	61	42	34	32	16
Figueiredo and Barraca, 1963*	Portuguese coast	15	21	23	12	22	34	35	32	28	24	16	13
Vives and Suau, 1963*	East coast of Spain	24	42	52	65	54	62	48	33	38	14	17	23
Karlovac, 1953	High Adriatic	41.3	61.6	67.2	63.3	58.2	48.3	43.4	41.1	43.3	-	39.0	-

* extrapolated values

TABLE IX

Percentage occurrence of ovigerous females in samples taken throughout the year

Authority	Area	Percentage ovigerous females of total number of females											
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Thomas and Figueiredo, 1964	Scottish waters	–	–	2.1	–	1.3	1.0	1.1	6.7	15.7	5.9	6.6	2.4
Thomas and Figueiredo, 1965	Scottish waters	–	–	2.0	–	1.3	1.0	1.1	6.7	18.7	5.9	6.6	2.4
Storrow, 1912	Northeast England	0	0	–	0	5	7	7	17	25	13	8	6
Symonds, 1972a	Northeast England	0.0	0.2	1.0	0.3	3.1	0.0	0.0	2.9	4.0	3.7	1.5	0.0
O'Riordan, 1964	Irish waters	3.3	–	–	–	–	–	–	0.2–55.3	13.6–89.2	16.4–58.5	1.7–10.0	0.6
Hillis, 1972d*	Irish Sea	0	0	0.5	0	2.0	0.8	0.4	4.6	18.4	10.4	1.3	0.8
Farmer, MS	Irish Sea	0	0	2	3	8	0	3	4	12	3	1	.0
Figueiredo and Barraca, 1963*	West coast of Portugal	40.0	41.7	7.7	15.5	33.7	5.7	3.4	54.5	65.3	36.1	14.4	46.9
Karlovac, 1953*	Adriatic Sea	33.3	0.9	0.0	0.0	0.0	0.0	58.8	24.6	53.9	–	64.8	–

* extrapolated values

- Nesting habits

During incubation it is generally thought that ovigerous females tend to remain within their burrows, thus explaining the disproportion of the sexes in samples except during the period from egg-hatching to egg-laying. See section 4.11.

- Reproductive isolation

N. norvegicus is geographically isolated from its most closely related species, Metanephrops spp.

Reproductive isolation probably occurs to quite a large extent between discrete populations in different areas. Evidence suggested for this includes the significant differences which have been reported in body proportions from different areas (see section 1.32) and the relative incidence of the parasite Stichocotyle nephropis (see section 3.35).

- Induction of spawning

There are no known methods of inducing spawning in N. norvegicus. According to Farmer (1972a, in press a) mature females do not readily lay eggs in the laboratory unless supplied with a layer of mud in which to burrow. He found that a large proportion of mature females ready to spawn resorbed their oocytes when kept in tanks without a suitable substrate, whereas other females kept in tanks supplied with suitable mud were able to burrow and spawn successfully.

3.17 Spawn

- Morphology

The newly-laid eggs of N. norvegicus are spheroidal in shape and dark green due to the presence of ovoverdin (a protein bound to astaxanthin) (Goodwin, 1951). The eggs when newly laid have an approximate diameter of 1.5 mm according to Karlovac (1955) and Schellenberg (1928). Storrow (1912) (also quoted by Havinga, 1929) gives the size range of the eggs as 1.3 x 1.4 mm to 1.5 x 1.6 mm. These measurements agree closely with those of Figueiredo and Barraca (1963) who found that the minimum and maximum diameters were 1.05 and 1.55 mm respectively, with a mean value of 1.34 mm.

When newly laid the eggs show no cleavage divisions, and contain large numbers of small globules evenly distributed throughout the entire volume of the egg (Farmer, in press a).

For details of the various membranes surrounding the egg, and the method of attachment, see section 3.16 - Nature of the spawning act.

3.2 Pre-adult phase

3.21 Embryonic phase

- General features of development of embryo

According to Farmer (1972a, in press a) yolk cleavage divisions take place, giving the eggs a mosaic appearance. Once the yolk cleavage divisions are complete, further development is arrested for up to 7 months, during which time the eggs remain dark green. After this period of inactivity, development continues fairly rapidly until the larvae are ready to hatch. Farmer (1972) suggested that cleavage is determinate. The development of the embryos has been described by Dunthorn (1967), Figueiredo (1971), Figueiredo and Barraca (1963), Figueiredo and Vilela (1972) and Fontaine and Warluzel (1969). Representative stages of the embryonic development are shown in Fig. 12.

During development the mean diameter of the eggs increases from 1.34 mm (range 1.05-1.55 mm) to 1.66 mm (range 1.35-2.05 mm) (Figueiredo and Barraca, 1963). As the embryo develops within the egg, there is a gradual change in colour from dark green, through pale green to pink/orange. This is due to the release of astaxanthin from ovoverdin (astaxanthin bound to a protein) (Goodwin, 1951). At all times the yolk remains green and the embryo pink/orange, but the relative proportion of these two parts of the egg changes during development to give rise to the overall change in colour.

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

The periods of incubation from egg-laying to egg-hatching in different areas are given in Table V, showing a variation from 6 months to 10 months. There appears to be a general correlation between water temperature and the rate of embryonic development. The work of Dunthorn (1967) and Farmer (1972a) which is included in Fig. 13 substantiates this view. During incubation there is a progressive loss of 10 percent of the eggs attached to the pleopods per month, with the result that by the time that the eggs are ready to hatch, only 30 percent of the original number laid remain (Figueiredo and Nunes, 1965).

During incubation the female beats the pleopods to create a flow of water through the burrow, so that the water around the eggs remains oxygenated. The female uses the fifth pair of pereiopods to clean the eggs and to sort through them, removing detritus (Farmer, 1974, in press a).
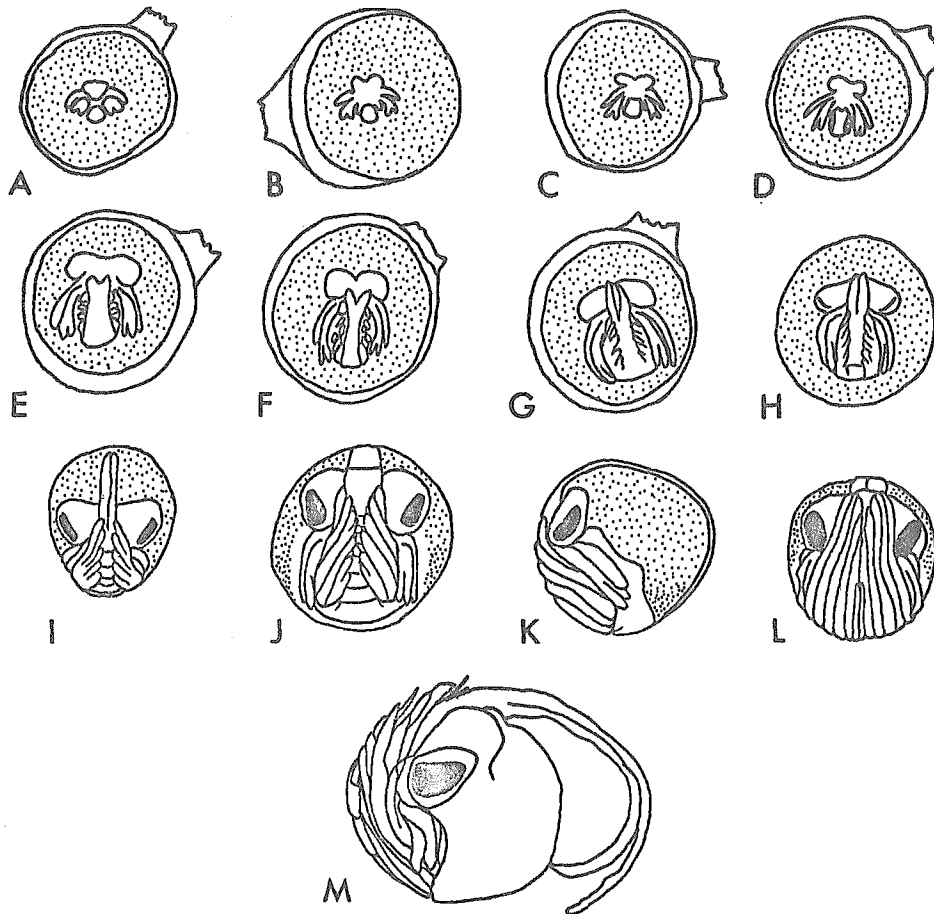
Fig. 12 Embryological development of N. ncrvegicus (after Fontaine and Warluzel, 1969).
         (A) General view of embryo in relation to the egg; (B) and (C) nauplius stage I;
         (D), (E) and (F) metanauplius stage II; (G) and (H) stage III; (I) stage IV;
         (J) and (K) stage V; (L) and (M) stage VI (equivalent to the first larval stage)

- Parasites and predators

According to Farmer (1972a) large numbers of eggs died whilst attached to the pleopods during laboratory rearing experiments. Since neither penicillin nor streptomycin appeared to control the pathogen responsible, he suggested that the deaths might be due to a fungal rather than a bacterial infection.

- Effect of environment, subpopulations,
  density on rates of development and
  survival

The effect of temperature on the rate of development has already been covered in the section above. See Fig. 13.

- Mode of hatching

Egg-hatching in the laboratory has only been observed at night, with batches of larvae being released over a period of several days (Farmer,

in press). During egg-hatching the female beats the pleopods rapidly, with the result that the larvae are discharged posteriorly in a fairly strong current. If egg-hatching takes place in the burrow, this action would help to ensure that the larvae are blown out through the rear entrance of the U-shaped burrow. While beating the pleopods, the female rocks slowly backwards and forwards on the tips of its walking legs. Farmer (in press) suggests that the outer membranes surrounding the egg may be burst by its internal pressure of water, whereas the inner membrane is probably burst by the ventilation movements of the pleopods. The inner membrane of isolated eggs does not rupture unless there are vigorous water movements. Farmer (1972a) suggested that the females leave their burrows during egg-hatching.

3.22 Larval phase

- General features of development

The larval stages of N. norvegicus were
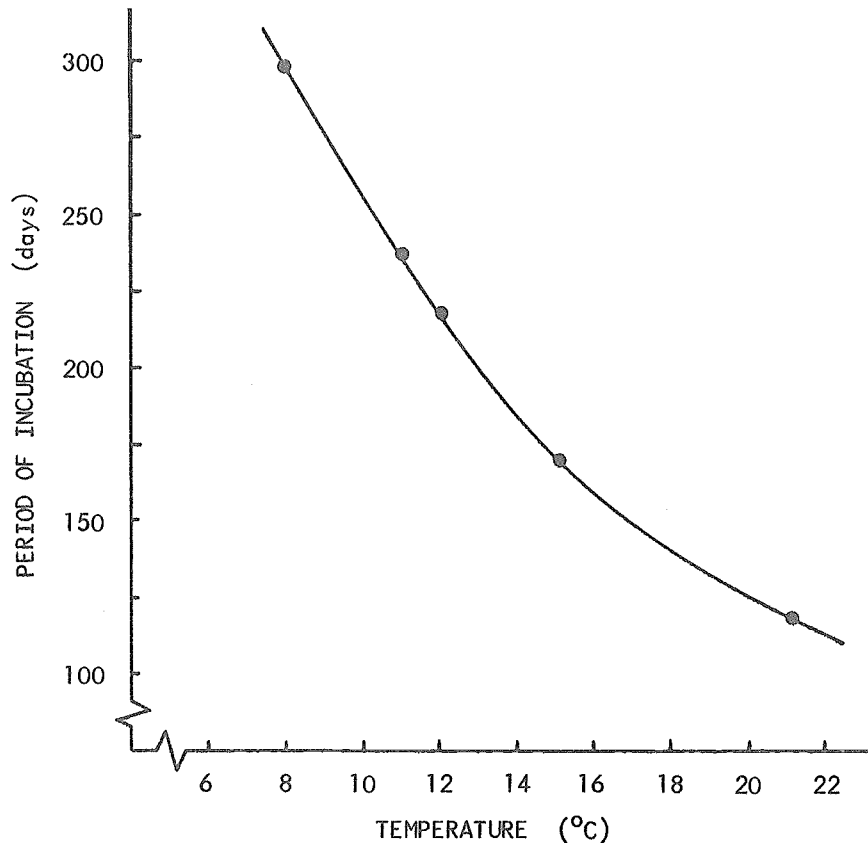
Fig. 13 N. norvègicus. Periods of incubation of eggs whilst carried on the pleopods
         at different temperatures. (After Dunthorn, 1967; Farmer, 1972a)

first described by Sars (1884, 1890) and later by
Jorgensen (1925) and Santucci (1926, 1926a, 1926b,
1927). Details of the rostrum and telson have
been given by Andersen (1962) and Kurian (1956).
According to Farmer (in press) there is a brief
pre-zoeal larval stage which is unable to swim,
since the natatory appendages are devoid of setae,
and moults soon after hatching to produce the
1st zoeal stage. The pre-zoeal stage corresponds
to the newly-hatched larva figured by Fontaine
and Warluzel (1969) (see Fig. 12(M)). The free-
swimming larval stages are shown in Fig. 14. The
diagnostic characters of the various larval stages
are as follows:

Pre-zoea: generally similar to 1st zoea,
           except smaller, and without setae
           on the natatory appendages. More
           or less curled up in the position
           of the embryo.

1st zoea: length 5.5-7 mm overall. 3rd,
           4th and 5th abdominal segments
           each bear one median dorsal spine.
           6th segment with two divergent
           dorsal spines. Telson divided
           into two lateral projections.
           Uropods absent, pleopods present
           as minute limb buds.

2nd zoea: length 7.5-10 mm overall.
           Dorsal spines and telson more
           or less as 1st zoea. Uropods
           absent, pleopods on the 2nd to
           5th abdominal segments present
           as biramous limbs, but devoid of
           setae. Supra-orbital spines
           present. Eyes stalked.

3rd zoea: length 10.5-12 mm overall.
           Dorsal spines and telson more
           or less as 1st zoea. Uropods
           present, and pleopods, with short
           setae, although pleopods still
           absent from 1st abdominal segment.
           Supra-orbital spines present.

According to Farmer (in press) all four larval
stages have yellow spots present at the bases and
joints of the pereiopods, in addition to the
orange/red chromatophores present over most of
the body surface.

 - Rates and periods of development and
   survival, and factors affecting these

According to Poulsen (1946) the larval stages
of N. norvegicus probably last 2-3 weeks. More
accurate estimates of the duration of the larval
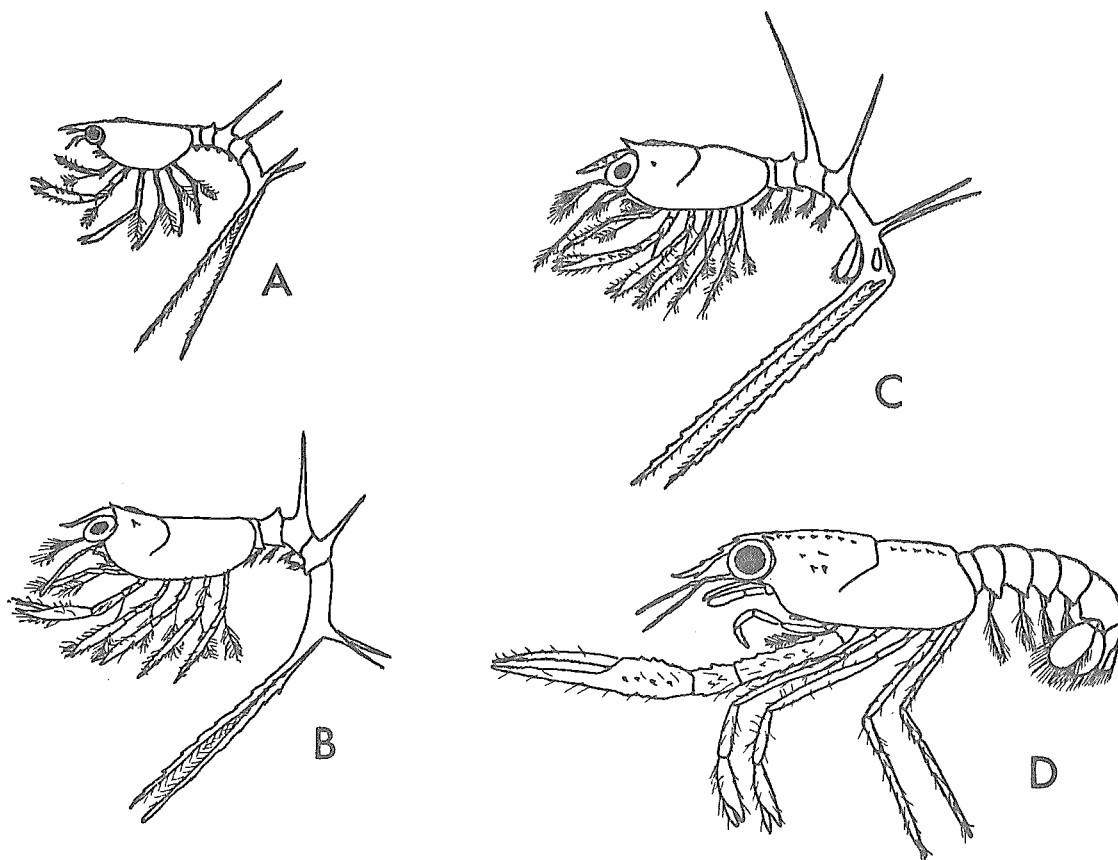
Fig. 14 Larval development of <u>N. norvegicus</u>. (A) stage I, total length 6.5 mm;
(B) stage II, total length 9 mm; (C) stage III, total length 11.6 mm;
(D) early post-larval instar, total length 15.6 mm. (From Santucci, 1926)

TABLE X

Duration of the larval stages of <u>N. norvegicus</u> maintained under laboratory conditions

Authority	Temperature °C	Duration in days		
		1st zoea	2nd zoea	3rd zoea
Farmer, 1972a	10–18	10	15	–
Figueiredo, 1971	11–14	11	–	–
	13–15	9	–	–
	15–18	5– 6	–	–
Figueiredo and Vilela, 1972	7–10	14–15	14–15	–
	11–14	10–11	10–11	–
	13–17	5– 6	5– 6	–
Hillis, 1972d	9–14	–	13	16
	17–19	–	7– 9	8–12

phase are available only from laboratory experiments; see Table X. Each successive larval stage is longer than the preceding stage. There appears to be a general trend for development to be faster at higher temperatures.

Survival of the larval stages under laboratory conditions is covered in section 7.4.

There is no parental care of the larvae.

- Diseases, parasites and predators

Anderson and Conroy (1968) have reported the infestation of N. norvegicus larvae by the ciliate Zoothamnion sp. The complete body surface of living larvae was covered by the sessile protozoans, and death was thought to have resulted from trauma and interference with respiration.

The natural predators of N. norvegicus larvae are likely to include ctenophores, medusae, plankton-feeding fish, and other N. norvegicus larvae. This is based on the observations of Farmer (MS) when using mixed zooplankton for feeding the larvae. The isopod, Eurydice pulchra, has been reported to feed on the larvae under laboratory conditions (Farmer, 1972a).

- Time of first feeding

Feeding commences at the 1st zoeal stage.

- Type of feeding

N. norvegicus larvae are carnivorous and under unnaturally high densities cannibalism takes place. The larvae probably feed on copepods, small mysids, other decapod larvae, small Sagitta sp. etc. in the natural environment (Farmer, MS). They capture their prey by active swimming movements, and grasp their food with the chelipeds before transferring it to the mouthparts.

- Behaviour

According to Foxon (1934) N. norvegicus larvae "... orientate themselves with the telson and abdomen towards the light, but with the head and thorax in a plane at right angles to them. In this posture all the specimens moved towards the light telson first."

3.23 Adolescent phase

Very few early post-larval stages of N. norvegicus had been reported until Farmer (1972a) and Hillis (1972a) started to use beam trawls and conventional trawls with fine-mesh covers for routine sampling. Earlier records include Jorgensen (1925), Santucci (1926, 1927), Karlovac (1953), Andersen (1962) and O'Riordan (1964). It appears that the apparent absence of small juveniles is due to the use of inadequate mesh sizes.

The juvenile stages are bottom-living, and construct burrows similar to those of the adults (Crnković, 1968; Farmer, 1974a).

The morphology of the juveniles, including the early post-larval instars, of N. norvegicus is similar to that of adults except in size. However, at sexual maturity there is a change in claw morphology and in certain body proportions (see sections 1.31 and 1.32). Throughout the adolescent phase there is a gradual development of the external sexual characters (Farmer, in press c). Sexual maturity is reached in males at a carapace length of approximately 26 mm, whereas sexual maturity in females is usually reported to occur at a carapace length of approximately 20 mm (see section 3.12 and Table VI).

- Rates and periods of development and
   survival, and factors affecting these

Farmer (1973) provides details of growth rates and estimates of mean sizes for animals of different age groups from the Irish Sea. From his data, the adolescent phase in males lasts about 3 years and in females about 2 years. Similar estimates are not available for other populations of N. norvegicus.

There are no data available on the survival of juveniles.

Throughout the adolescent phase there is no evidence of parental care.

- Diseases, parasites and predators

Diseases, parasites and predators of juvenile N. norvegicus have not been specifically noted, since these are likely to be similar to those of the adults (see sections 3.34 and 3.35).

- Type of feeding

The diet and feeding behaviour of the juvenile stages of N. norvegicus is similar to that of the adults (see section 3.4).

3.3 Adult phase

3.31 Longevity

- Average age

The average age of N. norvegicus from the Irish Sea, extrapolated from the size/age data quoted by Farmer (1973) is given below:

Males: mean size (carapace length): 26-35 mm
          mean age: $2\frac{1}{2}$-$4\frac{1}{2}$ years.

Females: mean size (carapace length): 22-29 mm
          mean age: 2-$3\frac{1}{2}$ years.

For details of the mean size of individuals from different populations see Table XI and section 4.13.

TABLE XI

Mean and maximum recorded sizes (carapace length) of N. norvegicus from different areas, partly from Figueiredo and Thomas (1967a)

Authority	Area	Depth (m)	Mean size (mm)		Maximum size (mm)	
			males	females	males	females
Leloup, 1959	Iceland	–	54*	–	80*	–
Sigurdsson, 1965	Iceland	108	–	–	74	44
Andersen, 1962	Faeroes	25– 88	–	–	77*	56*
Poulsen, 1946	Kattegat and Skagerrak	17–240	49*	44*	80*	58*
Höglund, 1942	Kattegat and Skagerrak	40–250	–	–	77*	–
Leloup, 1959	North Sea	–	43*	–	70*	–
Cole, 1962, 1965	North Sea	55– 91	–	–	75	–
Storrow, 1912	Northeast England	70– 85	47*	37*	66*	50*
Cole, 1962, 1965	Northeast England	–	48	–	75	–
Thomas, 1965b	Firth of Forth	24– 69	38	–	67	–
Thomas, 1965b	Moray Firth	29– 99	32	–	57	–
Thomas, 1965b	West Orkney	128–163	36 ·	–	62	–
Cole, 1962, 1965	North Minch	–	33	–	60	–
Thomas, 1965b	North Minch	57–130	40	–	72	–
Cole, 1962, 1965	South Minch	–	38	–	70	–
Thomas, 1965b	South Minch	73–181	32	–	62	–
Barnes and Bagenal, 1951	Clyde	40	–	–	80*	42*
Thomas, 1965b	Clyde	42–126	34	–	57	–
O'Riordan, 1965	Northwest Ireland	22– 48.	–	–	62	37
Cole, 1962, 1965	Irish Sea	18–101	–	–	55	–
O'Riordan, 1965	Irish Sea	27– 55	30	–	50+	42
Farmer, 1972a, MS	Irish Sea	28–121	–	–	55	38
O'Riordan, 1965	South Ireland	37– 59	35	–	57	42
O'Riordan, 1965	West Ireland	–	–	–	47	22
Leloup, 1959	Irish waters	–	42	–	73	–
Cole, 1962, 1965	Celtic Sea	256–586	–	–	80	–
Figueiredo and Barraca, 1963	West Portugal	95–549	48	–	92	74
Matta, 1959	Tyrrhenian Sea	36–440	39*	–	60*	47*
Karlovac, 1953	North Adriatic Sea	50–400	38*	31*	65*	51*
Karlovac, 1953	High Adriatic	50–400	35*	29*	72*	55*

* recalculated values, originally quoted as total length

– Maximum age

No data are available on the maximum age
attained by N. norvegicus. Recorded maximum sizes
are given in Table XI and section 4.13.

3.32 Hardiness

– Limits of tolerance to changes in or of
environment and feeding

Throughout the geographical range of
N. norvegicus the bottom seawater temperature
varies from 4.3–15.0°C in the Adriatic Sea
(Karlovac, 1953) to 7.0–13.0°C in the Irish Sea
(Farmer, 1973). It is not known whether these
temperatures represent the limits of tolerance.

The maximum recorded salinity from
N. norvegicus grounds is 38.77°/oo in the Adriatic
(Karlovac, 1953). According to Poulsen (1946)
salinities as low as 29–30°/oo are tolerated in
the southeastern Kattegat. Poulsen suggested that
this represented the lower limit of tolerance for
the species, thus explaining its absence from the
Baltic Sea (Höglund, 1942). Thomas (1970a) reports
that under estuarine conditions N. norvegicus is
able to withstand sea water dilution by about
12 percent fresh water.

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

Simpson and Symonds (1968) and Symonds and
Simpson (1971) have studied the survival of small
N. norvegicus returned to the sea during commercial
fishing. Their results show that after an initial
high mortality, probably caused by damage to
animals during trawling or on hauling the net, the
mortality decreased significantly, resulting in at
least 40 percent of the small individuals, which
would normally be rejected in a commercial opera-
tion, being alive when returned to the sea after
being out of water for up to 2 hours. As Thomas
(1960c, 1961) has pointed out, live animals
returned to the sea may not necessarily survive,
as airlocks in the gill chambers can result in
asphyxiation. Relative claw damage is an important
factor in the survival of N. norvegicus, as the
following figures show (Symonds and Simpson, 1971):

    percentage survival with both claws   69%;
    percentage survival with only one claw   50%;
    percentage survival with no claws   22%.

Further mortality is likely to result from
predation, if the animals do not find burrows soon
after reaching the bottom, or if the eyes have been
damaged by high surface light intensities as shown
by Loew (1974).

N. norvegicus can be maintained in aquaria
for relatively long periods, without the need for
special treatment. Thomas (1965d) has kept speci-
mens alive for periods up to 30 months, and
Farmer (MS) for periods up to 22 months. They
will feed on most fish or shellfish offered, and
can on occasion go without food for long periods
without apparent permanent harm (Dunthorn, 1967;
Farmer, 1974a; see also section 3.41). Given a
suitable substrate N. norvegicus will produce
typical burrows within the confines of an experi-
mental tank (see section 3.55).

Farmer (1974a) suggested that there might be
a critical distance within which aggressive
responses were elicited. It may be necessary to
consider this factor when deciding on the stocking
density of experimental tanks.

– Variations in hardiness with age, size
and physiological states

During studies on the survival of small
N. norvegicus returned to the sea during commercial
fishing, it was found that the survival rate of
smaller individuals appeared to be better than
that of larger individuals (Symonds and Simpson,
1971).

3.33 Competitors

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

Various fish species which occur in areas
where N. norvegicus is found must be considered
as potential competitors for food (see section
4.6). Other species which may in certain areas
compete for food include Munida rugosa, Macropipus
spp., Polycheles typhlops, etc., and various
cephalopods, although they are unlikely to be
present in sufficiently large numbers to be of
great importance.

Competition for suitable areas of substrate
in which to burrow is unlikely, although the
following burrowing species may be of importance
if present in unusually large numbers:
Calocaris macandreae, Jaxea nocturna, Alpheus glaber,
Callianassa subterranea, Goneplax rhomboides,
Lesueurigobius friesii and Buenia jeffreysii.

3.34 Predators

– Types of predators

According to Gauss–Garady (1912, 1913) the
main predators of N. norvegicus in the Adriatic Sea
are: the anglerfish (Lophius piscatorius and
L. budegassa); angelshark (Squatina squatina);

electric ray (Torpedo sp.); sting ray (Dasyatis sp.); eagle ray (Myliobatis sp.); lesser-spotted dogfish (Scyliorhinus canicula); smooth hound (Mustelus mustelus); the spur dogfish (Squalus acanthias and S. blainvillei); humantin (Oxynotus centrina); weevers (Trachinus spp.); gurnards (Trigla spp.); scorpionfish (Scorpaena spp.); stargazer (Uranoscopus scaber); turbot (Psetta maximus); whiting (Merlangius merlangus); poor cod (Trisopterus minutus); hake (Merluccius merluccius); octopus (Eledone moschata) and the swimming crab (Macropipus depurator).

In the Clyde (Scotland), the cod (Gadus morhua) was found to be the only species feeding on N. norvegicus (Bagenal, 1952). However, Thomas (1961a, 1965a) and DAFS (1963a) found that the following species were the most important throughout Scottish waters generally: long rough dab (Hippoglossoides platessoides); cod; lesser-spotted dogfish; skate (Raia clavata); hake; whiting; haddock (Melanogrammus aeglefinus); conger (Conger conger); halibut (Hippoglossus hippoglossus); catfish (Anarhichas lupus) and four-bearded rockling (Enchelyopus cimbrius). N. norvegicus was found in 80 percent of cod stomachs examined, in 51 percent of lesser-spotted dogfish and 52 percent of skate.

On the east coast of Spain, poor cod has been found to be an important predator of N. norvegicus (Planas and Vives, 1952)

In the Irish Sea, Farmer (1972a) found that lesser-spotted dogfish, cod, whiting, skate, hake and anglerfish feed on N. norvegicus.

Rae (1967, 1967a, 1968) in studies on the food of cod in Scottish, Faeroese and Icelandic waters, found that N. norvegicus was the most important part of the diet in those areas where the species occurs. It was found in up to 68 percent of cod stomachs examined. In Icelandic waters, N. norvegicus was a less important constituent of the diet compared with Faeroese and Scottish waters. In all three areas N. norvegicus was eaten mainly by the larger cod.

According to Höglund (1942) many species of the larger demersal fish are predators on N. norvegicus in the Kattegat and Skagerrak, cod probably being the most important. Fontaine and Warluzel (1969) found that poor cod, pout (Trisopterus esmarki), greater forkbeard (Phycis blennoides), poutassou (Micromesistius poutassou), whiting and Gadiculus argenteus thori were the principal predators off the coast of Gascogne.

- Defence reactions

According to Rice and Chapman (1971) the burrows of N. norvegicus function mainly as refuges, and must contribute greatly to the animals' chances of survival, since the animals appear to spend the greater part of their lives within the confines of the burrow. Chapman and Rice (1971) suggested that the pattern of diurnal activity shown by N. norvegicus may be related to the availability of prey species, and that by remaining in their burrows during poor feeding periods, the risk of predation by fish is probably reduced. Atkinson (1971) and Atkinson and Naylor (1973) have postulated that the precise and persistent activity rhythm of N. norvegicus assists in restricting activity to particular times of day without the need for periodic exploratory movements toward the burrow entrance, where assessment of environmental variables (e.g., light intensity) can take place.

See also sections 3.53 and 3.55.

- Variations in defence reactions with age, size and physiological state

Farmer (1974a) found that during laboratory studies large males did not produce burrows when supplied with suitable substrates, although smaller males and females would construct burrows readily under these conditions. The large males merely dug slight depressions into the substrate and retreated into these when not foraging.

See also sections 3.53 and 3.55.

- Predation as a controlling factor of size, density and size composition of the population

There are no data available on the effects of predation.

3.35 Parasites and diseases

- Types

Cunningham (1887) described the trematode, Stichocotyle nephropis, from the hind-gut of N. norvegicus from the Firth of Forth, Scotland. A detailed description of the morphology of the parasite and additional information on its way of live have been given by Odhner (1898, 1910). There have been various reports on the relative infestation of the parasite in different populations of N. norvegicus (DAFS, 1962a; MacKenzie, 1963; Symonds, 1969, 1972).

Thomson (1896) described an unidentified parasitic copepod from the vas deferens of N. norvegicus. He found only four parasites in a total of 500 specimens of N. norvegicus. It would appear that the presence of the parasite may result in degeneration of the vas deferens.

The gregarine Porospora nephropis has been described from the gut of N. norvegicus from

Roscoff, France (Léger and Duboscq, 1915; Tuzet and Ormière, 1961; Sprague, 1970; Sprague and Couch, 1971).

Necrosis often develops at sites of injury to the exoskeleton in N. norvegicus, producing a characteristic brown coloration. It is likely that chitinoclastic bacteria are involved in the destruction of the exoskeleton at the site of the injury.

Farmer (MS) has found cysts in the hepato-pancreas of several specimens from the Irish Sea. These have not been identified.

— Modes of infection

It is not known how Stichocotyle nephropis and Porospora nephropis infect N. norvegicus.

— Stages of parasites

The final host for Stichocotyle nephropis is probably the skate (Raia clavata) (Odhner, 1898, 1910). Since the skate is an important predator of N. norvegicus it seems likely that infection occurs by this route.

The intermediate molluscan host of Porospora nephropis has not been determined.

— Intensity of individual and population infection

As many as 34 cysts of Stichocotyle nephropis have been found in a single specimen of N. norvegicus. The relative infestation of this parasite in different populations is given in Table XII.

TABLE XII

Infestation of N. norvegicus by Stichocotyle nephropis (Trematoda: Aspidogastridae) in different areas

Authority	Area	Percentage infestation
DAFS, 1962a	Minch	50+
MacKenzie, 1963	North Minch	5.0–10.0*
Symonds, 1969, 1972	North Minch	8.2
Symonds, 1969, 1972	South Minch	7.6
MacKenzie, 1963	Tiree Passage	1.0–12.0*
Symonds, 1969, 1972	Tiree Passage	1.8
MacKenzie, 1963	Sound of Jura	4.0–48.0*
Symonds, 1969, 1972	Sound of Jura	20.3
MacKenzie, 1963	Moray Firth	0.0
MacKenzie, 1963	Firth of Forth	0.0
MacKenzie, 1963	Firth of Clyde (Irvine Bay)	1.8– 6.4*
MacKenzie, 1963	Firth of Clyde (Ailsa Craig)	3.0– 9.0*
Symonds, 1969, 1972	Irish Sea (Dundalk Bay)	0.0
Farmer, 1972	Irish Sea (Isle of Man)	0.0
Farmer, 1972	Irish Sea (Cumberland coast)	0.0
Symonds, 1969, 1972	Smalls	0.5
Symonds, 1969, 1972	Labadie Bank	2.0
Symonds, 1969, 1972	Great Sole Bank	0.0
Symonds, 1969, 1972	Farne Deeps	0.0

* range of infestation over 10 mm size groups (carapace length 20–29, 30–39, 40–49, 50+ mm)

3.36 Epifauna and epiflora

– Types

Andersen (1962) has reported the following species as being epizoic on N. norvegicus in Faeroese waters: Podocoryne carnea, Balanus porcatus, Heteranomia squamula, Hiatella striata and Triticella pedicellata, which is probably a synonym of T. koreni. Occasional specimens of N. norvegicus carried an extremely rich growth of epizoites: one specimen with a carapace length of approximately 50 mm carried 155 Balanus porcatus, 10 Heteranomia squamula and 1 Hiatella striata, in addition to hydroids.

The following species have been observed on specimens from the Irish Sea (Farmer, 1972a): Triticella koreni, Balanus crenatus, Electra pilosa, Eudendrium capillare, Sabella pavonina, Serpula vermicularis and a foraminiferan, probably Cyclogyra sp. While keeping N. norvegicus in the laboratory, Farmer found that in addition to some of the species already listed, species of Spirorbis were very common epizoites, and that the algae Ulva lactuca and Pylaiella littoralis often produced dense growths, particularly on the carapace.

Barnes and Bagenal (1951) recorded large numbers of Balanus crenatus living on N. norvegicus at certain times of the year in the Clyde area (Scotland). By ageing the barnacles, it was possible to obtain estimates of the period that had elapsed since the last moult. Details of the intermoult period and moulting activity throughout the year are included in section 3.43.

3.37 Injuries and abnormalities

A number of sexual abnormalities have been recorded from N. norvegicus, details of which are given in section 3.11.

Malformations of the rostrum have been reported by Santucci (1932) and Farmer (1972). The abnormalities reported were: lateral curvature, reduction in rostral length and bifurcation. It is likely that these were the result of regeneration following injury. Legendre (1929) described an example of trifurcation of the propodite of one of the major chelipeds of an individual obtained from the Iles de Glenans, France.

Regeneration of appendages following either injury or autotomy occurs in the usual decapod fashion. A limb bud is formed initially, which at the next moult is replaced by a miniature limb or replacement of the lost part. Several moults may be required for the replacement limb to reach its normal size, particularly in the case of the major chelipeds.

3.4 Nutrition and growth

3.41 Feeding

– Time of day

N. norvegicus forages for its food away from its burrow at certain times of the day. These periods of activity form a regular pattern and are probably synchronized to changes in light intensity at the seabed. Details of the diurnal activity of N. norvegicus are provided in section 3.53.

– Place; general area

Foraging presumably takes place within the approximate vicinity of the burrow, since Chapman and Rice (1971) have shown that some N. norvegicus continue to return to the same burrow for several days. However, it was also found that some individuals occupied different burrows within a few days, indicating a somewhat loose attachment to a particular burrow, and perhaps more extensive foraging.

– Manner; methods of capture, selection

The following description of feeding in N. norvegicus is based on the laboratory observations of Thomas and Davidson (1962a). N. norvegicus is capable of catching active prey by using the major chelipeds and walking legs in a grasping fashion. Alternatively, the animal walks about until, on finding possible food material lying on or within the surface of the substrate, it will close the walking legs around the food. The food is transferred to the mouth with the chelate second and third pereiopods, with the aid of the third maxillipeds. Occasionally N. norvegicus has been observed to pick up particles of stone and work these round the mouthparts. Such action could enable the animal to graze off small stones, shells, etc., organisms such as hydroids, polyzoa, and perhaps algae, which, owing to their small size, may otherwise not be available.

The functional morphology of the mouthparts, with particular reference to the distribution of different types of setae, has been covered by Farmer (1974).

According to Thomas and Davidson (1962a) it appears that the minimum size of particle which can be manipulated and passed to the mouth is 1 mm, whereas the largest rigid object which can be passed from the mandibles into the mouth is 5 mm. Polychaetes are ingested lengthwise, and lengths of up to 6 cm of such food can be taken whole into the stomach.

- Frequency

The frequency of feeding is related to the periods of foraging activity (see section 3.53). There is no specific information on the frequency of feeding.

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

Poulsen (1946) investigated the relationship between total weight and carapace length of N. norvegicus from the Skagerrak and Kattegat. He found that on the whole there was little difference in weight between males and females of the same carapace length, the non-berried females being slightly lighter, and the berried females slightly heavier, than the males. Poulsen calculated an expression for the coefficient of nutrition (see section 1.32) and found that males generally showed a higher coefficient than both berried and non-berried females. He also found that the coefficient was much higher in the autumn than in spring.

According to Dunthorn (1967) the feeding rates of female N. norvegicus are related to temperature, and berried females eat less than non-berried females, particularly during the later stages of embryonic development. It appears that berried females are less attracted to food, and Dunthorn suggests that in the open sea, where food may not be so readily available as it was in the laboratory experiments, they may well not forage at all.

- Abstention from feeding

Farmer (1974a) has shown that berried female N. norvegicus can go without food for as long as 333 days, apparently without ill effect. The observations of Dunthorn (1967) suggest that, whilst carrying eggs, females may not feed at all (see section above).

3.42 Food

- Types eaten and their relative importance in the diet

During studies on the morphology of the digestive system, Yonge (1924) found that N. norvegicus stomach contents consisted mainly of the following: torn pieces of muscle, crustacean appendages and parts of carapaces, vertebrae and bones of small fish, hydroid stems, spines, long filamentous strips of algae, and other organic fragments. According to Höglund (1942) stomach contents were usually so finely ground that only in exceptional circumstances could food fragments be identified, viz. fragments of mussel shell and chitinous parts of smaller Crustacea.

Andersen (1962) working on N. norvegicus from Faeroese waters lists the following species as occurring in stomach contents: Foraminifera, Radiolaria, polychaetes including Nereidae and ?-Lepidonotus sp., Syndosmya nitida, Tellina fabula, Nucula sp., Margarita ?groenlandica and Onoba striata. In the Golfe du Gascogne, it has been found, from stomach contents, that N. norvegicus feeds mainly on Crustacea of the families Crangonidae, Alpheidae and Sergestidae (Fontaine, 1967; Fontaine and Warluzel, 1969). Bivalves and small gastropods are also an important part of the diet, which also includes annelids, echinoderms, fish and Foraminifera.

The most detailed studies of the stomach contents of N. norvegicus have been made by Thomas and Davidson (1962, 1962a) (see also DAFS, 1962a). The relative importance of the recorded food organisms is indicated in Table XIII. They found that the composition of the diet in five areas studied was markedly uniform and that there was very little seasonal variation. It appears that N. norvegicus is, in general, a varied feeder regardless of sex or size, and takes indiscriminately the available food organisms occurring on or just within the sea bottom.

- Volume of food eaten during a given feeding period

There are no data available on the absolute quantity of food ingested by N. norvegicus, although it has been shown that animals kept at 15°C consume 27 percent more food than those kept at an average of 10°C (DAFS, 1972).

3.43 Growth rate

- Moulting; manner and moulting cycle

Moulting in N. norvegicus has been described and figured by Santucci (1932a). It takes place in the normal decapod fashion, with the animal escaping from the old exoskeleton between the carapace and the first abdominal segment. The complete moult takes about 30 minutes.

The changes which occur in the entegument of N. norvegicus during the moulting cycle have been described in detail by Charuau (1973). The study was based on the microscopic examination of the pleopod setae, resulting in the recognition of four stages of development.

- Moult increment

According to Santucci (1932a) the percentage increase in carapace length (females only) on moulting ranged from 0.98 percent to 2.04 percent. Höglund (1942) stated that the increase in total length per moult of N. norvegicus 10-15 cm in total length is on average 4 mm. Using data from

TABLE XIII

N. norvegicus. Percentage occurrence of various food species in fore-guts containing food (from Thomas and Davidson, 1962, 1962a)

Species	%	Species	%	Species	%	Species	%
POLYCHAETA (total)	66	CRUSTACEA (total)	67	MOLLUSCA (total)	64	ECHINODERMATA (total)	50
Errantia (unident.)	6	Ostracoda	15	Solenogastres	1	Ophiuroidea	16
Aphroditidae	1	Philomedes sp.	+	Gastropoda	8	Amphiura sp.	1
Aphrodite aculeata	+	Copepoda	5	Bullomorpha	2	A. chiajei	+
Polynoinae	+	Harpacticoida	5	Turbonilla sp.	+	A. filiformis	1
Sigalioninae	+	Nebalia bipes	+	Scaphandridae	+	Ophiura sp.	1
Nereidae	4	Cumacea	6	Philinidae	1	Echinoidea	28
Nephthydidae	2	Leuconidae	1	Scaphopoda	8	Irregular Urchins	12
Glyceridae	9	Campylaspis costata	+	Lamellibranchia	59	Holothurioidea	+
Goniada sp.	1	Tanaidae	1	Nucula sp.	20	Echinoderm (unident.)	17
G. norvegica	+	Isopoda	1	Pectenidae	+	PISCES	13
G. maculata	1	Cirolana borealis	+	Cyprina islandica	+	FORAMINIFERA	41
Eunicidae	1	Amphipoda	7	Mysella sp.	+	COELENTERATA (Hydroid)	3
Lumbriconereis sp.	1	Ampeliscidae	4	Cardium sp.	3	NEMERTINI	+
Sedentaria (unident.)	30	Phoxocephalidae	+	Veneridae	8	ECHIUROIDEA	+
Spionidae	1	Amphilochidae	+	Abra sp.	18	INSECTA	+
Chlorhaemidae	1	Oedicerotidae	+	Tellinidae	+	PHORONIDEA	1
Ammotrypane aulogaster	5	Lembos longipes	+	Solenidae	+	POLYZOA	3
Capitellidae	+	Caprellidae	+	Corbula gibba	+	PARTICULATE MATTER	68
Oweniidae	5	Mysidae	+	Hiatella sp.	+		
Owenia fusiformis	3	Natant decapoda	5	Mya sp.	+		
Myriochele sp.	2	Processa sp.	+	Cephalopoda	2		
Pectinaria sp.	14	Crangon sp.	3	Unidentified mollusca	+		
Hydroides norvegica	+	Reptant decapoda	21				
Unident. polychaetes	12	Nephrops norvegicus	+				
		Galantheidae	1				
		Porcellana sp.	+				
		Thallassinidae	2				
		Paguridae	+				
		Anapagurus laevis	+				
		Portunus sp.	4				
		Corystes cassivelaunus	+				
		Unidentified crustacea	35				

+ present, but in less than 1 percent of fore-guts examined

animals which had moulted in the sea after tagging, Andersen (1962) found that the percentage increase in carapace length was 5.88-7.14 percent (values recalculated from the total lengths originally quoted).

The percentage increase in carapace length at moulting in males ranges from 4.7 percent to 7.1 percent, and in females from 5.4 percent to 7.8 percent, according to DAFS (1960, 1961a, 1963a, 1964a) and Thomas (1960b, 1965d). Farmer (1973) found that the mean percentage increment ranged from 21.2 percent in the first post-larval instar, to 6.1 percent in large males with a carapace length of 55 mm. Using data obtained from the first three post-larval instars, percentage increase in carapace length was 22.2 percent to 18.2 percent (Hillis, 1972).

Various attempts have been made to obtain data on growth rates using the 'Petersen' method for separating the moults or year groups. Jensen (1962, 1963, 1965, 1965a, 1967) attempted to

separate the moults of N. norvegicus using this method, and suggested that the moult increment for males of total length 100-140 mm was 8-9 mm. Andersen (1962), using the same method, postulated that males of total length 140-170 mm increased in length by about 10 mm at each moult.

According to DAFS (1969c) the moult increments at $7-10^\circ C$ and $15^\circ C$ were similar.

– Moulting frequency and intermoult period

Moulting in N. norvegicus occurs throughout the year, although there are usually periods of peak moulting activity which have been summarized in Table XIV. Peak periods of moulting activity of males are generally less pronounced than those of females.

Barnes and Bagenal (1951) studied the age of epizoic barnacles (Balanus crenatus) on the exoskeleton of N. norvegicus. They found that no barnacles were more than one year old, and

TABLE XIV

Peak periods of moulting activity in N. norvegicus

Authority	Area	Sex	Period
Andersen, 1962	Faeroese waters	males females	Mar.-June –
Thomas, 1960b	Scottish waters	males and females	Mar.-Apr. and July-Nov.
Thomas, 1965	from Scottish waters, but kept in aquaria	males females	July-Nov. Apr.-Aug.
Storrow, 1912, 1913	Northeast England	males females	Feb.-Apr. June-Sep.
O'Riordan, 1960	Irish Sea	males females	June Apr.-Aug.
O'Riordan, 1964	Irish Sea	males and females	Apr.-Sep.
Gibson, 1967	Irish Sea	males females	Aug. and Sep. June-Aug.
Hillis, 1972d	Irish Sea	males females	June-July and Sep. May -June and Sep.
Farmer, 1973	Irish Sea i) in the sea	males females	Feb.-May and Aug. May -July
	ii) in the laboratory	males females	no peak June-Aug.

concluded that all size groups of N. norvegicus moult at least once per year. According to Andersen (1962) about 75 percent of all adult males moult every year. Exceptionally, individuals may live for up to 3 years without moulting, based on the age of an epizoic bivalve (Heteranomia squamula). Thomas (1960b) suggested that mature females moult only once per year, whereas, in general, males moult twice per year, except perhaps the larger specimens (DAFS, 1960). From Hillis (1972b) it would appear that immature specimens moult 4-5 times during their second year: this agrees very closely with the expected number of moults for this period given by Farmer (1973). Details of the number of moults per year for both males and females are given in Table XVa.

According to DAFS (1969c, 1972) growth rates at $15^{\circ}C$ were higher than at $13.5^{\circ}C$ and $7-10^{\circ}C$. It was found that the moult increments were similar at the different temperatures, but that the frequency of moulting had increased. Thomas (1965) found the moult increments of animals maintained in aquaria were successively smaller at subsequent moults. It was suggested that this was due to underfeeding.

According to Thomas (1965) the average intermoult period for N. norvegicus with carapace lengths of 20-55 mm was $6\frac{1}{2}$ months for males and

7 months for females. The previous estimate of the intermoult period by DAFS (1963a) gave an average of about 6 months for both males and females. Hillis (1971a, 1972, 1972b) found that the intermoult period varied from 16-22 days in the first three post-larval stages, to 6-7 months in a mature male.

- Absolute growth pattern

DAFS (1969c) suggested that N. norvegicus with a carapace length of 21.5 mm may be at least 3 years old, based on the moult increments and frequency of moulting observed in the laboratory. Using laboratory growth rates in conjunction with data on the sizes of larvae, it was suggested that N. norvegicus reach 20 mm carapace length in the first 12 months, and reach marketable size (30 mm) in about $3\frac{1}{2}$ years (DAFS, 1972).

Hillis (1971a, 1972a, 1972c, 1972d), using a combination of carapace length/frequency modes, laboratory growth rates (particularly of the early post-larval instars) and measurements from juvenile specimens caught with fine mesh covers fitted to an otter trawl, calculated growth rates for the first three years. The results are summarized in Table XVb. Hillis (1972d) also found that the time of year exerted a marked influence on growth rate, in that moult increment was greatest and the intermoult period shortest during May-June.

TABLE XV

N. norvegicus.

a) Expected mean carapace lengths of males and females from the Irish Sea,
   at yearly intervals from metamorphosis (August until the following July)
and expected numbers of moults required to reach these sizes (after Farmer, 1973)

Year	0	1	2	3	4	5	6	7
Size - males (mm)	3.3	14.0	20.8	25.8	30.4	34.5	38.0	41.5
No. of moults	$4\frac{1/}{}$	10	5	3-4	2-3	2	1-2	1
Size - females (mm)	3.3	14.0	20.8	22.9	25.1	27.3	29.6	31.9
No. of moults	$4\frac{1/}{}$	10	5	1	1	1	1	1

1/ including the pre-zoeal moult

b) Estimates of carapace length of males and immature females from the Irish Sea
   at yearly intervals from metamorphosis (August until the following July)
       (after Hillis, 1971a, 1972a, 1972b, 1972c)

Year	0	1	2	3	4	5
Size (mm)	4	12	19	26	31	36
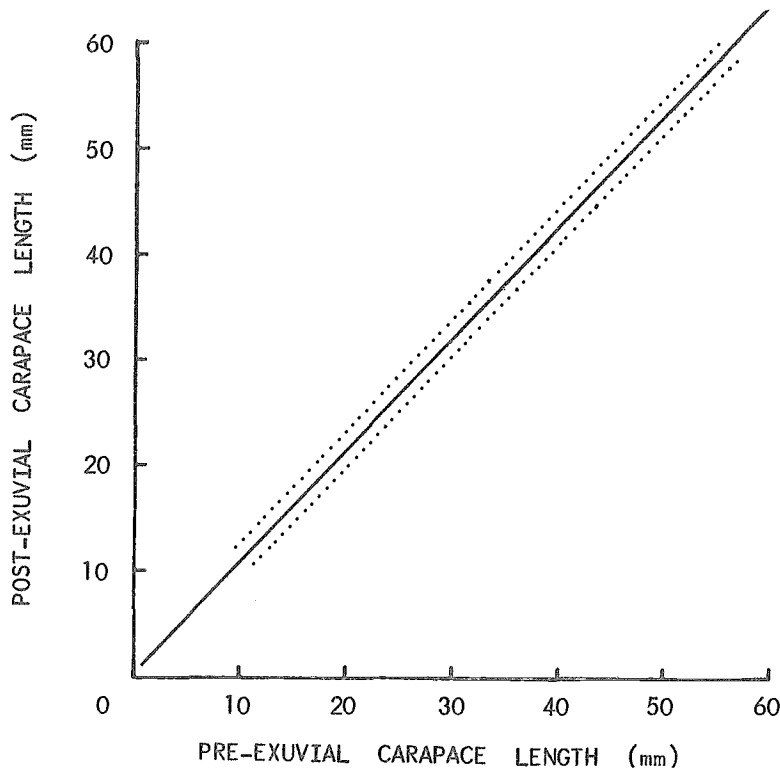
Fig. 15 N. norvegicus. Post-exuvial carapace length plotted against pre-exuvial carapace length; the 95% confidence limits of the regression line $(y = 1.0144x + 0.1848)$ are indicated by dotted lines. (After Farmer, 1973)

Farmer (1973) has produced a composite relationship between post-exuvial and pre-exuvial carapace length from his own data, and that of Andersen (1962) and Thomas (1965): see Fig. 15. Combining these results with carapace length/frequency modes, he calculated the expected mean carapace lengths at yearly intervals and the number of moults expected to occur each year: see Table XVa.

Farmer (1973) was unable to find any useful relationship between carapace length and the number and thickness of the lamellae in the endocuticle of the carapace, and the number of aesthetasc-bearing segments on the exopodite of the antennule – relationships which have in the past been used to obtain data on age and growth in other Crustacea. The relationship between propodus length and carapace length was of little assistance in separating different year-classes of N. norvegicus (Hillis, 1972d).

– Condition factors (Ponderal index)

Poulsen (1946) calculated a coefficient of nutrition. His results are included in sections 1.32 and 3.41.

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

Increased temperature does not appear to affect the moult increment, but does increase the frequency of moulting (DAFS, 1969c, 1972). It has been suggested that the reduction in successive moult increments observed in N. norvegicus maintained in the laboratory are due to underfeeding (Thomas, 1965). The growth rate of mature females is very slow, since they are only able to moult once per year: after the previous batch of eggs has hatched, and before laying the next.

See also section 2.35.

– Relation of growth to population density

No data are available.

– Food/growth relations

No data are available.

3.44 Metabolism

- Metabolic rates

No data are available.

- Respiration

The mechanism of respiration in N. norvegicus has been investigated by Bohn (1901) and Atkinson (1971a). According to Atkinson, both forward and reverse pumping using the scaphognathites were active processes, although Bohn had suggested that current reversals had a physiological effect in resting the muscles of the scaphognathite. The scaphognathite beat is more intense during reverse pumping, although there may be an inactive period following reversal. The purpose of the reversal of the respiratory currents appears primarily to be the removal of mud and other particulate matter from the gills. This behaviour is presumably connected with its burrowing activities in very fine substrates.

The respiration of muscle tissues of N. norvegicus has been studied by Mattisson (1959, 1961, 1961a). The concentration of cytochrome C was found to be highest in the muscles of the walking legs, slightly less in the chelae, and low in the abdominal muscles. Cytochrome activity and oxygen consumption followed the same pattern. The activity of cytochrome oxidase was inhibited by cyanide, azide, antimycin A and malonate, but not by inhibitors of copper enzymes. Activity was increased by methylene blue and succinate (Mattisson, 1961). Although the presence of flavins has been demonstrated, the concentrations are low and suggest that respiration is based on a cytochrome system rather than flavo-proteins.

Carbonic anhydrase has not been found in the blood of N. norvegicus (Goor, 1948; Wolvekamp and Waterman, 1960).

- Endocrine systems and hormones

Carstam (1942) found that extirpation of the eyestalks in N. norvegicus resulted in chromatophore contraction, and that injection of eyestalk extract resulted in re-expansion. However, when embryos were treated with extract, the chromatophores contracted from their normally expanded state.

Extracts of sinus glands, and eyestalks minus sinus glands, from N. norvegicus have been tested by Kleinholz et al. (1962) on Palaemon adspersus for retinal pigment hormone activity. Both extracts were found to produce light-adaptation of the distal retinal pigment.

According to Farmer (1972) the androgenic gland in N. norvegicus does not appear to function in the same way as reported to be the case in Orchestia gammerella and O. cavimana, since both testis and ovary appear to have developed normally in the bilateral gynandromorph described.

Farmer (in press) has suggested that pheromones may be involved during copulation, and may have an inhibitory effect on the normal feeding response of mature males.

- Digestion

The process of digestion in N. norvegicus has been examined by Yonge (1924) (also summarized by Vonk, 1960). The ferment cells of the hepatopancreas furnish the digestive enzymes. Although it was found to be possible to remove starch, coagulate calcified milk, and split butyrin by means of extracts from all parts of the alimentary canal, thus revealing the presence, intracellulary, of amylolytic, proteolytic and lipolytic enzymes, there is no evidence that any extracellular enzyme is produced in any part other than the hepatopancreas.

The secretion is faintly acid. Experiments showed that the enzymes secreted were capable of digesting starch, glycogen, sucrose, maltose and lactose, but not insulin or raffinose. There was no trace of any enzyme able to digest cellulose or hemicelluloses. The optimum temperature for starch digestion appeared to be $57^{\circ}C$, with enzyme destruction occurring at $76-78^{\circ}C$.

The enzymes produced by the hepatopancreas are capable of splitting olive oil and the following esters: methyl acetate, amyl acetate, butyl acetate, and ethyl acetate. A powerful proteolytic enzyme is present which works best in alkaline media.

The brown pigmentation of the hepatopancreas is apparently due to the presence of a lutein. The hepatopancreas acts as a storage organ for glycogen and fat, although cholesterol was not detected.

Absorption of the products and digestion is carried out by the mid-gut and its diverticula and by the absorption cells of the hepatopancreas.

- Osmotic relations

Robertson (1949, 1953, 1957, 1960) has investigated the composition of various body fluids with particular reference to osmotic

TABLE XVI

N. norvegicus. The mean composition of various body fluids and tissues and their osmotic relationships
(after Robertson, 1949, 1953, 1957, 1960, 1961)

	Na	K	Ca	Mg	Cl	SO_4	HCO_3	Lactate	Total* P	Total	Water (g/kg)
	(mmol/kg water)										
Whole muscle	83.2	166.6	5.21	19.1	109.9	3.1	-	-	144.8	532	756
Blood plasma	517	8.6	16.2	10.4	527	18.7	4.13	0.26	0.81	1 103	-
Sea water	457	9.8	10.1	52.2	535	27.5	-	-	-	1 092	986
Muscle cells	24.5	188	3.72	20.3	53.1	1.02	1.90	8.8	164.2	466	-
Ratio: muscle cells/plasma	0.047	21.9	0.23	1.97	0.101	0.055	0.46	33.8	203	0.42	-
Antennal gland secretion (% of plasma values)	98	83	81	130	101	106	-	-	-	-	-
Concentration in plasma as percentage of concentration in plasma dialysed against sea water	113	77	124	17	99	69	-	-	-	-	-

*as trichloroacetic acid-soluble P

TABLE XVII

N. norvegicus. Mean concentrations of components, additional to those in Table XVI, in various body fluids and tissues (after Robertson, 1961)

Component	Plasma	Muscle
Acid-soluble phosphate fractions		
Inorganic phosphate	–	18.3 mmol/kg water
Arginine phosphate	–	71.0 mmol/kg water
Adenosine triphosphate	–	11.6 mmol/kg water
Hexose phosphate, etc.	–	14.4 mmol/kg water
Total phosphate	–	115.2 mmol/kg water
Nigrogenous constituents		
α – amino acids	–	476.0 mmol/kg water
Trimethylamine oxide	–	59.0 mmol/kg water
Betaine	–	65.7 mmol/kg water
Ammonium ions	–	2.9 mmol/kg water
α – amino acids	–	512.0 mmol/kg water
Proline	–	102.0 mmol/kg water
Arginine	–	93.0 mmol/kg water
Glycine, taurine, etc. (by difference)	–	317.0 mmol/kg water
Glutamine	–	28.4 mmol/kg water
Soluble carbohydrates		
Reducing sugar	0.83 mmol/kg water	8.1 mmol/kg water
Lactate	0.26 mmol/kg water	17.7 mmol/kg water

regulation. The results are summarized in Tables XVI and XVII. Active absorption of sodium and calcium ions by the gills takes place against a concentration gradient, whereas potassium, magnesium and sulphate diffuse inwards in accordance with the concentration gradient. Differential excretion by the antennal glands tends to eliminate magnesium and sulphate, whilst conserving sodium, calcium and potassium.

- Composition of body fluids and tissues

Studies on the blood of N. norvegicus have been carried out by Halliburton (1885). However the results were mainly treated collectively with Homarus gammarus, the shore crab (Carcinus maenas) and the freshwater crayfish (Austropotamobius pallipes), which he found to be very similar.

The blood, which is colourless or has a faint reddish tinge, has an opalescent appearance due to the presence of numerous amoeboid cells. The blood of N. norvegicus was found to consist of 89.06 percent water, 10.94 percent solids (4.60 percent proteins, 3.57 percent other organic matter and 2.77 percent salts). It is faintly alkaline and of specific gravity 1.025–1.030. Iron and copper were present, and the organic matter included fatty bodies and a low concentration of urea.

Coagulation begins almost immediately the blood is shed. A network of white fibres forms, entangling the cells. The fibres contract and separate from a clear liquid, which within only minutes sets to a firm light violet jelly, the colour being due to oxidation of the dissolved

haemocyanin. In the few hours the clot extrudes
a clear, light violet, liquid serum. The clot,
which possesses properties very like vertebrate
fibrin, is similarly formed by the precipitation
of existing soluble fibrinogen. This action,
which is caused by an enzyme secreted by the
amoeboid blood cells, can be prevented by the
addition of four parts of a saturated solution of
magnesium sulphate to one part of blood, or by
the addition of saturated sodium chloride solution
in the ratio 9–10:1. Clotting is retarded at
lower temperatures and inhibited at $0°C$.

The haemocyanin dissolved in the blood plasma
performs a respiratory function. Colourless when
deoxygenated and blue when oxygenated, it is
responsible for the colour of the blood when
leaving the gills.

According to Florkin and Blum (1934) (also
quoted by Florkin, 1960) the blood plasma of
N. norvegicus contains 3.33–4.97 g of protein
per 100 ml plasma.

Svedberg and Pedersen (1940) found that the
sedimentation rate of N. norvegicus haemocyanin
was 24.5 cm x 10^{-13}/s/dyn at 20°C.

According to Goor (1948) carbonic anhydrase
is absent from the blood of N. norvegicus.

Details of the composition of muscle in
N. norvegicus are given in Tables XVI and XVII
(Robertson, 1961).

The composition of the integument has been
investigated by Lafon (1941, 1943) and Welinder
(1974). Their results are included in Table XVIII.

Chevaillier (1967, 1967a, 1969) and
Chevaillier and Maillet (1965a) have investigated
the biochemical composition of the developing
spermatozoids and spermatozoa of N. norvegicus.
The nuclei contain DNA, basic proteins and
sulphur compounds. The capsule has a double
structure: an outer layer and an inner one, the
former polysaccharidic in nature, the latter
composed of proteins revealed by their contents
of basic amino acids and sulphur compounds. The
capsule has an apical granule which is also
composed of basic proteins and sulphur containing
amino acids.

– Pigments and vitamins

According to Newbiggin (1897) the pigment
responsible for the characteristic colour of
N. norvegicus may be extracted with boiling
alcohol after decalcification; the subsequent
addition of sodium hydroxide produces an orange-
red precipitate, leaving a clear yellow liquid
containing a yellow pigment. Newbiggin suggested
that the red pigment was a derivative of the
yellow hepatochrome of the hepatopancreas.

The occurrence of astacene (= astaxanthin)
in oil extracts from N. norvegicus was reported
by Burkhardt et al. (1934).

Kuhn and Lederer (1933) and Fabre and Lederer
(1934) found that the pigment astaxanthin ($C_{27}H_{32}O_3$)
was present in the hypodermis and ova of
N. norvegicus, as the esterified and unesterified
forms respectively. This was subsequently confirmed
by Goodwin and Srisukh (1949), who also reported
the presence of a third form of astaxanthin bound
to a protein (ovoverdin) (see also Goodwin, 1960).
The absorption spectrum (λ max) of ovoverdin
dissolved in water was 660 and 476 nm, whereas
that of free and sterified astaxanthin in various
organic solvents was 467–506 nm depending on the
solvent used. Thommen (1967) has discussed the
chemical relationship and synthesis of various
carotenoids including astaxanthin, from β-carotene.

The distribution of vitamin A and β-carotene
in N. norvegicus has been reported by Fisher,
Kon and Thompson (1954), and Fisher and Kon (1959)
see Table XIXa). Astaxanthin and xanthophylls
were also present. There were no marked seasonal
variations in the concentration of vitamin A or
β-carotene throughout the year. 3 percent of the
total vitamin A present in the eyes of light-
adapted animals was in the form of retinene. This
increased to 5 percent in dark-adapted individuals.
The highest concentrations of vitamin A were found
in the eyes, generally in the form of the 11-cis
geometric isomer conjugated with protein. The
β-carotene was mainly confined to the hepato-
pancreas. The origin of the carotenoids is
probably in the food of N. norvegicus.

Vitamin B_{12} has been reported from
N. norvegicus as the analogues, Factor B and
pseudovitamin B_{12} (Cowey, 1956). Its distribution
is given in Table XIXb.

Euler and Euler (1933) have found vitamin C
(=ascorbic acid) in the gonads (22 mg/100 g fresh
tissue) and hepatopancreas (23 mg/100 g), although
Nespor and Wenig (1939) have demonstrated its
presence in crustacea only in the hepatopancreas
and alimentary canal.

Drummond and Hilditch (1930) have reported
extremely low concentrations of vitamin D in
N. norvegicus.

– Trace metals

An investigation of the concentrations of
certain trace metals in N. norvegicus has been
made by Topping (1973). The results are given
in Table XX. Although the data permit only
limited conclusions to be made, it is suggested
that the differences may be attributed more to
natural effects than to man-induced effects.

TABLE XVIII

N. norvegicus

a) The composition of the integument, estimated by different decalcifying agents, as a percentage of the weight of dried cuticle.

Authority	Content of calcium salts			Chitin* (%)	Protein* (%)
	5% nitric acid	0.1 M EDTA	10% TCA		
Lafon, 1941, 1943					
i) dorsal carapace	–	–	) 72.2	77.5	22.5
ii) abdominal segments	–	–	)	76.7	23.7
Welinder, 1974 pronotum	69.6	63.9	69.4	69.8	30.2

* percentage by weight of decalcified dried cuticle. EDTA = ethylenediaminetetra- acetic acid (disodium salt); TCA = trichloroacetic acid

b) The amino acid composition of the cuticle (from Welinder, 1974)

Amino acid	%
Aspartic acid	9.28
Threonine	5.46
Serine	7.84
Glutamic acid	1.37
Proline	8.13
Glycine	2.23
Alanine	9.21
Valine	6.51
Methionine	0.53
Isoleucine	3.53
Leucine	4.26
Tyrosine	7.52
Phenylalanine	4.08
Lysine	2.89
Histidine	3.35
Arginine	3.83
Cystine	0
Cysteic acid	0
Hydroxyproline	0
Hydroxylysine	0
3, 4-Dihydroxyphenylalanine	0

TABLE XIX

N. norvegicus

a) Distribution of oil, vitamin A, β-carotene and total·carotenoids in animals from the Clyde Sea area; range of concentration over 12 months (after Fisher, Kon and Thompson, 1954)

Tissue	Oil (% wet wt.)	Vitamin A (i.u./g)	β-carotene (μg/g oil)	Total carotenoids	
				(μg/g wet wt.)	(μg/g oil)
Whole animal	0.6– 2.0	0.01–0.09	4.7–18	4.3– 8.9	280– 889
Eyes	0.2– 1.5	1.9 –7.7	0	2.6–12	686–5 120
Eye stalks	8.5	0	0	12	137
Hepatopancreas	4.6–29	0–1.2	5.2–19	2.7– 9.6	22– 74
Cardiac fore–gut	0.2– 0.8	0	0	1.2–19	239–5 972
Alimentary canal	0.7	0	0	9.4	1 343

b) Distribution of vitamin B_{12} analogues (after Cowey, 1956)

Tissue	Analogues present	Activity expressed in terms of vitamin B_{12} (μg/g wet wt.)	
		Escherichia coli	Ochromonas malhamensis
Exoskeleton	None	0.03	0.02
Muscle	None	0.03	0.03
Gills	None	0.03	0.02
Alimentary canal and contents	Factor B and pseudovitamin B_{12}	0.08	0.05
Hepatopancreas	Factor B and pseudovitamin B_{12}	0.12	0.11

TABLE XX

Concentration of trace metals in N. norvegicus, homogenate of whole body (from Topping, 1973)

Locality	Metals (mg/kg wet wt.)			
	Copper	Zinc	Cadmium	Lead
North Minch	4.4	10.2	<0.03	<0.2
Anstruther	11.3	12.2	<0.03	0.5
Lossiemouth	4.0	12.2	<0.03	0.5

3.5 Behaviour

3.51 Migrations and local movements

– Extent of movements or migrations

The results of marking and tagging experiments have shown that in general N. norvegicus does not undertake migrations, although local movements may occur.

Storrow (1912, 1913) released 565 males and females which had been marked by punching out part of the telson. Only two recaptures were recorded and these were close to the area of release. According to Höglund (1942) the depth at which the largest catches were taken in the Kattegat was not constant throughout the year. The depth of maximum catch gradually increased from winter to summer and decreased from summer to winter. Höglund suggested that this might indicate that the main body of the population carried out a regular migration from shallow to deeper water during the first half of the year, and in the opposite direction in the latter half of the year.

Andersen (1962) marked several thousand N. norvegicus, by cutting notches in the telson and uropods, and released them in various areas in the Faeroes. 0.71–2.9 percent of the marked animals were recaptured, but no reference was made to any indication of migration.

Tagging experiments in the Skagerrak and Kattegat, using plastic tags usually attached to the tail, have been carried out by Jensen (1962, 1963, 1965, 1965a, 1967). Recaptures ranged between 3 and 11.5 percent. With the exception of a single animal, which was reported by a Danish fisherman 70 miles from the place of release (a record which Jensen discredits), movements averaged about 4 miles, with a range of 0–11 miles. Since the distanced covered by the trawl during fishing in these areas is about 8 miles, Jensen concluded that N. norvegicus does not migrate.

Gibson (1967) (see also DAFD, 1965a) used coloured rubber bands placed over the right cheliped as tags in an area off southwest Ireland. The maximum rate of recapture was 1.1 percent. Gibson did not make any reference to any indication of migration.

According to DAFS (1964a, 1965a) the results of tagging 6 400 N. norvegicus, of which 70 were recaptured, show that the distance between the positions of release and recapture was less than 5 miles, with the single exception of an individual which appeared to have moved 22 miles. The conclusion was that N. norvegicus do not undertake extensive migrations.

The distribution patterns of various size ranges of N. norvegicus off the east coast of Ireland indicate two adjoining populations, each with a definite nursery ground in the shallower part of the area (Hillis, 1972d). This would indicate that juveniles may make a gradual movement to join the main part of the population as they grow older.

3.52 Schooling

Schooling behaviour has not been observed in N. norvegicus.

3.53 Responses to environmental stimuli

– Electro-mechanical stimuli

The morphology and innervation of the proprioceptors of the mouthparts and pereiopods have been covered in section 1.33.

The electro-mechanical properties of the exoskeleton of N. norvegicus have been investigated by Cerquiglini et al. (1967).

– Chemical stimuli

See section 3.13 for the suggestion that a pheronome may be involved in copulation.

Presumably chemical stimuli are involved in the attraction of N. norvegicus to baited creels, and during normal feeding, although there appears to have been no experimental work in relation to this.

– Thermal stimuli

No data are available.

– Light

Large variations in the size of catches of N. norvegicus over relatively short periods of time have frequently been reported by fisherman and more recently substantiated by experimental evidence (see section 4.22 and Table XXI).

According to Andersen (1962) the size and composition of the catches of N. norvegicus vary diurnally in Faeroese waters. Andersen used the theoretical altitude of the sun as a measure of light intensity, and found that the size of the catch as well as the proportion of the large individuals is a function of the light intensity. In daylight he obtained catches of exclusively large animals, whereas at night catches were large and contained mostly the smaller individuals. Farmer (1974b) found some indication that the larger males represented a greater proportion of the catch during those periods of low catches, although the absolute number showed a decrease.

TABLE XXI

N. norvegicus. Times of increased catches and observed periods of emergency from burrows

Authority	Area	Depth (m)	Time of year	Times of increased catches (precise times G.M.T.)
Andersen, 1962	Faeroes	30– 50	July-Aug.	Night
DAFD, 1969	West Irish Sea	20	Aug.–Sep.	Midnight and sunset
DAFD, 1969	West Irish Sea	40	Aug.–Sep.	Sunrise and sunset
DAFD, 1969	West Irish Sea	60	Aug.–Sep.	Midday
DAFD, 1969	West Irish Sea	80	Aug.–Sep.	Sunrise and sunset
DAFD, 1970	West Irish Sea	20– 40	Nov. onward	Sunrise and sunset
DAFD, 1970	West Irish Sea	80–100	Nov. onward	Middle of day
Farmer, 1974d	East Irish Sea	28– 34	Mar.	3/4 h before sunset
Farmer, 1974d	West Irish Sea	75– 90	Feb.	2 h before sunset
Farmer, 1974d	West Irish Sea	75– 90	Mar.	1/4 h after sunrise and 2 h before sunset
Farmer, 1974d	West Irish Sea	75– 90	Mar.	Sunrise
Farmer, 1974d	West Irish Sea	75– 90	May	2 h after sunrise and 2 1/4 h before sunset
Farmer, 1974d	West Irish Sea	75– 90	Aug.	1 1/2 h before sunset
Farmer, 1974d	West Irish Sea	75– 90	Aug.	1 1/2 h after sunrise and 3 1/2 h before sunset
Farmer, 1974d	West Irish Sea	75– 90	Nov.	1/2 h before sunset
Farmer, 1974d	West Irish Sea	75– 90	Dec.	3/4 h after sunrise and 1/4 h before sunset
Fontaine, 1967	Golfe de Gascogne	100	–	Sunrise and sunset
Froglia, 1972	Central Adriatic	200	–	Sunrise and sunset
Gauss–Garády, 1912	Adriatic	>50	–	Night
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	20	Aug.–Sep.	Midnight and sunset
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	40	Aug.–Sep.	Sunrise and sunset
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	60	Aug.–Sep.	Sunrise and midday
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	80	Aug.–Sep.	Sunrise
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	110	Aug.–Sep.	Sunset
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	130	Aug.–Sep.	Midday
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	20	Nov.	61 min before sunrise and 75 min after sunset
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	30	Nov.	29 min before sunrise
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	40	Nov.	17 min before sunrise and 20 min after sunset
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	60	Nov.	42 min after sunrise
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	90	Nov.	113 min after sunrise
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	30	Oct.	60 min before sunset
Hillis, 1971, 1971b, 1972, 1972d	West Irish Sea	60	Dec.	>60 min before sunset

| Authority	Area	Depth (m)	Time of year	Times of increased catches (precise times G.M.T.)
Höglund and Dybern, 1965	Northern Kattegat	58	Jan.	Sunrise and sunset
Höglund and Dybern, 1965	Northern Kattegat	58	Feb.	2½ h before sunset and 2½ h after sunrise
Höglund and Dybern, 1965	Northern Kattegat	58	Mar.	Night
Höglund and Dybern, 1965	Northern Kattegat	58	May	Sunrise and sunset
Höglund and Dybern, 1965	Northern Kattegat	58	June	Sunrise
Höglund and Dybern, 1965	Northern Kattegat	58	Aug.	Night and sunset
Höglund and Dybern, 1965	Northern Kattegat	58	Nov.–Dec.	Sunrise and 1 h before sunset
Höglund and Dybern, 1965	Northern Kattegat	120–135	May	Sunrise and sunset
Höglund and Dybern, 1965	Northern Kattegat	205–220	May	Middle of day
Jensen, 1962, 1963, 1965a	Skagerrak and Kattegat	>70	Summer	Night
Jukić, 1971	Central Adriatic	200	May –Feb.	Sunrise and sunset
Jukić, 1971	Central Adriatic	200	Mar.–Apr.	Middle of day
O'Riordan, 1961, 1961a, 1964	West Irish Sea	27– 58	Sep.	Sunrise and 1½ h before sunset
Simpson, 1962, 1965	West Irish Sea	20– 35	July	04.30 and 21.00
Simpson, 1962, 1965	West Irish Sea	60	Apr.	04.30 and 20.00
Simpson, 1962, 1965	West Irish Sea	60	Sep.	06.00 and 18.00
Simpson, 1962, 1965	North Minch	120–130	Sep.	12.00 to 16.00
Simpson, 1962, 1965	South Minch	145–160	Sep.	08.00 to 18.00
Simpson, 1962, 1965	Northeast England	75	Sep.	05.00 to 17.00
Atkinson, 1972	Laboratory	–	–	Night
Atkinson and Naylor, 1973	Laboratory	–	–	Night
Chapman and Rice, 1971	Loch Torridon	30	June	21.10 to 03.30
Chapman et al., 1972, 1973; Chapman, 1973	Loch Torridon	23	Sep.	Night
Chapman et al., 1972, 1973; Chapman, 1973	Loch Torridon	30	June	Night
Chapman et al., 1972, 1973; Chapman, 1973	Loch Torridon	51	May	½ h before sunrise and 3/4 h after sunset
Chapman et al., 1972, 1973; Chapman, 1973	Loch Torridon	60	Apr.	½ h after sunrise and sunset
Chapman et al., 1972, 1973; Chapman, 1973	Loch Torridon	71	Apr.	1/4 h after sunrise and 3/4 h before sunset
Chapman et al., 1972, 1973; Chapman, 1973	Loch Brollum	42	Apr.	3/4 h before sunrise and 1¾ h after sunset
Chapman et al., 1972, 1973; Chapman, 1973	Loch Carron	93	May	3/4 h after sunrise and 1 1/4 h before sunset
Chapman et al., 1972, 1973; Chapman, 1973	Sound of Jura	103	Apr.–May	2 h after sunrise and 5 h before sunset
DAFS, 1969d	Loch Torridon	30	–	Sunset and sunrise
DAFS, 1972	Loch Torridon	30	Sep.	18.20 to 05.30
DAFS, 1972	Loch Torridon	60– 80	Apr.–May	Daylight
DAFS, 1972	Sound of Jura	60– 80	Apr.–May.	Daylight
Cole, 1967	West coast of Scotland	40	–	Sunset and sunrise
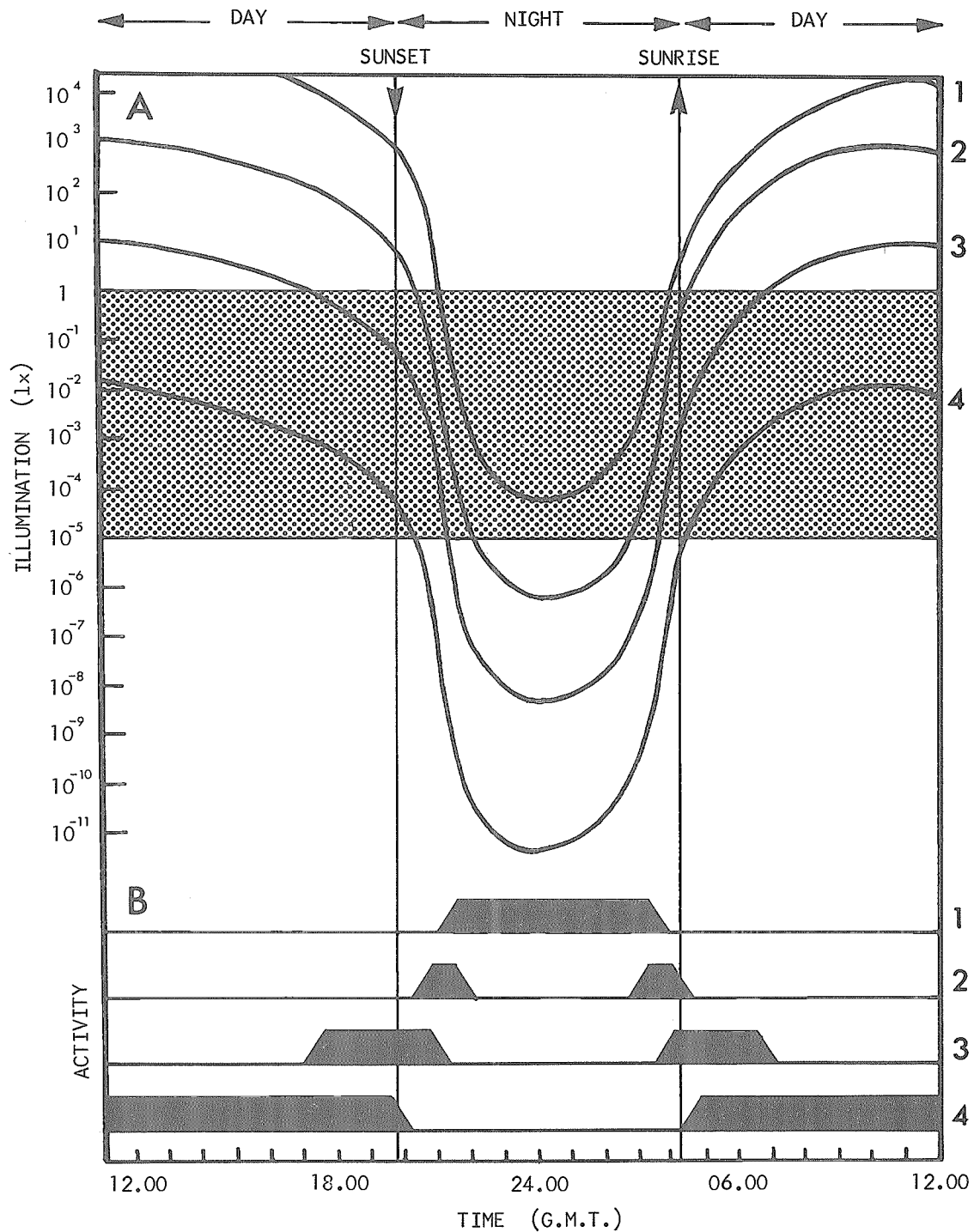
Fig. 16 N. norvegicus. Diagram showing (A) hypothetical illumination curves for
         four depths (1-4), and (B) the periods of activity (1-4) that would be
         expected at these depths on the basis of an optimum illumination concept.
         The optimum range of illumination is shown by the stippled area. (After
         Chapman, Priestley and Robertson, 1972)

More recent work on the effect of light on
N. norvegicus by under-water television camera
and by diving has confirmed that the changes in
the size of catches reflect the diurnal behaviour
pattern of the animals (Cole, 1967; DAFS, 1964a,
1969d, 1972; Chapman, 1973; Chapman et al., 1968,
1970, 1972, 1973; Chapman and Rice, 1971).
Observations on diurnal activity at different
depths have shown that in shallow water (30 m)
animals are active during the middle of the night,
whereas in deeper water (40-90 m) there are two
periods of activity which tend to move further
apart (from midnight) with increasing depth
(Chapman, Priestley and Robertson, 1972; Chapman,
1973; Hillis, 1971b, 1972d). It has been
suggested that in very deep water N. norvegicus
is active during the middle of the day. Measure-
ments of light intensity at the seabed have shown
that animals only become active when the light
intensity is within the range 1 to 10^{-5} lx (day-
time levels of illumination may reach 10^4 to
10^5 lx at sealevel in the Irish Sea). It has
therefore been suggested that the periods of
activity are related to absolute light intensity
(see Fig. 16). According to Chapman (pers. comm.),
it has been found since these light measurements
were taken, that the spectral sensitivity of the
meter was imperfectly matched to the eye of
N. norvegicus (see Loew, 1974). Therefore the
absolute units given by Chapman, Priestley and
Robertson (1972), Chapman (1973) and Hillis
(1971b, 1972d) are inaccurate, although the
general principle whereby the times of emergence
of the animals at different depths are related to
the levels of illumination, is still valid.

Chapman and Rice (1971) (see also DAFS, 1972)
have observed that animals are present in the
burrow entrance most frequently before and after
foraging - Fig. 17.

Atkinson (1971) and Atkinson and Naylor
(1973) have demonstrated a persistent endogenous
rhythm in male N. norvegicus after entrainment
to a 12 h:12 h light/dark cycle. It is suggested
that this is related to its fossorial mode of
life. Such a rhythm allows the animal to return
to its burrow after foraging, before the onset of
unfavourable conditions. It may also conserve
energy, in restricting activity to particular
times of day or permit animals to remain in their
burrows for one or more cycles without constant
reference to environmental variables at the sur-
face. Attempts to entrain ovigerous females to
a 12 h:12 h light/dark cycle were unsuccessful,
although a rhythm was entrained in the only non-
ovigerous female available. This observation may
be significant in that ovigerous females are
usually rare in trawl catches, since they probably
remain in their burrows and do not emerge to feed
(see sections 3.16 and 3.41).

- Lunar cycle

According to fishermen, catches of
N. norvegicus are higher during neap tides and
slack water than during spring tides or at the
height of the ebb or flood (Storrow, 1912;
Thomas, 1960). Storrow (1912) found that there
was a certain amount of correlation between the
two, particularly during the months of March to
July, although in August the highest catches
were obtained during the spring tides. Hillis
(1971, 1972d) has reported that at depths of
80-120 m, catches are influenced by tidal
currents, with catches being lowest during
spring tides (see also DAFD, 1969).

- Miscellaneous

Farmer (1972a) reported that a single
specimen of N. norvegicus produced a loud noise
intermittently for about 2 minutes, by grinding
the molar processes of the mandibles together.
This occurred on the deck of the ship immediately
after hauling the net.

3.54 Responses to artificial stimuli

- Electrical stimuli

Atwood (1963) has demonstrated the presence
of both 'fast' and 'slow' motor axons in the
first and second pairs of walking legs of
N. norvegicus. Most of the proximal muscle
fibres showed large 'fast' post-synaptic poten-
tials in response to single stimuli, but very
small 'slow' responses at any frequency of
stimulation. Single stimuli applied to the
'fast' axon produced a small twitch response of
the muscle. Tension was developed when fre-
quencies of 30 Hz were applied to the 'slow'
axon. It was estimated that the membrane poten-
tial threshold for tension development induced
by potassium chloride depolarization was 58 mV.

The reactions to electric fields of
N. norvegicus living in burrows in the laboratory
have been investigated by Stewart (1971). Using
electrodes placed near the burrow entrances and
applying pulses of various types (either square
or expotential) it was found that animals could
be forced out of the burrows. Electrical fields
of 8 V/ft (26.24 V m^{-1}) were insufficient to
make the animals emerge quickly, but at higher
voltages a significant number emerged in 5 s
or less. Results using a beam trawl with two
codends (only one side electrified at any one
time) have been encouraging. Work on the
development of an electrified otter trawl for
N. norvegicus is currently being carried out
at Aberdeen, U.K. (Stewart, 1973, 1974).

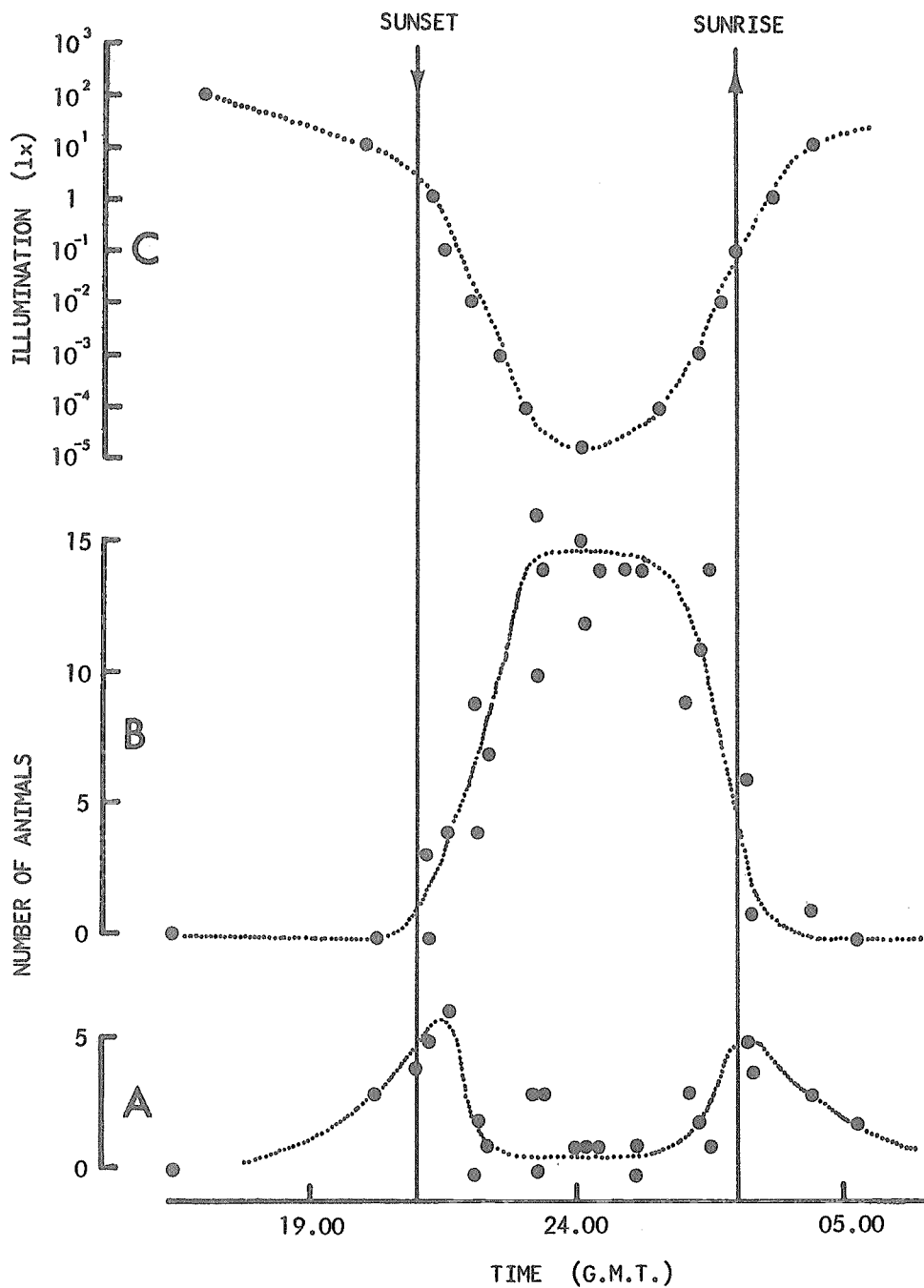Fig. 17 N. norvegicus. Counts of animals observed by diving in Loch Torridon (depth 30 m)
between 16.00 and 06.00 h G.M.T. during the period 12-19 June 1970. (A) animals
emerging from their burrows; (B) animals foraging away from their burrows;
(C) illumination on the seabed. Vertical lines marked by arrows indicate times
of sunset and sunrise. (From Chapman, Priestly and Robertson, 1972; Chapman and
Rice, 1971)

3.55 Burrows and burrowing behaviour

- General features

According to Höglund (1942) N. norvegicus has the ability to construct burrows in suitable mud in the laboratory, and therefore undoubtedly makes use of this under natural conditions also. This view was reiterated by Poulsen (1946). Barnes and Bagenal (1951) have shown that juvenile N. norvegicus will also construct burrows in the laboratory. Thomas (1960b) found that N. norvegicus did not produce burrows in the laboratory, but merely dug slight depressions. He suggested that this may have been due to changes in the characteristics of the mud incurred during collection. It was not until a series of photographs from the Fladen ground in the North Sea were published (DAFS, 1964b) that it was established that the animals inhabited burrows in their natural habitat.

Dybern (1965) and Dybern and Höisaeter (1965) have since carried out diving investigations in conjunction with laboratory experiments. It was found that, in general, burrows had two openings, and that they occurred in groups of 5-10, with each group well separated from the next. The dimensions of the burrows were proportional to the sizes of the animals inhabiting them. It was suggested that the rear opening of the burrow was to facilitate the flow of water through the tunnel.

Other records of burrows in the natural habitat include those of Cole (1967); DAFS (1968b, 1969a, 1969b, 1969d); Chapman, Kinnear and Dalgarno (1968) and Hillis (1972d).

Chapman and Rice (1971) have carried out observations of the burrows of N. norvegicus in Loch Torridon (Scotland), by diving and with the use of underwater television. The use of tags has shown that there is a somewhat loose attachment of individuals to particular burrows. The burrows were not evenly spaced throughout the area examined, nor were they distributed at random. The burrows were shown to be clumped to some extent, although there was no indication of the discrete groupings observed by Dybern and Höisaeter (1965).

According to Atkinson (1974) the spatial distribution of N. norvegicus burrows in Loch Aline is random.

- Details of construction

According to Dybern (1965) and Farmer (1974a) males and females (including ovigerous females) construct similar burrows. However Rice and Chapman (1971) suggested that females may always construct burrows with at least two openings, since only males were found in tunnels with a single opening. Farmer (1974a) found that large males did not burrow, but produced shallow depressions in suitable mud in the laboratory.

The method of burrow construction has been described by Dybern (1965), Rice and Chapman (1971) and Farmer (1974a). Initially a small depression is produced in the mud by loosening the surface with the chelae of the second and third pairs of pereiopods; the loose mud is gathered together by means of the third maxillipeds and the second and third pereiopods, together forming the sides and bottom of a 'basket', and pushed to one side. Continued digging produces an oval depression with a mound of mud in front of it. The chelae of the first pereiopods are then used to break up the mud at the bottom of the depression opposite the mound. Sometimes the animal lies on its side to be in a better position to use its chelipeds. Loose mud is dragged slightly away from the working surface. The animal then turns round and pushes the mud out of the depression onto the mound with the third maxillipeds and second and third pereiopods. Digging is continued downward at an angle until an entrance is formed. The shape of the tunnel is produced by the animal lying on its back or side and cutting at the surface of the mud with the small chelae of the second and third pereiopods. After continuing to burrow more or less horizontally for a short distance the tunnel is brought up to the surface at a steep angle (often nearly $90°$) until it just breaks the surface to form the rear opening. Loose material in the burrow is removed with a strong water current produced by the pleopods.

An additional side tunnel may be constructed, to form a T-shaped burrow. More complex types of burrows may be the result of additional side tunnels, where parts of the original burrow have collapsed. Rice and Chapman (1971) have illustrated various types of burrows formed in the natural environment. See Fig. 18 for photographs of burrow casts.

Atkinson (1974) has described a complex type of burrow which appears to have been occupied by N. norvegicus, Goneplax rhomboides and the goby, Leseurigobius friesii.

According to Crnković (1968) the early post-larval instars of N. norvegicus produce burrows of the same type. One specimen constructed a burrow with 5 openings in 5 days.

- Density

Chapman and Rice (1971) found that the density of burrows in Loch Torridon was $1/2.1$ m^2 in 1968 and $1/1.4$ m^2 in 1969. Densities of N. norvegicus were $1/7.8$ m^2 and $1/5.5$ m^2 respectively. About 70 percent of the large burrows were found to be occupied by N. norvegicus; many of the smaller burrows contained L. friesii.

Densities of burrows in the Sound of Jura, reported by Chapman, Priestley and Robertson (1973), were estimated at about $10/m^2$. Two
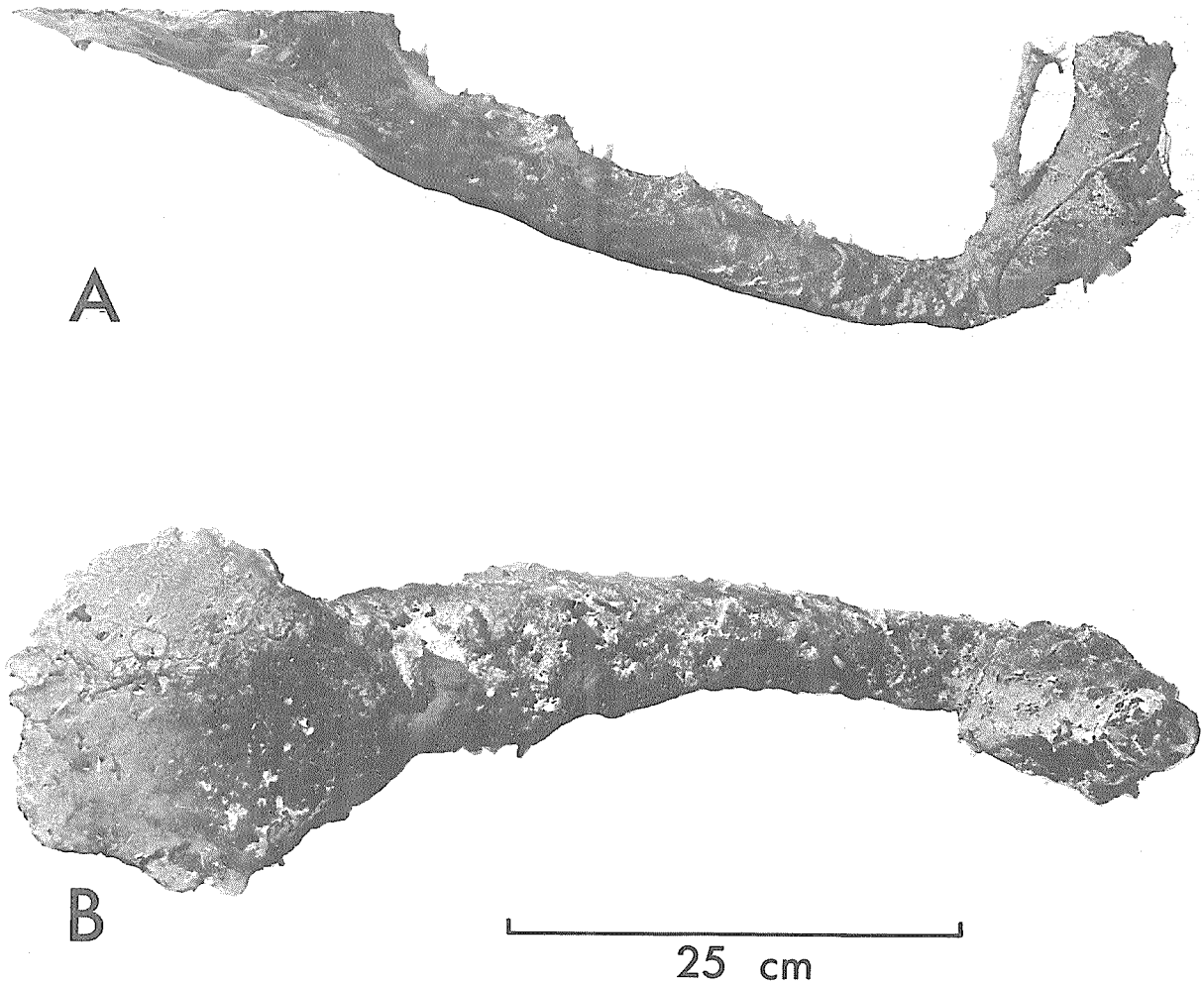
Fig. 18 _N. norvegicus._ Polyester resin cast of a burrow with one entrance and smaller
        rear opening. (A) side view; (B) view from above. (From Rice and Chapman, 1971,
        reproduced by kind permission of the Editors of "Marine Biology".)

types of burrow were distinguised _viz._ (i) small
circular openings on the surface leading into
vertical.shafts formed U-shaped chambers, and
(ii) horizontal tunnels with much larger openings.
The former were occupied by the thalassinid
Calocaris macandreae, and the latter by
N. norvegicus. It was estimated that the density
of the animals was about $3-5/m^2$ of each species.
Densities of burrows reported by DAFS (1966a,
1968b) ranged from $9/m^2$ to $12/m^2$, although
according to Chapman (pers. comm.) these figures
refer to numbers of openings and not burrow
systems.

Estimates of burrow densities in the Irish Sea
have been carried out by Hillis (1972d). The
density of burrows was found to range from
1 burrow/2.1 m^2 to 1 burrow/9.3 m^2. The equi-
valent densities of _N. norvegicus_ ranged from
$1/2.5$ m^2 to $1/8.9$ m^2.

– Associated behaviour

The diurnal behaviour pattern of _N. norvegicus_
has been summarized in section 3.53. In addition
to the foraging behaviour away from the burrow,
there are periods of activity in the burrow
entrance, both slightly before and after the main
period of foraging (Chapman and Rice, 1971; DAFS,
1972); see Fig. 17. A photograph of _N. norvegicus_
in the vicinity of the burrow entrance is shown
in Fig. 19.

Barnes and Bagenal (1951) examined the
distribution of the barnacle _Balanus crenatus_ on
the integument, particularly of the claws, of
N. norvegicus. It was found that the smaller
individuals carried no barnacles at all, whereas
relatively large numbers of barnacles were present
on some of the larger animals. The highest levels
of infestation were on the carpopodites, propodites
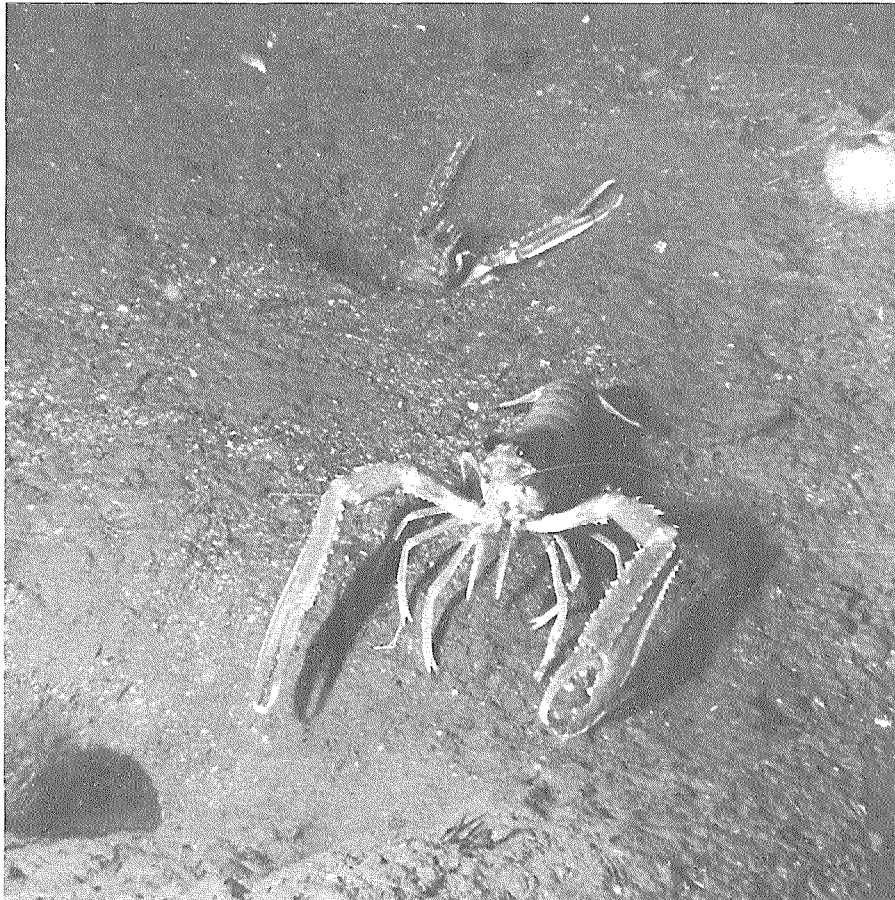
Fig. 19   Photograph of large burrow occupied by two _N. norvegicus_ which have emerged in response
to the presence of the diver (from Chapman and Rice, 1971, reproduced by kind permission
of the Editors of "Marine Biology")

and dactylopodites of the first pair of pereiopods.
Furthermore, the great majority of barnacles were
present on the upper surfaces of the chelipeds.
It was therefore suggested that the larger indi-
viduals spend more time in the entrances to the
burrows, where larval settlement of barnacles
could occur. This agrees with the observations
of Chapman and Rice (1971) and Mundey (1968),
that usually only large males were observed during
the day in the burrow entrances, whereas the small
animals (including most of the females) remained
completely hidden. Presumably the larger males
are less vulnerable to predation than the smaller
individuals in the population, which is possibly
illustrated by their readiness to leave their
burrows during daylight to investigate distur-
bances (Chapman, pers. comm.). This would explain
the reports of Andersen (1962) and Farmer (1974b)
that during periods of low catches large males
represent a larger proportion of the total catch,
since these animals are more likely to be caught
in a trawl. It may also be related to the obser-
vation that large males did not produce burrows
under laboratory conditions, but merely shallow
depressions, suggesting that they are less burrow-
dependent (Farmer, 1974a), although a more likely
explanation is that the laboratory conditions were
not ideal and the resulting behaviour not typical
of that occurring in the natural environment
(Chapman, pers. comm.).

Fighting behaviour in N. norvegicus has been
noted by DAFS (1968b); Chapman, Kinnear and
Dalgarno (1968); Chapman and Rice (1971) and
Farmer (1974a). Farmer has suggested that
N. norvegicus is strongly territorial (based on
laboratory observations) and that there is a
critical distance at which agonistic responses to
other N. norvegicus occur. The aggressive
behaviour takes the form of a very stylized
lateral merus display, with clashing of the cheli-
peds if neither contestant retreats. According
to Rice and Chapman (1971) there was little
indication that the burrows act as centres for
territorial behaviour. Claw damage, indicative
of fighting, has been observed in a high propor-
tion of animals in Loch Torridon (males 62 percent,
females 41 percent), suggesting that fighting
between individuals is common in the natural
environment (Chapman and Rice, 1971).

4   POPULATION

   4.1 Structure

      4.11 Sex ratio

   - Sex ratio of the population

   No data are available.

   - Sex ratio of the catch

   Details of the sex ratio in catches of
N. norvegicus have been reported by: Andersen
(1962); Barnes and Bagenal (1951); DAFD (1965);
Farmer (1972a); Faure (1965); Figueiredo and
Barraca (1963); Figueiredo and Thomas (1965,
1967); Fontaine and Warluzel (1969); Froglia
(1972); Gibson (1967); Hillis (1972d); Jensen
(1962); Jukić (1971); Karlovac (1953, 1955);
Lüling (1951a, 1952); McIntosh (1904, 1908, 1911);
Matta (1959); O'Riordan (1960a, 1964); Storrow
(1912, 1913); Symonds (1972a); Thomas (1954,
1960a, 1969); Thomas and Figueiredo (1964, 1965)
and Vives and Suau (1963).

   In general the males outnumber the females,
although the percentage of males may range from
96 percent to 31 percent - see Table VIII.

      - Variations of ratios with size, age and
        season

   Although the overall proportion of males in
the catches is generally higher, the proportion
of females usually increases as the size of the
animals decreases, until, in the case of the
smallest animals the females outnumber the males
(Andersen, 1962; Figueiredo and Barraca, 1963;
Karlovac, 1953; Matta, 1959; Thomas, 1954, 1960a;
Thomas and Figueiredo, 1964, 1965; Vives and
Suau, 1963). This is shown in Fig. 20.

   Andersen (1962) has attributed the variation
in the proportion of the females to the difference
in the frequency of moulting in males and females
(mature females are only able to moult once per
year, whereas males and immature females moult
more frequently - see section 3.43). According to
Figueiredo and Thomas (1967) the reduced growth
rate of females, compared with that of males,
results in a higher percentage of females in the
length classes just before the onset of the
diminished growth rate, followed by a falling
off in the proportion of females to males in the
larger size classes.

   The proportion of females in the catches has
been found to vary according to the time of year
(Table VIII). There is a general tendency for
the percentage of females to increase during the
period between egg-hatching and egg-laying (see
section 3.16). At this time the large proportion
of females which would otherwise be carrying eggs
are available for capture by fishing gear
(Storrow, 1912; Thomas and Figueiredo, 1964,
1965). Normally the catches of females are
reduced, because the berried females remain
within their burrows. This is substantiated by
Dunthorn (1967) who showed that under laboratory
conditions berried females eat less than non-
berried females, particularly during the latter
stages of embryonic development, and that in the
natural environment they may not feed at all.
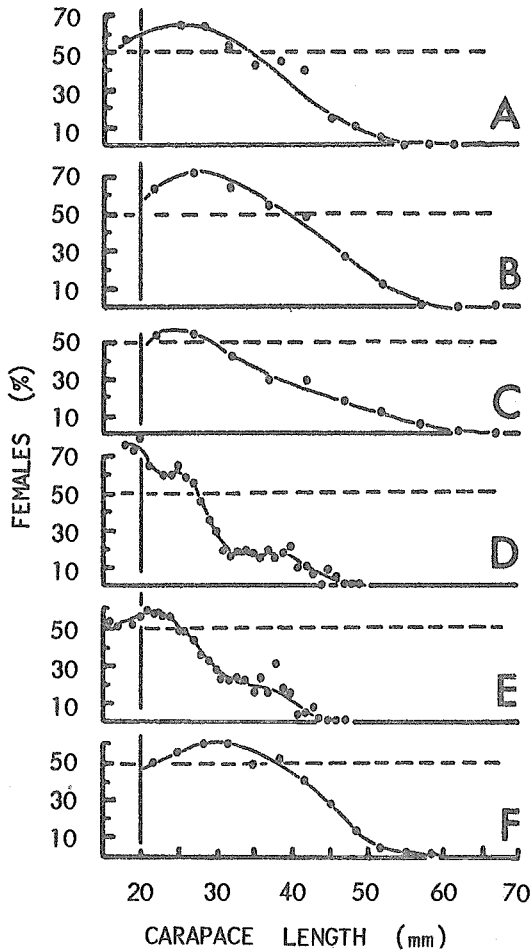
Fig. 20 N. norvegicus. The percentage of
females in the total catch, according
to size in different areas and seasons.
(A) High Adriatic, September 1949;
(B) West Portugal, June 1961-1964;
(C) West Portugal, October 1959-1964;
(D) Moray Firth, July 1963;
(E) Moray Firth, September/October 1963;
(F) Faeroes, July-August 1937-1939.
(After Figueiredo and Thomas, 1967)
Sexual maturity in females is marked
by the solid vertical line (Farmer,
in press)

– Sex ratio on the spawning grounds

There are no data available, as the spawning
grounds correspond to the normal geographical
distribution of the species.

4.12 Age composition

– Age composition of the population as a
whole

No data are available.

– Age distribution of the catch

Both Hillis (1972d) and Farmer (1972a) have
reported modal and mean carapace lengths for
N. norvegicus of different year-classes; see
section 3.43. However, neither author has
separated the samples into age groups, although
Hillis has attempted to correlate modes in size-
frequency distributions with tentative year-
classes.

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

No data are available.

– Age at first capture

Hillis (1972a, 1972d) and Farmer (1972a,
in press c) have reported catches of the earliest
post-larval instars using various types of
fishing gear with small meshes; see section 4.13.
These stages are 1-2 months old. Using commercial
fishing gear, the age at first capture is about
2 years.

– Age at maturity

Both Hillis (1972d) and Farmer (1973) have
reported mean carapace lengths for N. norvegicus
at yearly intervals. From these data it would
appear that sexual maturity in males is reached
when about 3 years old, and in females when
about 2 years old. See also section 3.12.

– Maximum age

No data are available.

– Density of age groups

No data are available.

4.13 Size composition

– Length composition of the populations
as a whole

Length frequency distributions for
N. norvegicus from different areas have been
reported as follows: Faeroes – Andersen (1962);
Skagerrak and Kattegat – Dybern (1967), Jensen
(1959, 1962, 1965, 1965a, 1967), Poulsen (1946);
Scottish waters – Barnes and Bagenal (1951),
Cole (1962, 1965), DAFS (1965a, 1966a, 1967a,
1968a), Faure (1965), McIntosh (1908), Thomas
(1954, 1960a, 1965b, 1969), Thomas and Figueiredo
(1964, 1968); North Sea – Cole (1962, 1965),
Leloup (1958, 1959), Storrow (1912, 1913),
Symonds (1972a); Irish Sea – Cole (1962, 1965),
Farmer (1973), Faure (1965), Gibson (1967),
Hillis (1971a, 1972, 1972a, 1972c), O'Riordan
(1961, 1962a, 1964, 1965); Golfe de Gascogne –
Faure (1965), Fontaine (1967), Fontaine and
Warluzel (1969); west coast of Portugal –

FREQUENCY (%)

Jan. (2174)

Feb. (2219)

Mar. (2156)

Apr. (2397)

May (758)

Jun. (634)

Jul. (519)

Aug. (1162)

Sep. (869)

Oct. (3374)

Nov. (3519)

Dec. (1800)

<23 23 28 33 38 43 48 53 58 63 68 73+

CARAPACE LENGTH (5 mm groups)
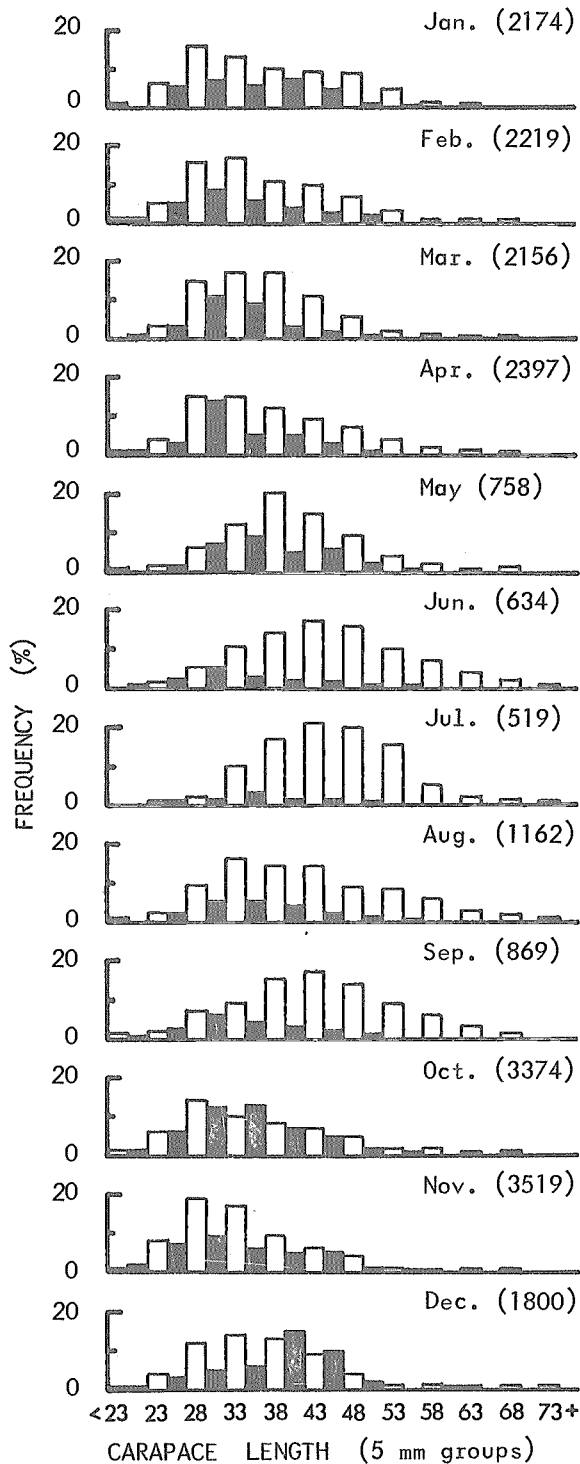
Fig. 21 N. norvegicus. Percentage carapace
length compositions of males and females
in laboratory samples, mean monthly
values from northeast England for 1962-
1968 inclusive. Figures in parentheses
are monthly totals of animals measured.
(After Symonds, 1972a)

Figueiredo and Barraca (1963); east coast of
Spain - Vives and Suau (1963); Tyrrenhian Sea -
Matta (1959); Adriatic Sea - Jukic (1971),
Karlovac (1953, 1955, 1955a).

As an example, the results of Symonds (1972a)
for the population of N. norvegicus off the coast
of northeast England, have been included in
Fig. 21.

- Length composition of the catch for each
  age group over the whole range of
  distribution of the species

Since carapace length/frequency distributions
for N. norvegicus do not show clear year-classes,
and since it is not possible to determine accu-
rately the age of a specific individual, the
length composition of the catch for each group
cannot be determined. See section 3.43. Mean
sizes of both males and females from different
areas are given in Table XI.

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

Variations in the length composition of
catches are generally small (Fig. 21). Farmer
(1973) and Hillis (1971a, 1972a, 1972c, 1972d)
used the movement of modes in length/frequency
distributions throughout the year in combination
with other data to obtain estimates of growth
rates. See section 3.43.

- Size at first capture

Hillis (1972a, 1972d) and Farmer (1972a, in
press c) have reported catches of the earliest
post-larval instars using various types of fine-
mesh fishing gear. The earliest post-larval
stages obtained in this way have a carapace
length of approximately 4 mm. However, the
smallest individuals normally captured using
commercial fishing gear have a carapace length
of about 20 mm.

- Size at maturity

Size at maturity is covered in section 3.12.

- Maximum size

The maximum recorded sizes of male and
female N. norvegicus from different areas are
given in Table XI.

- Density of size groups

No data are available.

- Length and weight relationship

The relationship between total wet weight
and carapace length has been covered in section
1.32.

4.2 Abundance and density (of population)

4.21 Average abundance

- Estimation of population size

Andersen (1962) estimated the size of N. norvegicus populations in the Faeroes by catch per unit effort and by marking. The estimated size of the habitat in each case was measured in trawling hours. Results from both marking and catch per unit effort were comparable, and ranged from 172 kg/h to 505 kg/h. The total population of large individuals varied from 9.25 tons to 88 tons in habitats of 134-435 trawling hours respectively.

Gibson (1967) used tagged N. norvegicus in an attempt to estimate the size of populations in the Irish Sea. From his recapture rates, Gibson estimated that the minimum density of N. norvegicus was 406 000/km^2, of which about 75 percent were of a commercial size.

4.22 Changes in abundance

- Changes caused by environmental conditions, food competition, predation, fluctuations and fishing

Large-scale variations in the number of N. norvegicus caught whilst fishing over relatively short periods have been frequently reported by fishermen. These observations have been confirmed by experimental investigations, which are summarized in Table XXI. It is generally accepted that the diurnal fluctuations in catches of N. norvegicus are related to the foraging behaviour of the animals during periods of optimum illumination - see section 3.53. For changes in commercial catches see section 5.43.

4.23 Average density

- Mean density

Details of the density of N. norvegicus burrows are given in section 3.55.

It has been estimated that, assuming each burrow represents one animal, only 0.5 percent of all N. norvegicus occurring in the path of the trawl were captured (DAFS, 1966a).

- Density of adult females

No data are available.

4.24 Changes in density

- Landings per unit of fishing effort

See section 5.41.

- Variations with depth

From the limited data available it appears that the density of N. norvegicus burrows increases with depth (Chapman and Rice, 1971; Chapman, Priestley and Robertson, 1973; DAFS, 1966a, 1968b; Hillis, 1972d). The recorded densities are: at 30 m - 1 burrow/2.1 m^2 to 1 burrow/1.4 m^2 (Loch Torridon); 1 burrow/9.3 m^2 to 1 burrow/2.1 m^2 (Irish Sea); at 110 m - 10 burrows/m^2 (Sound of Jura).

- Seasonal variations in available stock

See sections 3.16, 3.53 and 4.11.

4.3 Natality and recruitment

4.31 Reproduction rates

- Annual egg production rates

For details of fecundity see section 3.15.

- Survival rates (eggs, larvae)

According to Figueiredo and Nunes (1965) about 10 percent of the total number of eggs carried on the pleopods are lost per month during incubation, and not all the eggs attach to the pleopods during egg-laying.

No data are available on the survival rates of the larvae in the sea.

- Forecasting of potential yields

No data are available.

4.33 Recruitment

- Seasonal pattern of recruitment

Recruitment in N. norvegicus is annual, since there is only one brood of eggs per year. Recruitment into the fishable stock (carapace length 20 mm) takes place when the animals are 2-3 years old. The main period of recruitment to the fishable stock in the Irish Sea occurs in July to November (Farmer, MS).

4.6 The population in the community and the ecosystem

- Physical features of the biotope of the community

N. norvegicus inhabits areas of mud on the continental shelves of the northeastern Atlantic, and in the Mediterranean Sea. It is now generally accepted that the most important single factor determining the distribution of this species is the availability of a suitable substrate (see section 2.3 in general, and section 2.34 in particular).

N. norvegicus is a boreal species

- Species compositions of the community and
  relative sizes of their populations

Reports on the species composition of the
community are generally incomplete, since the
collecting gear used does not usually sample the
infauna adequately. Species associated with
N. norvegicus have been reported from the
following areas: Scottish waters – Chapman and
Rice (1971), DAFS (1969e, 1972b), Mundey (1968),
Rice and Chapman (1971); Irish Sea – Farmer
(1972a); Golfe de Gascogne – Fontaine (1967),
Fontaine and Warluzel (1969), Lagardère (1973);
Balearic Islands – Massuti (1971); Adriatic Sea –
Alfirević, Crnković and Gamulin-Brida (1969),
Gamulin-Brida (1965, 1968), Zupanovic (1968);
Mediterranean Sea in general – Brunelli (1947).

The major species of the N. norvegicus
community found in Scottish waters and the
Irish Sea are: Polychaeta – Nephtys incisa,
Glycera rouxi, Pectinaria koreni, Prionospio
malmgreni, Magelona sp.; Crustacea – Pandalus
montagui, Dichelopandalus bonnieri, Crangon
allmanni, Calocaris macandreae, Anapagurus laevis,
Goneplax rhomboides (in some areas); Mollusca –
Turritella communis, Aporrhais pes-pelicani,
Nucula spp., Abra spp.; Echinodermata –
Brissopsis lyrifera; Pisces – Lesueurigobius
friesii, Buenia jeffreysii. Densities of
1 300-2 000 animals/m^2 (macrofauna retained on a
0.5 mm mesh) have been recorded from N. norvegicus
grounds. Meiofauna studies have indicated popu-
lations in excess of 3 000 000/m^2 in some samples.
The overall biomass varied from 10.5 to 20.0 g/m^2
(wet weight) throughout the year (DAFS, 1972b).

The most important species of decapods found
in association with N. norvegicus in the Golfe
de Gascogne are: Sergestes articus, Solenocera
membranacea, Pasiphaea sivado, Dichelopandalus
bonnieri, Processa mediterranea, Philocheras
echinulatus, and Polycheles typhlops (Lagadère,
1973). Other important species recorded from
N. norvegicus grounds include: Munida rugosa,
Crangon allmanni, Alpheus glaber, Macropipus
tuberculatus, Polybius henslowi, Macropodia
tenuirostris, and Goneplax rhomboides (Fontaine
and Warluzel, 1969). Largely similar species
have been reported in association with
N. norvegicus in the Balearic Islands (Massuti,
1971). Aristeomorpha foliacea, Aristeus
antennatus, Parapenaeus longirostris, and
Plesionika spp. were found to be important.

The N. norvegicus community in the Adriatic
Sea is characterized by two species of algae viz.
Laminaria rodriguezii and Halarachnium spathulatum
fo. luxuriens, the octocoral Funiculina
quadrangularis and the sponge Thenea muricata
(Gamulin-Brida, 1965, 1968; Zupanovic, 1968). In
some localities F. quadrangularis is replaced by
Virgularia mirabilis. Other common species are:
Turritella communis, Pennatula phosphorea, Dorippe
lanata, and Cardium paucicostatum.

Numerous species of demersal fish, not
included above, are important predators on
N. norvegicus (see section 3.34). The food
species of N. norvegicus have been covered in
section 3.42.

5   EXPLOITATION

    5.1   Fishing equipment

        5.11   Gears

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

The most common gear used in the fishery
for N. norvegicus is a prawn trawl (the legal
limits on mesh sizes for this species are
covered in section 6.12).

The gear used off the northeast coast of
England is an otter trawl with a light groundrope
(= footrope) of 35-38 m, and headrope of
31.3-36.3 m. The mesh sizes are normally 70 mm
throughout the net, although in a few cases
larger mesh may be used in the wings (Symonds,
1971, 1972a).

In the Skagerrak and Kattegat the mesh size
for the codend of prawn trawls is normally
50-70 mm (Aker and Tiews, 1965; Figueiredo and
Thomas, 1967), although in Norwegian waters mesh
sizes of 30-36 mm are used (Thomas, 1970).

Prawn trawls used for N. norvegicus fishing
in Scottish waters have a mesh size of 70 mm
throughout (Fig. 22). The most usual size of
net has a headrope of about 27 m and a footrope
of 31 m (Figueiredo and Thomas, 1967; Thomas,
1970).

According to Thomas (1970) the mesh size of
nets used in the Irish fishery is about 50 mm or
less.

The N. norvegicus trawl used in Icelandic
waters has long wings and wire footrope. The
average length of the headrope is 41 m, and the
minimum mesh size is 80 mm (Thomas, 1970).
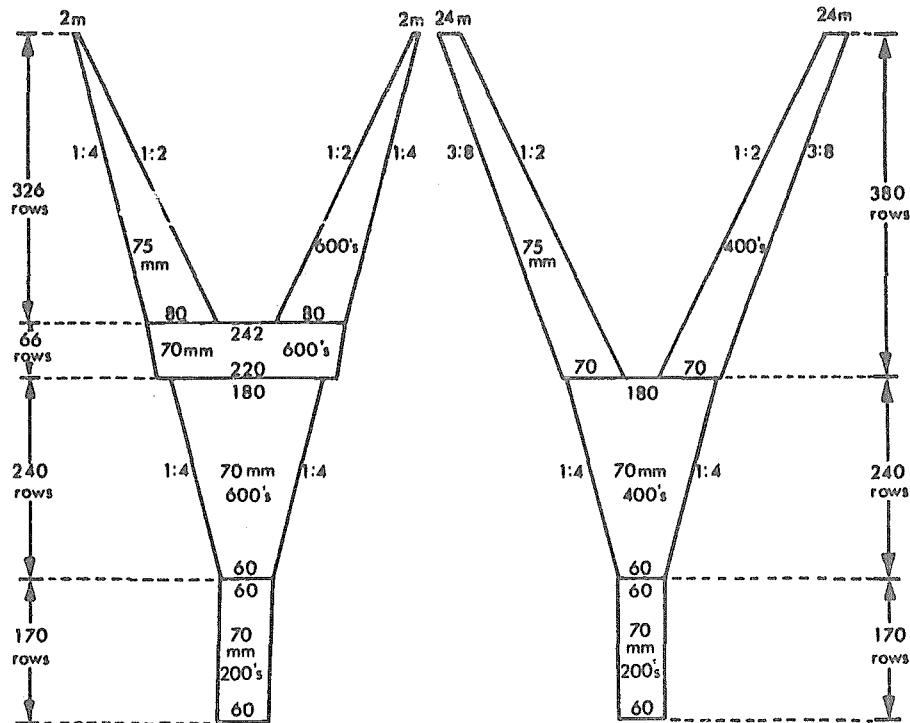
Fig. 22 Specification of a typical Scottish N. norvegicus trawl, after Figueiredo and Thomas (1967) and Thomas (1970). Headrope length 26.2 m, groundrope length 30.4 m.

Courlene (= polythene) is generally used for the manufacture of N. norvegicus trawls, which are usually rigged on terylene or polypropylene/steel core combination top and bottom ropes. The footrope may be weighted with light chain, leads or rubber discs.

According to Thomas (1967) there is a special beam trawl fishery for N. norvegicus by French vessels in the Bay of Biscay.

Since 1887 N. norvegicus has been caught by traps at depths of 50–100 m (Legendre, 1924) off Concarneau. In recent years a creel fishery has developed in some of the sea lochs on the west coast of Scotland, either where trawling is prohibited or where the nature of the bottom is unsuited to trawling (DAFS, 1966b, 1969c; Figueiredo and Thomas, 1967; Thomas, 1965, 1970a). An example of a Scottish creel for N. norvegicus is shown in Fig. 23.

– Changes in types of gear during the development of the fishery

According to Heydeck (1960) the usual fishing gear in the Kattegat was a trawl with 40 mm mesh in the wings, reducing to 25 mm or 20 mm in the codend. The overall size of the net varied considerably between 18.4 m headrope with a 21.2 m footrope, to 52.8 m headrope with a 56 m footrope.

Similar fishing gear, with a headrope of 16 m and a footrope of 20.7 m, has been used in the Golfe de Gascogne (Fontaine, 1967). Previously fishermen in the same area have used beamtrawls with meshes as small as 32–36 mm (Le Gall, 1937).

Initially (circa 1950) the fishery in Scottish waters employed seine nets with 70 mm mesh codends, as used for the capture of whitefish, but later (circa 1956) the mesh in the codend and bag was reduced to 55 mm. This net was worked with small otterboards and the headrope height reduced by restricting the number of floats. The wings were shortened and a wire footrope used. The modern N. norvegicus trawl, /with a 70 mm minimum mesh size, as originally used in Scottish waters, has been adapted from this (Figueiredo and Thomas, 1967; Pope and Thomas, 1965; Thomas, 1960).

– Use of echo-sounding or fish detectors

Echo-sounders and sonar are not able to detect the presence of N. norvegicus, since the animals live on or in the muddy substrate. However it is possible to recognize soft bottom deposits, which may support populations of N. norvegicus.
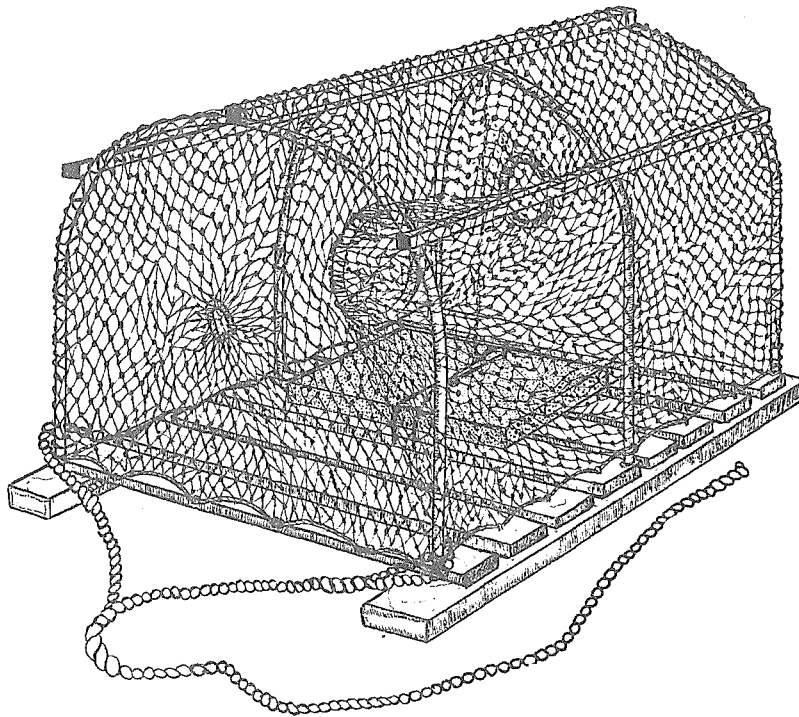
Fig. 23 Scottish creel for trapping <u>N. norvegicus</u>, from Thomas (1970a).
Mesh size 30 mm, internal diameter of entrance 64 mm.

5.12 Boats

- Type, size, power

There are restrictions on the size of boat
which may be used in fishing for <u>N. norvegicus</u>
in certain inshore waters. For details see
section 6.12.

In Icelandic waters the fishery is undertaken
mainly by side-trawlers. The average size of the
boat has increased from around 50 B.R.T. (British
Registered Tons) in 1964 to 70 B.R.T. in 1969. In
1969 the range was from 21 to 204 B.R.T., with
90-600 hp engines, the average being about 320 hp.
In the Faeroes, small cutters up to 40 hp are
used for <u>N. norvegicus</u> fishing. Vessels of about
20-100 B.R.T. are used in Danish waters (Thomas,
1970).

The Swedish <u>N. norvegicus</u> fishery is by
trawlers of 30-50 B.R.T., with engines generally
between 100 and 200 hp (Thomas, 1970).

According to Heydeck (1960) 17-m cutters are
used in the Kattegat. Fishing boats from the
Baltic coast measure 14-19 m, with engines between
90 and 150 hp, while the Finkenwerder boats are
19-24 m in length, and equipped with engines
between 90 and 200 hp (Aker and Tiews, 1965).

The Irish <u>N. norvegicus</u> fishery is under-
taken mainly by boats of 15-18 m, of about
30 B.R.T. and with engines averaging 100 hp.
A few boats up to 23 m are used (Thomas, 1970).
According to Symonds (1971) the vessels engaged
in the Irish Sea fishery are from 14-20 m in
length, with an average horsepower of about
130 hp. The Northern Irish boats from
Portavogie are from 15 to 20 m, equipped with
engines of about 150 hp. The boats fishing
from Kilkeel range from 18-21 m, with an
average horsepower of 220 hp.

The main <u>N. norvegicus</u> fishery in Scottish
waters is undertaken by trawlers of 12-28 m,
with engines of about 100-150 hp. There is
also a creel fishery using boats of 9-12 m, with
engines of 50-80 hp (Thomas, 1970).

The fishing vessels used in the fishery of
the northeast coast of England range from 12 m
to 20 m (average 15 m), with engines of 60-250 hp
(average 100 hp) (Symonds, 1971, 1972a).

5.2 Fishing areas

    5.21 General geographic distribution

- Geographic distribution

Land areas[1]/:

100 AFRICA, 111 Tunisia (GFCM, 1970);
112 Algeria (GFCM, 1970; Heldt and Heldt, 1931);
113 Morocco (GFCM, 1970; Heldt and Heldt, 1931;
Vilela, 1970).

500 EUROPE, 511 Denmark (Aker and Tiews,
1965; Höglund, 1942; Jensen, 1967); 512 Faeroe
Islands (Andersen, 1962; Höglund, 1942);
513 Iceland (Sigurdsson, 1965; Skuladottir,
1967); 514 Norway (Jensen, 1967; Poulsen, 1946);
516 Sweden (Aker and Tiews, 1965; Höglund, 1942;
Jensen, 1967; Poulsen, 1946); 522 Belgium
(Höglund, 1942); 524 France (Fontaine, 1967;
GFCM, 1970; Le Gall, 1933, 1937; Legendre, 1924);
525 Monaco (GFCM, 1970); 531 Ireland (Cole, 1965;
DAFD, 1965a; Hillis, 1972d; O'Riordan, 1961,
1961a, 1962a, 1964, 1965); 533 England, Wales
(Cole, 1965; Havinga, 1929; Storrow, 1912;
Symonds, 1971, 1972a); 534 Scotland (Cole, 1965;
Marine Laboratory, Aberdeen, 1971; Thomas, 1954,
1959, 1960, 1961a, 1965b, 1970a); 535 Northern
Ireland (Cole, 1965; O'Riordan, 1961a, 1964);
537 Isle of Man (Cole, 1965; O'Riordan, 1962a);
541 Portugal (Heldt and Heldt, 1931; Höglund,
1942); 542 Spain, Balearic Islands (de Buen, 1916;
GFCM, 1970; Massuti, 1970, 1971; Vives and Suau,
1963); 543 Italy (Alfirević, 1968; Froglia, 1972;
GFCM, 1970; Jukić, 1971); 551 Yugoslavia
(Alfirević, 1968; Jukić, 1971; Karlovac, 1955,
1955a,; Zupanovic, 1968); 561 Federal Republic
of Germany (Aker and Tiews, 1965; Höglund, 1942;
Jensen, 1967; Lüling, 1952a).

Sea areas[1]/:

ANE (Atlantic, N.E.) North Sea (Figueiredo
and Thomas, 1967a; Havinga, 1929; Storrow, 1912;
Symonds, 1971, 1972a); Skagerrak and Kattegat
(Aker and Tiews, 1965; Höglund, 1942; Jensen,
1967); Irish Sea (Cole, 1965; DAFD, 1965a;
Hillis, 1972d; Symonds, 1971).

ASE (Atlantic, S.E.) Bay of Biscay (Fontaine,
1967); western Mediterranean (Figueiredo and
Thomas, 1967a; Stephensen, 1923; Vives and Suau,
1963); Tyrrhenian Sea (GFCM, 1970; Santucci,
1930); Adriatic Sea (Alfirević, 1968; Figueiredo
and Thomas, 1967a; Jukić, 1971; Karlovac, 1953,
1955, 1955a; Santucci, 1930; Zupanovic, 1968).

The distribution of N. norvegicus throughout
the Mediterranean has been reported by Forest
(1973). The major fishing areas for N. norvegicus
have been given by FAO (1971) and Korringa (1969).

5.22 Geographic ranges

– Distances from the coast

Fishing for N. norvegicus occurs on the
northeastern Atlantic continental shelf and in
the Mediterranean Sea. Normally the fishing

grounds are fairly close to the coast, although
in the North Sea fishing grounds may be 150–200 km
from the coast. See Fig. 7 for the geographical
distribution of N. norvegicus, and section 5.21
for details of the commercial fishing grounds.

– Areas of greatest abundance

The areas of greatest abundance are: the
east and west coasts of Scotland; the North Sea;
the Atlantic coast of France; Icelandic waters;
the Irish Sea; the Skagerrak and Kattegat; the
Atlantic coast of Spain, and in the Mediterranean,
the Tyrrhenian and the Adriatic Seas.

– Differential abundance associated with
  hydrographical features

For details of temperature and salinity,
and their effects on the distribution of
N. norvegicus see sections 2.31 and 2.32.

5.23 Depth ranges

– Bathymetric contour

N. norvegicus occurs at depths from 15 m to
more than 800 m. The greatest recorded depth is
760–823 m off the island of Merettimo, west of
Sicily (Senna, 1903).

The depth range of N. norvegicus in different
areas is summarized as follows: Faeroes – 30–57 m
(Andersen, 1962); Skagerrak – 40–250 m (Höglund,
1942); Kattegat – 20–90 m (Aker and Tiews, 1965);
Scottish waters – 20–350 m (Thomas, 1965b;
Chapman, Priestley and Robertson, 1972); northeast
coast of England – down to 73 m (Symonds, 1971,
1972a); Irish Sea – 28–120+ m (Farmer, 1972a);
Golfe de Gascogne and Gulf of Cadiz – down to
400 m (Lagardère, 1973; Massuti, 1970); Atlantic
coast of Morocco – 322 m (Heldt and Heldt, 1931);
Mediterranean coast of Morocco – 250–500 m (GFCM,
1970); Mediterranean coast of Spain – 250–300 m
(GFCM, 1970); coasts of Sicily – more than 300 m
(GFCM, 1970); coast of Tunisia – 200–300 m (GFCM,
1970); coasts of Sardinia – 380–520 m (GFCM, 1970);
coasts of Corsica – 200–450 m (GFCM, 1970); Mare
Ligure – 50–150 m (Issel, 1930); Adriatic Sea –
66–400 m (Karlovac, 1953, 1955a)

According to FAO (1971) the depth range of
N. norvegicus is 55–160 m in the northwestern
Atlantic, and 190–390 m in the Mediterranean.

– Variations of density with depth

See section 4.24.

5.24 Conditions of the grounds

The bottom deposits of the grounds are
normally fine-grained muds or clays, although
sometimes the substrate may consist of muddy-sand.
See also section 2.34.

1/ Land and sea areas taken from Rosa (1965)

The associated species in the N. norvegicus community have been covered in section 4.6.

5.3 Fishing seasons

5.31 General pattern of seasons

- Pattern of seasons within whole fishing area

Strict seasons for N. norvegicus do not exist unless legally enforced (see section 6.1). Details of periods of peak landings are given in section 5.32.

5.32 Dates of beginning, peak and end of season

German landings of N. norvegicus are generally higher during the period June to September, although previously the landings were highest during October and November (Lüling, 1952a; Aker and Tiews, 1965). See Table XXII.

According to Lüling (1953) peak landings of N. norvegicus in the Danish fishery were during June to August, with secondary peaks during March/April and October/November. Jensen (1962) reported that landings were highest during June to November, with a smaller peak during March.

Scottish landings of N. norvegicus are generally highest during the months of July to October, and at their lowest during May (DAFS, 1961a; Thomas, 1954, 1960, 1970). The monthly landings of N. norvegicus in Scotland during 1969 in the various ICES statistical areas are given in Table XXIII.

Monthly landings at North Shields (England) during the years 1907-1911 were highest during September to January, with a peak in October/November. The smallest quantities landed were from March to July (Storrow, 1912). Symonds (1971, 1972a) has reported that landings at North Shields (1962-1970) are generally high

TABLE XXII

German monthly landings of N. norvegicus from the Kattegat (metric tons)

a) From Lüling, 1952a

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Total
1931	–	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	–	0.1	0.1
1932	–	–	0.3	0.0	0.0	0.0	0.0	0.0	0.0	–	–	0.5	0.8
1933	7.9	6.2	6.8	0.0	0.0	0.0	0.0	0.0	3.3	8.6	9.3	8.6	50.8
1934	8.9	7.2	2.9	0.0	0.0	0.1	1.1	0.7	6.6	19.0	25.2	13.9	85.0
1935	11.1	9.0	5.2	0.7	1.1	0.1	0.3	1.1	5.5	25.0	23.2	20.2	102.7
1936	15.0	5.9	4.8	7.7	1.4	1.3	–	1.8	20.6	47.2	35.2	11.4	151.8
1937	2.0	6.4	8.3	1.8	0.6	1.9	1.6	3.4	8.5	38.1	34.9	4.4	112.1
1938	11.1	2.8	1.9	0.3	–	–	–	1.0	9.1	22.4	29.9	12.4	91.2
1939	8.3	15.4	0.5	–	0.0	0.0	0.0	–	–*	–*	0.7*	–*	25.0
1949	0.1	2.1	0.6	0.2	0.1	0.4	–	–	3.6	2.8	8.5	2.8	21.3
1950	2.8	3.8	5.9	0.5	–	–	–	–	6.8	9.9	9.3	0.8	33.7
1951	–	–	–	0.1	–	–	–	2.7	4.4	14.5	14.9	2.0	43.8

*wartime months

b) From Aker and Tiews, 1965

1959	0.5	1.5	1.1	0.5	1.0	8.1	15.9	26.5	21.2	13.7	4.7	0.8	95.5
1960	1.5	1.1	1.8	0.5	3.1	17.2	19.5	23.6	22.7	17.0	3.7	3.3	115.0
1961	3.6	7.6	5.0	0.1	2.4	13.6	21.4	17.6	21.3	6.8	6.3	2.1	107.8

TABLE XXIII

Scottish monthly landings of N. norvegicus during 1969, from different ICES statistical areas (metric tons), from Thomas (1970)

Area	Jan.	Feb.	Mar.	Apr.	May	Jun.	July	Aug.	Sep.	Oct.	Nov.	Dec.	Total
IVa	121.5	37.2	29.8	36.5	81.7	153.9	173.2	412.6	422.9	69.7	19.1	17.1	1 575.2
IVb	111.4	40.0	82.0	134.2	39.7	53.3	55.9	103.8	148.0	161.2	84.9	97.9	1 112.3
VIa North of 57°30'N	110.0	115.2	167.8	138.3	141.7	73.5	184.9	172.1	60.6	50.5	67.1	103.4	1 385.1
VIa South of 57°30'N	89.5	70.8	189.7	374.0	535.9	447.6	585.9	580.1	384.8	377.6	166.4	97.3	3 899.6
Total	432.4	263.2	683.0	469.3	799.0	728.3	999.9	1 268.6	1 016.3	659.0	337.5	315.7	7 972.2

TABLE XXIV

Monthly landings (metric tons) of N. norvegicus from 1962 to 1970 at North Shields (England), from Symonds (1971)

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Total
1962	-	-	-	-	-	5.2	1.3	11.9	27.9	38.3	14.4	29.3	128.3*
1963	3.0	1.1	4.8	4.1	1.1	0.0	0.1	0.7	9.2	24.1	72.0	20.5	140.7
1964	43.5	24.2	27.0	28.7	0.2	0.0	0.0	0.0	2.6	6.9	11.0	20.5	164.6
1965	8.1	17.9	79.6	35.9	0.8	0.3	1.5	1.6	4.9	20.4	17.5	37.0	225.5
1966	18.3	23.3	48.8	9.5	40.1	7.9	18.0	13.7	67.4	39.6	84.3	75.3	446.2
1967	45.3	31.8	3.5	2.0	9.2	12.2	6.9	27.9	73.2	54.2	74.1	40.7	381.0
1968	28.4	28.5	2.7	1.6	0.0	0.0	0.0	4.3	44.4	169.8	88.4	98.4	466.5
1969	58.6	7.0	21.3	6.1	0.1	0.0	0.0	0.0	53.5	114.5	94.2	49.7	405.0
1970	1.1	0.3	0.0	0.0	0.0	0.0	0.9	4.6	63.1	73.3	59.4	32.4	235.1

* incomplete total as records only cover 7 months

TABLE XXV

Portuguese monthly landings of N. norvegicus as a percentage of the total annual landing
for the years 1959-63, from Figueiredo and Barraca (1963)

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Total (metric tons)
1959	0.6	2.5	2.7	11.9	16.3	16.6	19.5	14.4	7.1	2.7	4.1	1.6	97.4
1960	1.2	2.6	10.1	9.8	18.9	20.0	16.4	8.3	5.9	1.2	2.0	3.7	84.8
1961	3.8	3.2	6.6	13.1	16.7	12.1	17.6	9.2	7.0	5.7	4.0	0.9	75.4
1962	2.3	3.1	2.5	8.6	15.7	13.9	17.5	12.5	10.4	5.0	4.4	4.1	61.7
1963	0.8	5.2	7.1	13.7	4.5	15.6	5.9	18.4	18.3	4.3	3.1	3.1	67.3

during the months September to January, and low or
even nil during March to August (see Table XXIV).

Irish landings of N. norvegicus are highest
during the months June to October, except on the
west and south-west coasts, where landings are
somewhat irregular (Hillis, 1972d).

Landings at the port of Guilvinec (France)
were generally lowest during October to March;
the largest quantities landed were normally in
April to June (Fontaine and Warluzel, 1969).

According to Figueiredo and Barraca (1963)
Portuguese landings are highest during April to
August, whereas during the remainder of the year
landings are generally low. See Table XXV.

5.33   Variation in date or duration of
        season

- Variations caused by climate, availability,
  regulations, economic factors, etc.

During the years 1931-1939 German landings
were highest during October and November, simi-
larly during the years 1949-1951 landings were
also highest at this time of year (Lüling, 1952a).
However, according to Aker and Tiews (1965), peak
landings during 1959-1961 were in July to
September. This change in the season of maximum
landings has not been explained.

5.4   Fishing operations and results

5.41   Effort and intensity

- Type of unit of effort

The most usually employed unit of effort is
the catch or landing expressed in kg/h. However,
kg/day, cwt/100 h, cwt/boat/day, and number/½ h
have also been used.

- Landings/catches per unit of fishing
  effort

In Icelandic waters reported catches range
from 172 kg/h to 6 kg/h, with an average of
about 70 kg/h (Sigurdsson, 1965; Skuladottir,
1967; Thomas, 1970).

According to Andersen (1962) catch per unit
effort in Faeroese waters ranged from 544 kg/h
to 0.4 kg/h (including undersized animals, which
would normally be rejected). The mean catch
varied from 229 kg/h to 17 kg/h in different
areas. The proportion of large animals (carapace
length >47 mm) ranged from 23 to 100 percent.

The catch per unit effort for Scottish
commercial landings in 1969 in various ICES
statistical areas was 24.5 to 15.4 kg/h. Throughout
the year the variation in monthly mean values was
35.7 to 9.0 kg/h (Thomas, 1970). In an exploratory
survey in Scottish waters during 1959, catches
of 10 176 to 4 animals/h were recorded (Thomas; 1959).

Mean annual catches of N. norvegicus landed
at North Shields (England) ranged from 24.1 to
13.5 kg/h. Variation throughout the year was
pronounced, with catches up to 36.8 kg/h being
recorded during the winter months, and falling to
4.1 kg/h during the late spring and early summer
(Symonds, 1971). Symonds (1972a) quoted the same
data but in cwt/100 h.

O'Riordan (1962b, 1964) has reported catches
of 14.7 to 3.6 cwt/boat/day in the Irish Sea. The
highest catches were taken during the months of
April to June. Off the west coast of Ireland
catches of 27 to 4 kg/h have been recorded by
O'Riordan (1965).

According to Froglia (1972) the Italian
catches per unit effort have steadily dropped in
the Adriatic Sea from 1960 to 1970. The highest
catch per unit effort throughout this period was
generally recorded in the spring.

Catches of N. norvegicus by Yugoslav trawlers in the Adriatic Sea have shown a gradual decline between 1956 and 1962 in terms of catch per unit effort (from about 70 kg/day to 15 kg/day). From 1963 to 1965 catches rose steadily to 40 kg/day (Zupanovic, 1968). According to Jukić (1971) the mean catch in Yugoslav coastal waters during 1948/49 was 4.54 kg/h, and in 1968 it was 5.17 kg/h, whereas the mean catch in the Adriatic international waters (fished mainly by Italian trawlers) had fallen from 3.39 kg/h to 1.69 kg/h in the same period.

- Fishing effort per unit area

No data are available.

- Total fishing intensity

According to Skuladottir (1967) the total fishing effort for N. norvegicus in Icelandic waters during 1966 was 56 161 hours, and the estimated effort for 1967 was 45 698 hours, assuming that a given year's stock is caught over an eight-year period. It was suggested that the optimum effort was 65 500 hours, which would result in the catch per unit effort falling from 61 kg/h to 45 kg/h.

Gulland (1971) gives details of the relative degree of exploitation of the various stocks of N. norvegicus in the northeastern Atlantic (see Table XXVI). The estimated potential yield from this region is 60 000 metric tons annually, compared with 38 200 metric tons landed in 1972 (see Table XXVII). The production in the Mediterranean has remained extremely constant over the last 15 years. No figures for the potential production in the Mediterranean of N. norvegicus specifically have been given, although the total crustacean production is expected to increase by approximately 20 percent on the 1965 figures.

TABLE XXVI

N. norvegicus. Degree of exploitation in various stocks in the northeastern Atlantic
(from Gulland, 1971)

Country	Area	Degree of exploitation	1965 Production (10^3 metric tons)
Iceland	Near seas	Moderate	3.7
Faeroes	Coastal areas	Light	0.1
Norway	Coastal areas	Light	0.2
Sweden	Kattegat	Heavy	0.3
	North Sea	Moderate	0.0
Denmark	Kattegat	Heavy	0.8
	Skagerrak	Moderate	0.3
	North Sea	Moderate	0.0
Germany	Kattegat	Heavy	0.1
Holland	North Sea (by-catch)		0.0
Belgium	South North Sea		0.5
Scotland	North Sea (near seas)	Moderate	3.5
	West coast	Light to moderate	3.0
England and Wales	North Sea (near seas)	Moderate	0.4
Northern Ireland	Irish Sea	Moderate	0.9
Eire	Irish Sea	Moderate	1.0
	Celtic Sea	Light	0.0
France		Moderate	7.4
Spain	Near seas	Moderate	3.8
Portugal	Near seas	Light	0.2
TOTAL			26.4

TABLE XXVII

Total annual catches (10³ metric tons) of N. norvegicus by fishing area and by country for 1955–1973, from FAO (1947 et seq.) and Figueiredo and Thomas (1967)

Fishing area/country	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
ATLANTIC, NORTHEAST	...	...	...	...	...	...	...	...	...	27.4	25.1	27.3	27.8	29.7	34.7	33.0	33.8	38.2	38.0
Belgium	0.4	0.4	0.6	0.8	0.9	0.8	0.9	0.7	0.8	0.8	0.5	0.7	0.5	0.5	0.5	0.5	0.4	0.3	0.4
Denmark	1.0	1.5	1.7	1.7	1.5	2.2	1.5	1.7	1.8	2.2	1.7	1.2	1.5	1.7	1.2	1.2	1.2	2.1	1.3
Faeroe Islands	...	...	...	...	0.0	0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	—
France	*5.1	*5.2	*7.4	T6.8	T7.2	T8.2	T8.9	T8.3	T8.7	T9.7	7.8	7.6	7.7	8.3	11.3	10.0	9.0	9.6	12.1
Germany, Federal Republic	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0
Netherlands	...	...	...	0.0	...	0.0	0.0	0.0	0.0	—	—	—	—	—	—	—	—	—	—
Iceland	...	...	...	...	1.4	2.1	1.5	2.5	5.2	3.5	3.7	3.5	2.7	2.5	3.5	4.0	4.7	4.3	2.8
Ireland	...	...	...	0.6	0.8	0.4	0.7	0.8	1.5	1.0	0.8	1.3	0.9	1.5	1.4	2.0	1.8	1.8	2.2
Norway	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.0	0.1	0.2	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0
Portugal	0.1	0.0	0.0	F0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.2	0.3	0.2	0.3	0.2	0.1	F0.1	F0.1
Spain	...	...	...	T2.5	T2.6	T2.3	T2.9	T2.7	T2.7	T3.2	3.1	3.6	4.1	4.1	4.2	3.2	F3.2	3.8	4.0
Sweden	0.7	0.7	0.8	0.7	0.7	0.7	0.7	0.5	0.6	0.8	0.5	0.4	0.5	0.6	0.4	0.3	0.4	0.5	0.5
U.K. (England and Wales)	...	...	...	0.4	0.3	0.4	0.8	0.3	0.3	0.4	0.4	1.1	0.8	1.0	0.9	0.6	1.0	0.9	0.8
U.K. (Scotland)	1.1	1.1	1.4	1.1	2.2	2.0	2.9	3.5	3.7	4.9	5.2	6.3	6.7	7.2	8.2	8.2	9.0	10.8	9.8
U.K. (N. Ireland)	...	...	...	0.8	0.7	0.5	0.9	0.8	1.4	1.3	0.9	1.4	2.0	1.9	2.7	2.8	2.9	4.0	F4.0
ATLANTIC, EASTERN CENTRAL	...	...	...	...	...	...	...	...	...	...	—	—	—	—	—	0.1	0.1	—	0.5
Spain	...	...	...	...	...	...	...	...	...	...	—	—	—	—	—	0.1	F0.1	—	0.5
MEDITERRANEAN AND BLACK SEA	...	...	...	...	...	...	...	...	...	2.5	2.9	4.3	2.9	2.6	2.4	2.2	2.3	2.6	2.5
Algeria	...	...	...	0.1	0.1	0.1	...	...	...	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0
France	...	...	...	...	...	...	...	...	...	...	—	1.4	—	0.0	—	—	—	—	—
Italy	...	...	...	1.5	1.3	1.5	1.6	1.3	1.3	1.3	2.0	2.1	2.1	2.0	1.8	1.6	1.7	1.9	1.8
Morocco	...	...	...	0.0	...	...	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spain	...	...	...	...	...	...	...	...	...	...	0.7	0.6	0.6	0.4	0.4	0.3	F0.3	0.5	0.5
Yugoslavia	0.2	0.2	0.3	0.4	0.2	0.3	0.2	0.1	0.1	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
TOTAL (nearest 10³ tons)	15.0	16.0	19.0	19.0	21.0	22.0	24.0	24.0	28.0	30.0	28.0	32.0	31.0	32.0	37.0	35.0	36.0	41.0	41.0

... data not available; unobtainable   — none; magnitude known to be nil or zero   F data estimated or calculated by FAO

° category or entry not applicable   T total for country regardless of fishing area   * including Algeria

0.0 magnitude known to be more than zero but less than half the unit or final digit used

- Causes of variation in fishing effort
  and intensity

No data are available.

5.42 Selectivity

- Selective properties of gear

Mesh selection of N. norvegicus is not a simple relationship dependent only on mesh size. N. norvegicus tend to cling to the meshes of the net and to each other with the pereiopods. This behaviour makes assessment of the selective properties of a net difficult (Thomas, 1970a).

Gulf of Mexico flat trawls have been found to catch more than twice the quantities of N. norvegicus caught using wing trawls (FAO, 1973).

- Changes in mesh size and their effect

According to O'Riordan (1960a, 1961) the mean carapace lengths of N. norvegicus caught when stretched mesh sizes of 70 mm, 65 mm, 60 mm and 50 mm were used were 32.5 mm, 31.0 mm, 31.0 mm and 30.0 mm respectively. The respective mean sizes of escapes from the various meshes into a codend cover were 26.0 mm, 26.0 mm, 25.8 mm and 30.0 mm. O'Riordan (1962b, 1964, 1965a) has reported that the 50 percent release points for 45-mm and 50-mm mesh nets were 18 mm carapace length. Using a 60-mm mesh, 50 percent release occurred at a carapace length of 19 mm, and with a 70-mm mesh at 21 mm carapace length.

Jensen (1965a) found that the 50 percent release point for a 69-mm mesh net was about 27 mm carapace length, and for a 117-mm mesh net about 46 mm.

By using fine mesh covers on the wings, bunt, belly, bating and codend of a 70-mm courlene net, Cole and Simpson (1965) found that the largest numbers of escapes through the meshes occurred in the bunt, the belly and the underside of the codend. The mean 50 percent release point for the 70-mm net was 33.5 mm carapace length.

According to Ancellin (1965) the 50 percent release point for a 63.9-mm mesh codend was about 27 mm carapace length.

Dybern (1967) has studied the effect of various mesh sizes on the catches of N. norvegicus, particularly in relation to the proportion of commercial and non-commercial sized animals.

Thomas (1954) reported that the 50 percent release point from a 70-mm mesh codend was about 27 mm carapace length. According to Pope (1960)

conflicting results have been obtained on the 50 percent release points of 70-mm manilla and nylon mesh in the codends of trawls, in that occasionally selection has been quite irregular or there has been no release. Similarly, using seine nets there is evidence of a general increase in the number of escapes with increasing mesh size, but most irregularly since there may be no significant losses up to mesh sizes of 70 mm. It was found that seines, even if used with otter boards, appeared to be less efficient both in the commercial fishery and in experimental fishing than trawls. Thomas (1965c) has found that the quantities of the small and large market categories of N. norvegicus caught by a 70-mm mesh trawl are approximately equal, whereas, using a net with 65-mm mesh in the square and bosom and 55-mm in the bag, but fitted with a 70-mm codend with 40-mm cover, the quantity of smalls was approximately double that of the large category.

Pope and Thomas (1965) have shown that the 70-mm mesh N. norvegicus trawl is considerably more efficient than the older style seine net. When fitted with a 63-mm codend the seine net averaged 11 N. norvegicus per haul, whereas the trawl averaged 1 660 per haul. The mesh selection curves of codends of different types of twine and mesh size are given in Fig. 24.

According to Fontaine (1967) the 50 percent release point for a trawl fitted with a 25-mm mesh codend was about 27 mm carapace length.

Abbes and Warluzel (1970) used two types of trawls, one fitted with a 35-mm mesh codend and 15-mm mesh cover, and the other with a double codend (35-mm and 15-mm mesh), to examine the effects of mesh selection on N. norvegicus. The 50 percent release point of the 35-mm mesh codend (fitted with cover) was 28.7 mm carapace length when towed for one hour; however, if towed for two hours the 50 percent release point was 33.7 mm. The equivalent values for the trawl fitted with the double codend were 29.5 mm and 32.8 mm respectively. There was little correlation between the state of the sea and the 50 percent release point in the 1-hour hauls, whereas the relationship in the 2-hour hauls was highly significant, in that the carapace length of the 50 percent release point increased as the sea became rougher. These results were explained by the behaviour of the N. norvegicus in clinging to the meshes of the net. The 50 percent release point of females was found to be generally higher than that of males.

Symonds and Simpson (1971), using a specially designed N. norvegicus trawl for releasing undersized roundfish, have found that, although the gear was more difficult to handle
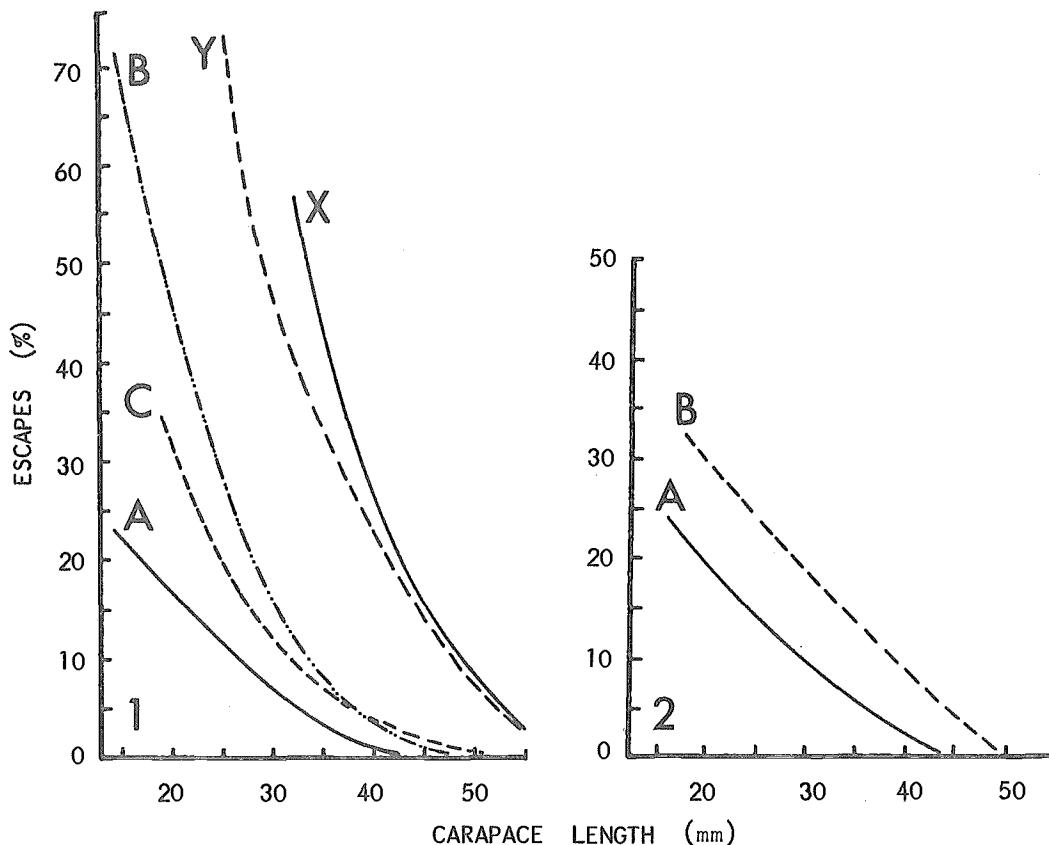
Fig. 24 N. norvegicus. Trawl codend selection curves. (1) A: 62-65 mm double manilla;
B: 68-74 mm double manilla; C: 77-83 mm double manilla; X: 61-64 mm single nylon;
Y: 69-70 mm single nylon. (2) A: 55-56 mm single cotton; B: 72-73 mm single
cotton. (From Pope and Thomas, 1965)

than conventional trawls, in general good separa-
tion of N. norvegicus from whiting was obtained,
with large numbers of undersized roundfish
escaping from the upper codend. The whole of the
upper surface of the net was made of 70-mm mesh,
whereas the lower surface was 50-mm mesh. The
codend was horizontally divided internally with
a 50-mm sheet of netting. It has been found that
80 percent of the total N. norvegicus caught are
retained in the lower portion of the horizontally
divided codend (FAO, 1973).

 — Other selection factors: type of twine

Differences in the selection curves of
codends made of different types of material are
given in Fig. 24.

5.43 Catches

 — Total annual yields

The total annual yields of N. norvegicus
by countries are given in Table XXVII. Annual
yields for the ICES statistical areas, for the
years 1954-1969, are given in Table XXVIII.

 — Total annual yields from different
   fishing grounds

Icelandic landings of N. norvegicus during
the years 1960-1962 have been given by Sigurdsson
(1965).

According to Höglund (1942) the total
landings for 1938 in Sweden were 365 metric tons
(value S.Kr. 111 000), and in Denmark 674 tons
(value D.Kr. 354 000). Danish landings from
the start of the N. norvegicus fishery in 1930
until 1943 have been reported by Poulsen (1946)
and Lüling (1953). Landings originating from
the Kattegat were generally higher than those
from the Skagerrak.

Details of the yield of N. norvegicus in
the Stagerrak and Kattegat have also been
reported by Jensen (1959, 1962, 1963, 1965a,
1967). Total landings (by-catch of the
Pandalus borealis fishery) by all countries from
the Skagerrak and Kattegat, between 1915 and
1932, have fluctuated between about 10 and
260 tons per year. From about 1960 onwards,
the Swedish catch had grown to about 900 tons

TABLE XXVIII

Annual catches (metric tons) of N. norvegicus by country and by ICES statistical areas, for 1954-1969 (from Thomas, 1970)

Year	Va 2	Vb 1	IIIa					IVa			IVb	IVa, b	VIa			VIIa	VIIb, c	VIIg, h, j, k
	Iceland	Faeroes	Denmark	Germany	Norway	Sweden	Total	Norway	Scotland	Total	Scotland	Germany	Ireland	Scotland	Total	Ireland	Ireland	Ireland
1954	-	3	-	40	19	584	643	-	316	316	231	15	-	29	29	-	-	-
1955	-	2	-	70	121	651	842	-	210	210	804	5	-	70	70	212	-	-
1956	-	2	-	73	72	722	867	+	337	337	665	2	9	56	65	197	-	2
1957	-	51	-	51	187	834	1 072	2	345	347	985	1	15	43	58	330	-	-
1958	728	91	-	94	87	679	860	1	297	298	685	+	25	162	187	569	14	-
1959	1 404	96	1 529	96	60	654	2 339	6	595	601	830	1	12	738	750	734	-	1
1960	2 081	73	2 228	115	68	716	3 127	1	538	539	501	1	2	930	932	392	3	-
1961	1 490	35	1 446	108	51	691	2 296	-	765	765	590	1	11	1 564	1 575	688	3	13
1962	2 662	39	1 661	90	49	511	2 311	3	898	901	632	+	1	1 950	1 951	649	2	188
1963	550	78	1 746	111	13	560	2 430	3	921	924	688	+	-	2 098	2 098	1 061	2	431
1964	3 521	54	2 228	141	102	782	3 253	1	1 543	1 544	908	3	33	2 677	2 710	540	81	366
1965	3 706	49	1 732	56	142	550	2 480	9	1 033	1 042	1 052	+	1	3 159	3 160	558	79	163
1966	3 465	43	1 140	23	19	436	1 618	2	1 438	1 440	1 963	4	4	2 943	2 947	888	87	268
1967	2 731	36	1 458	60	17	554	2 089	-	1 387	1 387	1 452	5	2	3 846	3 848	748	49	126
1968	2 489	-	1 711	64	84	613	2 472	-	1 500	1 500	1 132	+	11	4 570	4 581	906	17	559
1969	3 512	23	-	-	75	-	75	-	1 577	1 577	1 113	-	6	5 499	5 505	941	3	424
1970	4 026	-	1 232	6	18	335	1 591	-	1 092	1 092	1 654	-	-	5 431	5 431	1 258	18	743
1971	4 657	38	1 214	2	18	373	1 607	4	1 638	1 642	1 412	1	-	5 972	5 972	1 415	1	359
1972	4 321	31	2 085	1	24			5	1 304	1 309	1 904	1	-	7 556	7 556	1 626	46	151

TABLE XXIX

a) Weight (metric tons) and value (£ Sterling) of N. norvegicus landed at Scottish ports
for 1967-1970 (from DAFS, 1969, 1970, 1971)

Port	1967		1968		1969		1970	
	Weight	Value	Weight	Value	Weight	Value	Weight	Value
Eyemouth	217	40 783	237	48 957	165	34 343	252	48 071
Leith	688	115 374	511	89 163	577	106 130	759	139 485
Anstruther	444	82 418	299	61 013	349	69 395	601	140 212
Arbroath	103	22 361	84	18 656	19	4 372	40	9 084
Aberdeen	0.6	126	0.3	121	3	525	-	-
Peterhead	96	19 654	84	19 714	16	3 274	0.7	108
Fraserburgh	286	53 641	342	80 693	294	62 042	261	57 148
Macduff	13	1 576	34	4 329	9	922	38	6 877
Buckie	732	124 522	708	137 900	841	145 316	503	94 725
Lossiemouth	260	41 042	332	62 854	415	93 376	294	70 419
Wick	-	-	0.3	67	4	1 425	0.9	311
Lerwick	0.1	27	0.2	23	-	-	-	-
Stornoway	339	66 356	343	78 607	295	71 731	163	41 845
Ullapool	654	139 186	883	235 431	1 169	357 693	1 318	378 431
Mallaig	743	179 191	954	265 124	1 407	423 979	1 452	412 249
Oban	336	74 047	522	130 547	579	164 089	526	146 312
Campbeltown	669	123 071	802	184 502	865	226 279	709	161 964
Ayr	1 107	203 653	1 067	203 588	1 183	263 022	1 261	285 539
Total	6 688	1 287 028	7 601	1 621 289	8 190	2 027 913	8 179	1 992 780

b) Annual Scottish landings (metric tons) of N. norvegicus for certain areas
for 1966-1970 (after DAFS, 1972)

Area	1966	1967	1968	1969	1970 estimated
Firth of Clyde	1 308	1 776	1 869	2 049	2 073
South Minch	919	1 079	1 476	1 478	1 941
North Minch	716	993	1 226	1 463	1 321
Moray Firth	1 439	1 387	1 500	1 579	1 153
Firth of Forth	1 961	1 452	1 132	1 110	1 209
Others	1.9	0.7	0.5	2.8	-
Total	6 344.9	6 687.7	7 203.5	7 681.8	7 697

per year, and the Danish to about 1 700 tons per year. Approximately 100 tons are taken annually in the Norwegian P. borealis fishery, and a similar quantity by the German trawl fishery also operating in this area. The German landings of N. norvegicus are given by Lüling (1952a) and Aker and Tiews (1965). See also Table XXII.

Scottish landings have been published by DAFS (1961, 1962, 1963, 1964, 1965, 1966, 1967, 1968, 1969, 1970, 1971, 1972, et seq.). Further details of Scottish landings are available in Thomas (1954, 1960d, 1969, 1970b), Wood (1957) and Marine Laboratory, Aberdeen (1971). Recent landings separated into fishing areas and ports of landing are shown in Table XXIX. See also Table XXII.

Storrow (1912) provided records of the landings and values of N. norvegicus at North Shields (England) from 1895 to 1911. More recent figures have been recorded by Symonds (1971, 1972a) for the same area (see Table XXIV).

Irish landings of N. norvegicus have been reported by O'Riordan (1961, 1961a, 1962b, 1964) and Hillis (1972d). Approximate catches by all vessels fishing in the Irish Sea, grouped according to country of origin, for the years 1955-1960 have been given by O'Riordan (1964); see Table XXX.

Leloup (1955, 1958, 1959) and Leloup and Gilis (1965) have given the landings of N. norvegicus at Belgian ports from 1946 to 1960, separated according to the different fishing grounds. The largest proportion of the landings had originated from Icelandic waters; the central North Sea, and the Irish Sea and St. George's Channel were also very important.

Landings on the coast of France have been reported by Legendre (1924), Le Gall (1935), Fontaine (1967) and Fontaine and Warluzel (1969). 8-9 metric tons of N. norvegicus are normally landed per year at French ports, the most important of which is Concarneau.

Portuguese landings of N. norvegicus are given in Table XXV.

Values of the landings of N. norvegicus in the Balearic Islands for the years 1953 and 1964 have been published by Massuti (1971).

From 1877 to 1951 Yugoslav catches of N. norvegicus in the Adriatic Sea have risen steadily from 20 to 141 metric tons per year (Karlovac, 1955a). However, during the period 1956-1965 there has been a general decline to about 15 metric tons per annum (Zupanovic, 1968).

– Maximum equilibrium yield

See section 5.41 – Total fishing intensity, and Table XXVI.

5.44 By-catch

Fontaine (1967) and Fontaine and Warluzel (1969) have listed the important species of fish and shellfish in the by-catch of the N. norvegicus fishery off the French coast. The major species are: hake (Merluccius merluccius), poor cod (Trisopterus minutus minutus), pout (Trisopterus luscus), greater forkbeard (Phycis blennoides), poutassou (Micromesistius poutassu), whiting (Odontogadus merlangus merlangus), Gadiculus argenteus thori, megrim (Lepidorhombus whiffiagonis), sole (Solea solea), variegated sole (Microchirus variegatus), plaice (Pleuronectes platessa), edible crab (Cancer pagurus) and cephalopods.

TABLE XXX

Approximate catch of N. norvegicus by all vessels fishing in the Irish Sea (from O'Riordan, 1964)

Year	Catches (metric tons)					
	Ireland	Northern Ireland	England	France	Belgium	Total
1955	210	397	102	–	5	714
1955	195	534	57	–	1	787
1957	325	600	67	50	13	1 165
1958	560	845	106	146	17	1 674
1959	722	750	55	200	2	1 729
1960	392	495	1	67	89	1 044

The most important species in the by-catch of the N. norvegicus fishery off the northeast coast of England are: cod (Gadus morhua), whiting, haddock (Melanogrammus aeglefinus), plaice, skate/rays, and dogfish (Symonds, 1971, 1972a). In 1970 the total landing of N. norvegicus at North Shields was 235 metric tons, whereas the by-catch landed was 406.4 tons.

According to O'Riordan (1962b) the percentage composition of the landings of N. norvegicus by trawlers fishing solely for this species in the Irish Sea during 1960 and 1961 was: 74.7 and 86.3 percent N. norvegicus; 12.9 and 10.6 percent whiting; 11.8 and 3.0 percent cod; 0.6 and 0.0 percent plaice; and 0.0 and 0.1 percent hake. Equivalent figures have been reported by Aker and Tiews (1965) in the German N. norvegicus fishery in 1959 and 1960 viz.: 67.6 and 66.6 per-cent N. norvegicus; 9.3 and 7.1 percent plaice; 5.9 and 5.5 percent cod; 2.0 and 1.8 percent hake; 1.7 and 2.4 percent sole; 1.8 and 1.6 per-cent brill (Scophthalmus rhombus), and 0.5 and 0.8 percent turbot (Scophthalmus maximus).

Thomas (1965a) has carried out an extensive survey of the by-catch from the N. norvegicus fishery on different fishing grounds around the Scottish coast. The most important species were: whiting; long rough dab (Hippoglossoides platessoides); hake; dogfish; haddock; herring (Clupea harengus); witch (Glyptocephalus cynoglossus); dab (Limanda limanda); cod; and gurnards (Trigla spp.).

The by-catch from the Icelandic N. norvegicus fishery is shown in Table XXXI.

Thomas (1960c) has discussed the merits of seines and trawls in the N. norvegicus fishery, with particular reference to undersized whitefish, and has suggested ways of controlling the fishery for N. norvegicus on whitefish nursery grounds.

For details of predators see section 3.34 and for the community associated with N. norvegicus see section 4.6.

TABLE XXXI

Relative importance of the by-catch in the Icelandic N. norvegicus fishery
(all fish gutted with head on). After Sigurdsson (1965)

Species	1960		1961		1962	
	Total catch (kg)	%	Total catch (kg)	%	Total catch (kg)	%
N. norvegicus	2 080 918	33.3	1 490 107	28.3	2 662 277	41.5
Haddock	890 724	14.2	1 122 830	21.4	1 023 744	16.0
Cod	1 075 936	17.2	718 546	13.7	718 247	11.2
Witch	727 434	11.6	514 804	9.8	402 957	6.3
Redfish	478 183	7.6	246 834	4.7	515 364	8.0
Ling	317 805	5.1	353 129	6.7	486 844	7.6
Catfish	143 195	2.3	192 593	3.7	88 720	1.4
Lemon sole	132 967	2.1	182 917	3.5	82 324	1.3
Plaice	154 057	2.5	167 512	3.2	89 535	1.4
Halibut	96 956	1.6	89 370	1.7	51 914	0.8
Torsk	6 167	0.1	85 254	1.6	2 051	0.03
Megrim	37 423	0.6	18,650	0.4	30 676	0.5
Coalfish	29 254	0.5	11 003	0.2	17 796	0.3
Common skate	16 183	0.3	15 837	0.3	12 170	0.2
Other species and waste	65 081	1.0	48 334	0.9	229 646	3.6
Total	6 252 283	100.0	5 257 720	100.1	6 414 265	100.0
Total by-catch	4 171 365	66.7	3 767 613	71.7	3 751 988	58.5

5.45 Processing

The tails (=abdomen) of N. norvegicus are usually either sold fresh, frozen but uncooked, or canned and cooked (Le Gall, 1937; Thomas, 1970a).

According to Early (1966) N. norvegicus should either be landed live or already tailed, since the hepatopancreas in the carapace rapidly causes discoloration and a bad flavour, although there is the disadvantage that penetration of bacteria from the ice into the flesh is made easier (Hovart and Vyncke, 1964, 1964a).

In Belgian fishing ports, N. norvegicus are usually cooked shortly after auction and sold to customers in this state (Hovart and Vyncke, 1964, 1964a). 30 kg of N. norvegicus can be cooked in 150 l of water with the addition of 7-8 kg of salt, and optionally spices and vegetables to improve the flavour. Whole animals are placed in the boiling water and removed when the scum appears on the surface.

It has been found that washing the animals before they are cooked in 3 percent salt solution was more efficient in removing sand and mud than water alone (Hovart and Vyncke, 1964, 1964a). Experiments on cooking techniques have shown that the use of pressure cookers has the advantage of producing better flavour, less mechanical damage and higher nutritive value, although colours were duller, keeping qualities were reduced, and there was higher loss of weight. The ideal concentration for the cooking brine was found to be 7-9 percent. It appeared that animals cooked before storage had a better quality and kept their freshness longer than those stored in ice uncooked. Organoleptic studies and spoilage analyses confirmed these observations.

In the United Kingdom N. norvegicus are usually sold as uncooked, frozen, shelled meats, although smaller quantities of cooked tails are also sold (Early, 1966). Whole animals or unshelled tails should be boiled in water containing 5 percent salt for about 5-6 minutes. Removing the raw flesh from the tails is facilitated by either keeping the tails on ice for up to 72 h to allow the membrane which attaches the flesh to the shell to be digested, or by freezing the uncooked tails until required for processing, and then thawed. The tail meat is easily removed from the shell with a jet of compressed air in either case, although thawed frozen tails are of a higher quality, and produce less wastage. After cleaning, the tail meats can be refrozen singly or in blocks, glazed and wrapped, and can be stored at -20 F (= approx. -30 C) for at least 2-3 months.

According to Le Gall (1937) N. norvegicus tails are canned in factories along the coast of Brittany. By cooking the tails in slightly acidified water, blackening and discoloration is avoided.

Various studies have been carried out on the effects of sodium sulphite and sodium metabisulphite as preservatives for N. norvegicus (Caracciolo, 1965; Caracciolo and Pepe, 1965; Caracciolo and Perricone, 1965; Caracciolo, Perna and Pistola, 1965; Pistola, 1965; Angeli, 1966). It has been found that N. norvegicus may be immersed for 10 minutes in solutions of sulphite or metabisulphite (strength 2-3 percent, depending on the size of the animals) without exceeding the Italian regulation controlling the maximum permitted content of sulphur dioxide (350 mg/kg of flesh). Studies on the presence of formaldehyde and trimethylamine in the flesh of N. norvegicus have been carried out by Caracciolo (1966) and Perna, Mancini and Ruffo (1965).

According to Michel and Parent (1973) the preservatives sodium metabisulphite and boracic acid inhibit enzyme degradation, whereas sodium benzoate and, to a lesser extent, sodium metabisulphite and boracid acid, inhibits bacterial decay. Metabisulphite and boracic acid were found to be more effective in inhibiting the blackening of the N. norvegicus flesh. The characters used by Michel and Parent (1973) to define the stages of degradation are similar to those given by Early (1966).

Studies on the ammonia, trimethylamine and TVN (= total votile basic nitrogen) concentrations in N. norvegicus flesh have been carried out by Vyncke (1970). It was found that at 20°C cooked N. norvegicus spoiled after about 2 days, whereas at 0°C they were borderline after 11 days, when the concentration of ammonia had reached 45-50 mg N.

Changes in the refractive index of frozen or iced N. norvegicus muscle have been assessed by Elerian (1965) as a possible means of measuring quality. The refractive index of iced tails, and frozen tails stored at -1°C and -2°C, dropped with time, whereas the refractive index of tails stored at -4°C to -29°C increased. The water content of the uncooked muscle ranged from 77.1 to 78.1 percent. According to Early (1966) the water content of cooked N. norvegicus flesh is 72-75 percent.

The bacteriology of N. norvegicus has been studied by Walker, Cann and Shewan (1970), Hobbs et al. (1971) and Cann et al. (1971). After 8-10 days storage at 2.2°C the N. norvegicus tails became inedible due to the presence of strong, ammoniacal and sour odours and flavours. Bacterial counts rose sharply after the fourth

day. The initial flora consisted mainly of coryneform bacteria (80 percent), which gradually changed throughout storage until it consisted mainly of _Achromobacter_ spp. (70 percent). The bacterial flora of freshly caught _N. norvegicus_ consisted predominantly of coryneform organisms, with strains of the _Achromobacter-Acinetobacter_ group and the _Pseudomonas_, _Cytophaga_ and _Micrococcus_ genera also present. Apart from contamination during hand-peeling there was no significant change in the numbers of bacteria during processing.

According to Barker (1968) the proportion of edible material in whole cooked _N. norvegicus_ is 20 percent.

6 PROTECTION AND MANAGEMENT

6.1 Regulatory (legislative) measures[1]/

6.11 Limitations or reduction of total catch

– Limitation on the efficiency of fishing units, boats

In Faeroese waters the maximum horsepower permitted for vessels fishing for _N. norvegicus_ is 40 hp (Thomas, 1970).

– Limitation on the number of fishing units, boats

According to Thomas (1970) up to six small cutters are allowed to fish for _N. norvegicus_ in the Faeroes.

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

No data are available.

6.12 Protection of portions of the population

– Closed areas such as spawning or nursery grounds

The _N. norvegicus_ fishery in Icelandic waters is permitted only in water deeper than 60 fath (approx. 110 m) (Sigurdsson, 1965).

The use of trawl nets for the capture of _N. norvegicus_ was permitted in 1962 in certain

areas in the Firth of Clyde, Moray Firth and Firth of Forth, subject to restrictions on vessel size, the number, material of construction and dimensions of the otter boards, and the relative percentage by weight of fish landed. The maximum size of vessels permitted to fish in the Firth of Forth was 55 feet, and 70 feet in the Firth of Clyde and Moray Firth. The permitted fishing season was from 1 May to 30 September in the Firth of Clyde, 1 April to 31 October in the Moray Firth, and for a period of 3 years in the Firth of Forth. In 1968 the requirement that otter boards should be made of wood was relaxed, and fishing in the Moray Firth and Firth of Clyde was permitted throughout the year (Thomas, 1960; Pope and Thomas, 1965; DAFS, 1969).

– Closed seasons

Fishing for _N. norvegicus_ in Faeroese waters is permitted only from 15 June to 14 August (Thomas, 1970).

– Limitations of size and efficiency of gear

The minimum mesh size permitted in Icelandic waters is 80 mm (stretched mesh) (Skuladottir, 1967; Thomas, 1970).

In Scottish waters the minimum permitted stretched mesh size is 70 mm, although previously seine nets with meshes of 55 mm have been permitted (Thomas, 1960, 1969, 1970; Pope and Thomas, 1965; DAFS, 1964a).

– Restrictions based on sex or condition

Under French law, the landing, sale and transportation of female _N. norvegicus_ carrying eggs has been prohibited since 1967. However, the Directors of Marine Affairs may authorize the landing, transportation and sale of berried females for the purposes of restocking reserves.

– Restrictions based on size

From January 1936 the minimum size of _N. norvegicus_ permitted to be landed in Denmark was 160 mm total length (tip of rostrum to hind edge of telson). A convention in 1952 between Denmark, Norway and Sweden introduced a common total minimum length of 150 mm (Jensen, 1959, 1967). In 1959 this was amended to 130 mm, but Denmark retained the minimum total length of 150 mm. In 1965 the Danish minimum permitted size for _N. norvegicus_ was altered to 147 mm, and a minimum length for _N. norvegicus_ tails of 80 mm (from front edge of the first segment to the hind edge of telson) was introduced.

1/ The regulations quoted may not be complete or up to date. Absence of information for a particular country or area should not be inferred as evidence of the absence of legislation concerning _N. norvegicus_.

Fishing for, possession on board, buying, selling, transporting, etc., and the use for any purpose, particularly as animal fodder and fertilizer, of N. norvegicus with a total length (tip of rostrum to hind edge of telson) of less than 115 mm (fished north of 48°N) and 100 mm (fished south of 48°N) have been prohibited under French law since 1964.

In Spanish waters the minimum permitted size of N. norvegicus is 120 mm (from eye socket to base of telson).

Greek law prohibits the fishing and sale of N. norvegicus less than 100 dramia (100 g) in weight, with a tolerance of not more than 10 dramia (10 g).

6.3 Control or alteration of chemical features of the environment

6.31 Water pollution control

It has been suggested that the dumping of N. norvegicus remains after tailing is deleterious to the stock (DAFS, 1963b). This view is shared by French trawlermen, who are claimed to retain such offal on board for dumping later in areas removed from the recognized fishing grounds.

7 ARTIFICIAL CULTIVATION

7.1 Procurement of stocks

Stocks of berried females for breeding purposes have been obtained by trawling. Hillis (1972d) maintained larvae in the laboratory which had been caught in plankton nets.

7.2 Spawning

Spawning in the laboratory has been achieved, although resorption of the oocytes in the ovary occurred in some females (see section 3.16).

7.3 Development times

The durations of the larval stages are given in Table X.

7.4 Survival

According to Figueiredo (1971) survival of larvae from the first to the second zoeal stage was 7.7-13.2 percent, and to the first post-larval instar 0-7.3 percent. The optimum temperature for the incubation of the eggs and survival of the larvae was found to be 11-14°C. The best salinity was 38°/oo (Figueiredo and Vilela, 1972).

The survival rates of wild-caught larvae as reported by Hillis (1972d) are as follows:

zoeal stage I to stage II	16%
zoeal stage II to stage III	1.8-19%
zoeal stage III to post-larval stage I	2.3-26%
post-larval stage I to stage II	15%
post-larval stage II to stage III	4.8%
post-larval stage III to stage IV	3.2%

7.5 Foods, feeding

See section 3.22.

In laboratory experiments larvae have been found to feed satisfactorily on the following foods: mixed live plankton (Farmer, 1972a); Artemia salina nauplii (Figueiredo, 1971; Figueiredo and Vilela, 1972; Hillis, 1972d; Farmer, 1972a); and living eggs of the shrimp Crangon crangon (Figueiredo and Vilela, 1972). The post-larval instars have been fed successfully on minced Mytilus spp. (Figueiredo and Vilela, 1972; Hillis, 1972d), cephalopod flesh (Hillis, 1972d) and minced cockles (Figueiredo and Vilela, 1972).

7.6 Parasites, diseases and their control

See sections 3.22 and 3.35.

Antibiotics have been used by Figueiredo (1971), Figueiredo and Vilela (1972) and Farmer (1972a) to control the growth of bacteria.

7.7 Commercial applications

At present there are no commercial applications of cultivation using N. norvegicus. It is unlikely that this state of affairs will change in the near future, in view of the very slow growth rate of the juveniles and adults (see section 3.43).

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SYNOPSIS OF FISHERIES BIOLOGICAL DATA

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

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