On the Biology of the Norway Lobster, *Nephrops norvegicus* (L.)

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In view of the wide distribution, differences in the biology of *Nephrops norvegicus* are to be expected. The size composition of the stocks, which varies considerably, appears to be unrelated to latitude. The largest are found off Portugal and the smallest in the Irish Sea. The size of females at maturity also varies in a manner apparently unrelated to latitude. The 50% level of maturity in the High Adriatic is reached at 27 mm carapace length as compared with 33 mm off Portugal and 22 mm in the Moray Firth. The sex ratio varies seasonally because of the lower availability of berried females as compared with non-berried females and males. The percentage of females in the catch is lowest during the period between spawning and hatching. The extent of the seasonal variation is very marked in Scottish and Irish waters, but less so off Portugal and in the Adriatic. The period of egg-bearing in the Adriatic extends for about 30 weeks from June–July to January. Off Portugal spawning occurs in August–September and development takes only 28 weeks whilst around Scotland and Ireland spawning occurs around a peak in September and the incubation lasts about 34 weeks until hatching in May. Females are most abundant, relative to males, in the lowest size classes. With the onset of maturity the growth rate of the female decreases in comparison with that of the male of corresponding size. This results in a high percentage of females in the length classes about the maturity size followed by a falling off in the proportion of females to males. Annual spawning is normal throughout the distribution of the Norway lobster.

Introduction

The distribution of the Norway lobster extends from the northern part of the west coast of Africa to Iceland, into the Mediterranean as far as the Adriatic, and into the North Sea, the Skagerrak and the Kattegat. In view of the environmental differences occurring within this range, differences in the biology of *Nephrops* in the various areas are to be expected. The present comparative account of the biology of this species, throughout its geographical range, is based largely on data published by previous authors who have, however, frequently been concerned primarily with aspects other than the biology and whose

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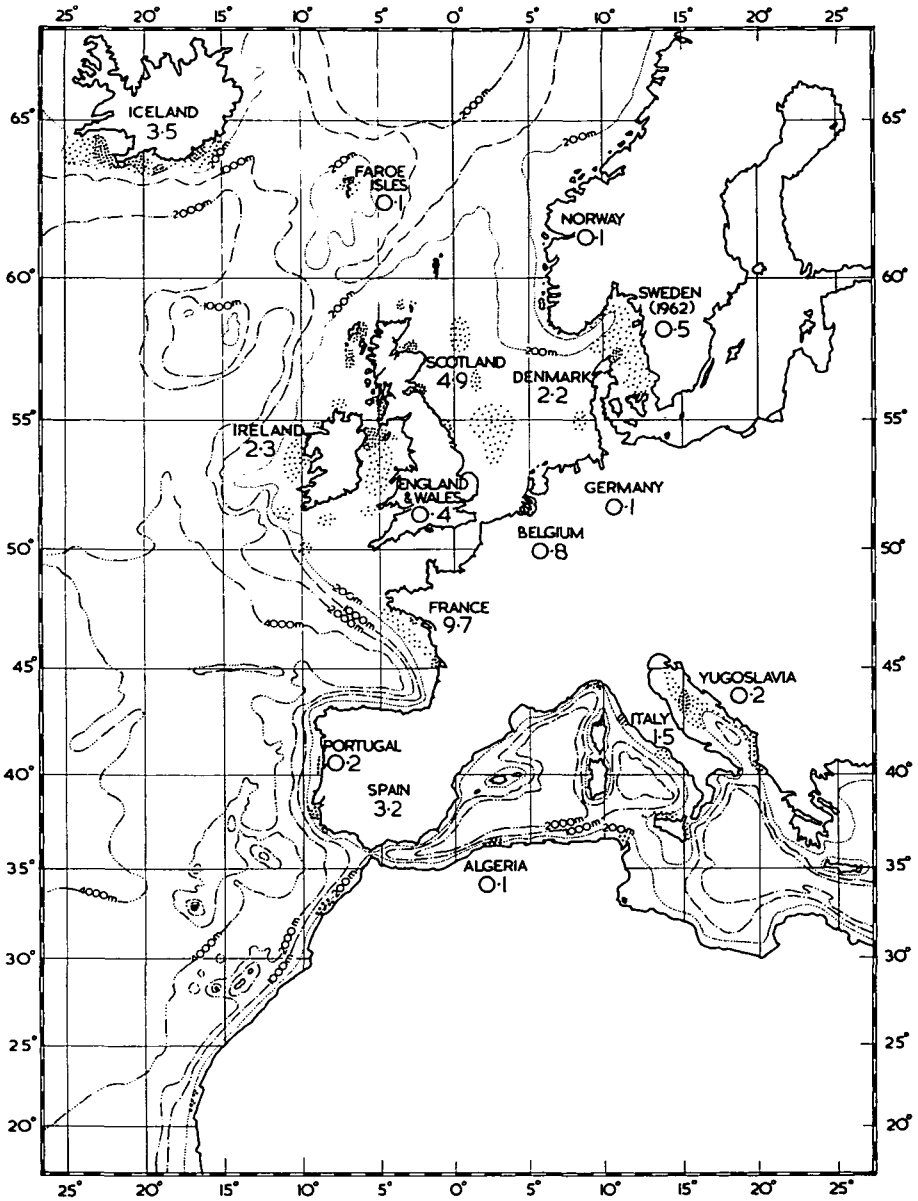

Figure 1. The distribution of the Norway lobster and the commercial landings (1000 metric tons) by country, for 1964 or, where not available, for the nearest recorded year.

results, as presented, are not directly comparable. The study, which has been undertaken at the Instituto de Biologia Maritima, Lisboa, and the Marine Laboratory, Aberdeen, has been facilitated by the collation of the authors' experience of Portuguese and Scottish *Nephrops* stocks.

Table 1

The mean size (mm carapace length) and the minimum and maximum recorded sizes of male Norway lobster taken by specified sampling on stated grounds

Area	Authority		Type of sampling vessel	Depth metres	Carapace length mm Mean	Min.	Max.
High Adriatic	KARLOVAC	(1953)	Research	50–400	34·7	12	72
North Adriatic	KARLOVAC	(1953)	Research	50–400	38·0	12	65
Northwest Italy	MATTA	(1959)	Commercial	36–440	39·4	22	60
West Portugal	FIGUEIREDO and BARRACA	(1963)	Commercial	95–549	48·0	14	92
Celtic Sea	COLE	(1965)	Research	256–586	–	15	80
Ireland	LELOUP	(1959)	Commercial	–	41·7	–	73
South Ireland	O'RIORDAN	(1965)	Commercial	37–59	34·5	27	57
Irish Sea	O'RIORDAN	(1965)	Commercial	27–55	30·1	17	47
Irish Sea	COLE	(1965)	Research	18–101	–	15	55
Clyde	THOMAS	(1965)	Research	42–126	33·9	17	57
Northwest Ireland	O'RIORDAN	(1965)	Commercial	22–48	–	17	62
South Minch	THOMAS	(1965)	Research	73–181	32·5	17	62
North Minch	THOMAS	(1965)	Research	57–130	39·6	17	72
West Orkney			Research	128–163	36·4	21	62
Moray Firth	THOMAS	(1965)	Research	29–99	32·0	17	57
Firth of Forth	THOMAS	(1965)	Research	24–69	38·3	17	67
North Sea	COLE	(1965)	Research	55–91	–	20	75
North Sea	LELOUP	(1959)	Commercial	–	42·7	–	70
North Jutland	HÖGLUND	(1942)	Commercial	40–250	–	–	77
North Kattegat and East Skagerrak	POULSEN	(1946)	Commercial	17–240	49·0	23	80
Iceland	SIGURDSSON	(1965)	Commercial	108	–	26	74
Iceland	LELOUP	(1959)	Commercial	–	54·3	–	80

Methods

The Special Meeting of the Conseil International pour l'Exploration de la Mer held in 1962 to consider problems in the exploitation and regulation of fisheries for Crustacea, drew attention in the report to the rapid progress in the study of *Nephrops* and also recommended that carapace length be adopted as the standard dimension to be recorded in scientific work. Comparisons between areas by direct reference to the literature are complicated by the fact that the early work, in general, is reported in terms of total length. Where necessary, these values have been transformed into the corresponding carapace lengths using the equation, based on Scottish data, $C = 0{\cdot}3326L - 3{\cdot}22$ (POPE and THOMAS, 1960), where C = carapace length and L = total length, both in mm.

Most of the available information on *Nephrops* shows the catch-composition by size, sex and condition at particular seasons. However, these data reflect many aspects of the biology as demonstrated by THOMAS and FIGUEIREDO (1965), whose methods have been followed in this study.

Size Composition of the Stocks

The distribution of the Norway lobsters is shown in Figure 1. The areas of occurrence relate mainly to fisheries and probably do not, therefore, fully represent the actual distribution of the species. *Nephrops* is commonly found in depths between 10 and 600 m on bottoms composed of mud of a sticky con-

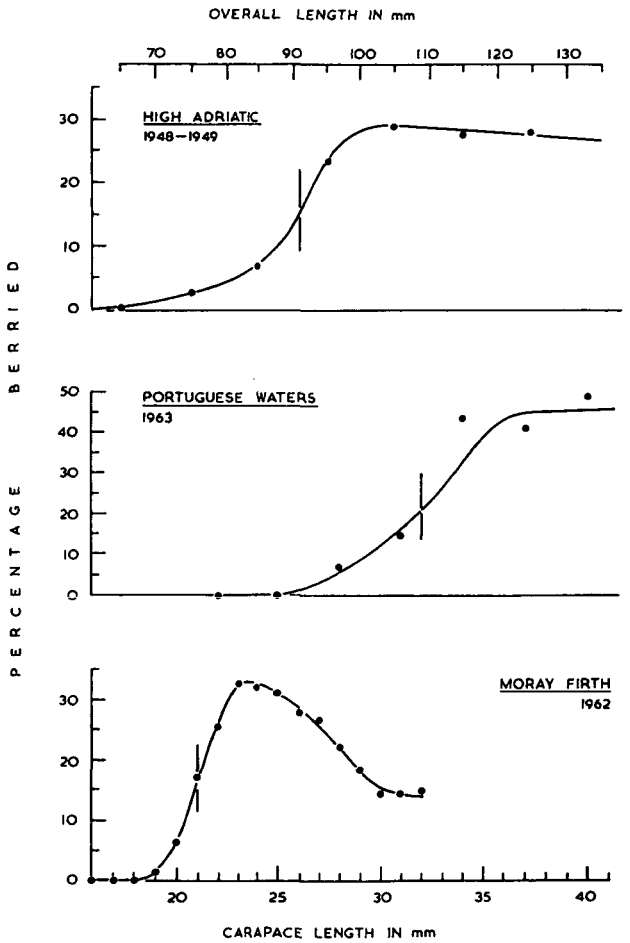

Figure 2. The percentage berried female Norway lobsters of total females by size in the High Adriatic (from KARLOVAC, 1953), Portuguese waters and the Moray Firth. The 50% maturity level is shown.

sistency. Size-composition data are derived from catches obtained using a variety of gears, mainly trawls. In the commercial fisheries where Norway lobsters are taken incidentally to the catch of white fish, for instance by Belgian trawlers, nets of mesh size 70 mm and upwards will have been employed. Where records are taken from commercial landings there is the further possibility of selection since, in some countries, for instance Ireland, the general practice is to reject small specimens. Because of these complications, research ship data provide the more reliable comparison of the size compositions of the catch in different areas. However, the maximum size of *Nephrops* taken in the various areas, by whatever means, also affords a reasonable comparison. Details of the size of male Norway lobsters in the various areas are shown in Table 1. From the research ship data the lowest mean size is found in the Moray Firth

whilst the highest is also off Scotland in the North Minch, followed by the High Adriatic. Considering the full data, the maximum recorded size of *Nephrops* is lowest from the Irish Sea (O' RIORDAN, 1965; COLE, 1965), and highest off Portugal, followed by the Celtic Sea, Danish waters and Iceland. It appears, therefore, that the size of Norway lobsters is not markedly related to latitude.

The decrease in the mean size of male *Nephrops* which has occurred from 1958 to 1962 around Scotland has been attributed to the increasing fishery (THOMAS, 1965a). A similar effect has been noted elsewhere (O'RIORDAN, 1964; JENSEN, 1965). Differences in the intensity of fishing would appear to be one factor responsible for area differences in the size of Norway lobsters. However, in Portuguese waters, where the fishery is relatively light, the maximum size of male Norway lobsters is 92 mm carapace length, whilst the largest Norway lobsters taken around Scotland in the "unfished" waters of the Inner Sound (57°41'N 05°57'W), where also predation is at a low level, attain no more than 75 mm. in *Nephrops* of this size, which are rare around Scotland, are relatively common the Portuguese catches. This difference must be attributable to some biological factor rather than fishing intensity. ANDERSEN (1962) expresses the opinion that small Norway lobsters are less readily caught in daylight than are large. Under these circumstances, shallow water fishing grounds mainly fished in daylight may give an above-average mean size, but this would not account for differences in the maximum recorded size. COLE (1965) finds that, around England, larger *Nephrops* are taken on the deeper fishing grounds, for instance the Farm area. Whilst the depth of water may itself affect the size composition of the Norway lobster stocks, its influence in this respect could well be an indirect reflection of the intensity of fishing. In any case, the maximum recorded size of 55 mm carapace length from depths of up to 101 m in the Irish Sea (COLE, 1965) is less than the maximum recorded on the Northwest Ireland grounds (62 mm) in depths of less than 50 m (O'RIORDAN, 1965) and the North Minch grounds (72 mm) in depths not exceeding 130 m (THOMAS, 1965a).

Area differences in size composition of the stocks of Norway lobsters certainly reflect the fishing intensity and predation. They appear to be unrelated to latitude. Light intensity and depth may have some influence on the size composition of the catch but there would appear to be some other major factor responsible for differences in the maximum size of Norway lobsters taken on the various grounds. A possible explanation is the differences which arise from the various levels of available food supply being reflected in different rates of growth.

Maturity Size in Females

The 50% maturity size, calculated from the percentage of females berried in each length class, for the Moray Firth, Scotland, the High Adriatic (data from KARLOVAC, 1953) and Portuguese waters is shown in Figure 2. In the Moray Firth 50% of female Norway lobsters are mature at 22 mm carapace length as compared with 27 mm in the High Adriatic and 33 mm off Portugal. As with the size composition of the stocks this wide variation between areas appears to be unrelated to latitude.

Data from other areas are insufficient to permit calculation of the 50% maturity size by the above method. However, a comparison can be made on the basis of the minimum recorded size of berried female. This figure is liable to

Table 2

The lowest recorded size (mm carapace length) of Norway lobster carrying external eggs

Area	Authority		No. females in sample	Mean size of females mm carapace length	No. berried	Lowest maturity size, mm carapace length
High Adriatic	KARLOVAC	(1953)	622	30·0	344	18
West Portugal	FIGUEIREDO and BARRACA	(1963)	2,355	36·9	527	26
Clyde	THOMAS	(1954)	2,343	26·7	171	20
Moray Firth	THOMAS and FIGUEIREDO	(1956)	11,321	27·4	1,567	21
Northeast England	STORROW	(1912)	2,036	38·4	118	23

bias owing to differences in the gear employed and the treatment of the catch, particularly in commercial catches and where the sample size is small. For this reason only samples of over 100 have been considered. The lowest recorded size of berried female in various areas is shown in Table 2. As with the 50% maturity size there is a considerable variation between areas. The highest figure is that for Portugal, 26 mm carapace length, the lowest for the High Adriatic, 18 mm. Around Scotland and the northeast of England the lowest recorded size of berried female is between 20 and 23 mm carapace length.

Whilst there is no discernible relationship between maturity size and latitude it may be significant that off Portugal, where maturity size is highest, also is the area in which Norway lobsters grow to their largest size.

Breeding Cycle

The sex ratio in the catch of Norway lobsters is highly variable. In the Adriatic, GAUSS-GARADY (1912) found that females outnumbered males at all seasons. KARLOVAC (1953), also in the Adriatic, found that the sex ratio varied seasonally, there being fewer females than males during the main period of egg-bearing, whilst females outnumber males during the months when females are mainly in a non-berried condition. THOMAS and FIGUEIREDO (1965) showed

Table 3

The percentages of females in the total catch of The peak periods of spawning

Area and date	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
High Adriatic, 1948–49 (KARLOVAC, 1953)	48 Spawn	43	41	38	–	39	–
West Portugal, 1959–64			33 Spawn	28	56	19	30
Scotland, 1960–63				46 Spawn	40	15	24
Irish Sea, 1958–62 (O'RIORDAN, 1964)				35 Spawn	20	20	18

that in Scottish waters the percentage of females in the catch followed the breeding cycle. Whilst males remain equally catchable at all seasons, egg-bearing females are less easily caught than non-berried females. This effect becomes more marked in the later stages of egg development. O'RIORDAN (1964) also noted the seasonal difference in the percentage of females in Irish waters and attributed this to migration of berried females off the fishable grounds. However, despite a marked reduction in availability, berried females in all stages of egg development are taken in Portuguese waters. In view of this and the marked variability in the catch between succeeding hauls on the same ground (THOMAS, 1965a) and between daylight and dark (SIMPSON, 1965), and also the fact that tagging experiments have not shown any migratory habit, it seems more likely that berried females remain on the grounds, but in some way, related to the burrowing habit, become less readily caught.

Because of the lower catchability of berried females as compared with non-berried females and males, seasonal variations in the sex ratio reflect the main spawning and hatching seasons. The percentage of females in the total catch of Norway lobsters by months on various grounds is shown in Table 3. The main seasons of spawning and hatching are also indicated. In all areas the percentage of females is lower during the period between spawning and hatching than during the season when females are non-berried. The extent of the seasonal variation in the sex ratio is very marked in Scottish and Irish waters but less so around Portugal and in the Adriatic. The percentage of females in the catch is highest in the Adriatic (see p. 96). As stated above berried females in all stages of egg development are frequently taken in Portuguese waters. Around Scotland on the other hand Norway lobsters bearing eggs at the eyed stages of development are rare. There appears to be a marked difference between the areas. A further factor contributing to the less marked variation in the sex ratio in southern latitudes may be that in warmer waters the egg-bearing period is less concentrated into a single season than in the north. These differences require further study (see also p. 98).

The peak period of egg-bearing in the Adriatic extends for about 30 weeks from June-July to January. Off Portugal spawning occurs in August-September and development takes only 28 weeks whilst around Scotland and Ireland spawning occurs in September and the incubation period lasts about 34 weeks until hatching in May. The spawning season differs markedly with latitude. Differences in the incubation period probably reflect mainly temperature differences but the possibility of other influences cannot be excluded.

Norway lobsters, by months, in specified areas. and hatching are also indicated

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
41	62	65	56	57	48	43			
Hatch					Spawn				
14	21	24	10	23	31	36	33	28	–
	Hatch						Spawn		
–	–	12	–	20	43	40	47	46	40
				Hatch				Spawn	
9	11	8	16	24	45	52	32	35	–
				Hatch				Spawn	

Table 4

The sex ratio, percentage females in the total catch, and the largest size group (mm carapace length) up to and including that in which females constitute at least 50% in stated seasons and areas

Area	Authority		Season	Number in sample	Size group up to which females predominate, mm	Percentage females
High Adriatic	KARLOVAC	(1953)	Mar.–Sep.	12,752	35	51·3
North Adriatic	KARLOVAC	(1953)	Apr.–June	5,677	38	56·5
Adriatic	GAUSS-GARADY	(1912)	June	50	38	80·0
Northwest Italy	MATTA	(1959)	September	180	35	48·9
West Portugal	FIGUEIREDO and	(1963)	Spring	1,875	44	30·6
	BARRACA	(1963)	Autumn	2,662	none	19·9
Irish Sea	O'RIORDAN	(1961)	Summer	not stated	27	not stated
			Winter	not stated	none	not stated
Clyde	MCINTOSH	(1904)	September	656	37	51·4
	BARNES and					
	BAGENAL	(1951)	July–Jan.	1,200	37	not stated
	THOMAS	(1954)	September	9,850	23	23·8
East Scotland	MCINTOSH	(1908)	Sept.–Apr.	5,165	23	12·9
Northeast England	STORROW	(1912, 1913)	All months	9,535	40	30·0
Denmark	POULSEN	(1946)	June–Aug.	1,248	33	27·2
Faroe	ANDERSEN	(1962)	July–Aug.	7,732	38	not stated

Sex Ratio and Size Frequency

The proportions of the sexes vary widely from area to area and even within the same area observations can be markedly different (Table 4). The sex ratio has been seen to vary seasonally owing to the decreased catchability of egg-bearing females (Table 3). Males and non-berried females do not show any marked seasonal variation in catchability. Off both Scotland and Portugal the sex ratio in size groups below the female maturity size reveals no seasonal variation. In size groups within the range of female maturity the percentage of females in the catch is markedly higher during the months when females are predominantly non-berried than when they are mainly egg-bearing (Table 5). Reported data on the seasonal catch composition from other areas do not allow of such comparison but the information relating to particular months suggests that this is a universal characteristic, although differing in extent (see also p. 94).

In all areas and at all seasons females are most abundant relative to males in the lowest size groups and, over the range below female maturity size, generally exceed 50% of the catch (Figure 3). However, even in the season when females are mainly non-berried, and therefore most abundant, the percentage of females in the catch of the higher size groups decreases markedly with increasing size (Table 5). The decrease in the percentage of females at higher sizes was noted by STORROW (1912) who attributed it to a lower moulting frequency of females as compared with males. BARNES and BAGENAL (1951) considered it due to differential mortality whilst KARLOVAC (1953) suggested a combination of both these factors. With the onset of maturity the moulting frequency of the female Norway lobster becomes less frequent than that of the male of corresponding

Table 5

The percentage of females in the total catch of Norway lobsters in each 5 mm carapace length group and overall by months for the Portuguese West Coast over the years 1959 to 1964 (A) and around Scotland over the period 1960 to 1963 (B)

A. Portuguese West Coast

Carapace length class in mm	March	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.
25 – 29	–	0	68·6	71·7	84·0	63·8	73·2	53·9	62·5	45·8
30 – 34	–	50·0	61·5	64·2	61·1	64·1	61·2	42·2	48·7	56·7
35 – 39	–	52·6	55·6	56·1	61·9	53·3	58·3	29·5	32·6	33·9
40 – 44	–	30·4	28·9	47·6	46·8	31·8	28·6	28·9	8·6	22·3
45 – 49	–	7·7	35·4	27·6	21·8	20·8	20·7	16·9	5·9	5·9
50 – 54	–	0	10·8	11·8	8·3	15·2	12·6	12·1	0	0
Overall	–	10·1	22·6	31·0	35·8	38·9	33·9	25·8	19·1	30·4
B. Scotland										
15 – 19	55·6	–	0	60·2	59·0	59·6	56·3	51·0	65·9	70·8
20 – 24	49·1	–	56·3	64·9	60·3	59·6	52·7	55·0	55·1	50·0
25 – 29	32·2	–	33·9	47·5	57·3	60·3	42·9	42·8	23·6	45·3
30 – 34	13·1	–	15·5	37·5	45·0	50·8	50·0	27·4	6·6	20·0
35 – 39	7·0	–	10·8	27·2	27·9	37·7	48·4	25·0	4·4	12·0
40 – 44	2·7	–	16·1	9·8	16·2	15·8	17·7	20·2	4·0	10·1
45 – 49	1·2	–	5·0	1·2	4·2	2·8	4·3	11·3	2·2	5·0
50 – 54	0·7	–	0	0	0·4	0	0	3·6	0·3	0
Overall	12·2	–	20·4	43·2	39·8	46·7	45·6	40·6	15·1	23·7

size (THOMAS, 1954). Furthermore, aquarium observations on the increase in size at the moult (THOMAS, 1965b) show that the percentage increase at the moult is less in mature females than in males of corresponding size. Together these factors result in the mature female Norway lobster having a much lower annual growth rate than the male. The effect of this on the sex ratio of the *stocks* will depend on the size at maturity of females, the difference in annual growth rates between the sexes and the level of total mortality of each sex. These, particularly mortality, will vary from area to area, and in any area, may well differ from year to year. In considering the sex composition of the *catch* there is the added complication of the seasonal variation in catchability of mature females, associated with egg-bearing. Because of this comparisons are more readily made between samples confined to the period when females are predominantly non-berried, and are fully represented in the catch, than at other times.

The reduced growth rate of females as compared with males results in a higher percentage of females in the length classes just above the onset of diminished growth rate, followed by a falling off in the proportion of females to males in the larger size classes (Figure 3). In any stock this effect will vary in extent according to the different levels of mortalities of males and females. The lowered catchability of berried females is a degree of natural protection which males do not have. This differential may be accentuated where the main fishing season is during the period when mature females are mainly berried and results in a high proportion of females to males in the catch.

Frequency of Spawning

It was shown (THOMAS, 1964), on the basis of ovary maturities, that at least 90% of mature female Norway lobsters in the Scottish stocks spawn annually. This subject was further investigated by THOMAS and FIGUEIREDO (1965) with the same conclusion. Whilst during the season when females are mainly non-berried the percentage of females in the total catch in the size classes above 25 mm carapace length is around 40 mm during the period November to March when females are mainly bearing eggs in other than a newly spawned condition the percentage is only 13 (Table 5B). In Portuguese stocks (FIGUEIREDO and BARRACA, 1963), in which the ovary maturities were examined throughout the year, with special reference to the state of ovary development in berried females, mature females generally spawn each year. In Portuguese stocks there is not, however, as great a decrease in the proportion of females in the total catch between the season of egg-bearing and when females are non-berried as there is in Scotland (Table 5). The difference is due to the fact that in Portuguese stocks berried females are caught to some extent in all stages of egg development and more so than around Scotland (see p. 95). A further factor may be the difference existing in the spawning seasons of the various size classes of Norway lobsters off Portugal (FIGUEIREDO, 1965).

Data from other areas, either on ovary development or on seasonal variations in stock composition, are insufficient to ascertain the frequency of spawning. In the Adriatic, however, KARLOVAC (1953) records that during the main period of egg-bearing 84% of females in the mature sizes were berried. He therefore concludes that mature females spawn annually. This direct observation is not possible in areas such as Scotland where berried females are rarely caught except in the earliest stage of egg development.

Whilst area to area variations in the frequency of spawning may well exist such limited evidence as is available for areas other than the Adriatic, Portugal and Scotland appear to accord with the position in these areas (THOMAS and FIGUEIREDO, 1965). It may, therefore, reasonably be assumed that annual spawning is normal throughout the distribution of the Norway lobster.

Discussion

Despite its wide distribution, in many respects the biology of the Norway lobster shows little variation with latitude, although there may well be differences at the northern limit of the distribution. Both the size composition of the catch and the maturity size of females vary considerably, but the differences appear to be more related to environmental factors such as food supply and possibly depth and light than to temperature. There is a marked variation with latitude in the season of spawning, and the rate of development of the external eggs appears to be closely affected by temperature, although other factors such as the amount of yolk could well be an influence. A marked difference exists in the behaviour of the berried females. In northern latitudes they are rarely taken except immediately after spawning, whilst in the Adriatic berried females with eggs at all stages of development are well represented in the catch. The position off Portugal appears to be intermediate. The reason for these differences is not clear. They have a marked effect on the composition of the stocks and certainly should be taken into account when considering the effects of

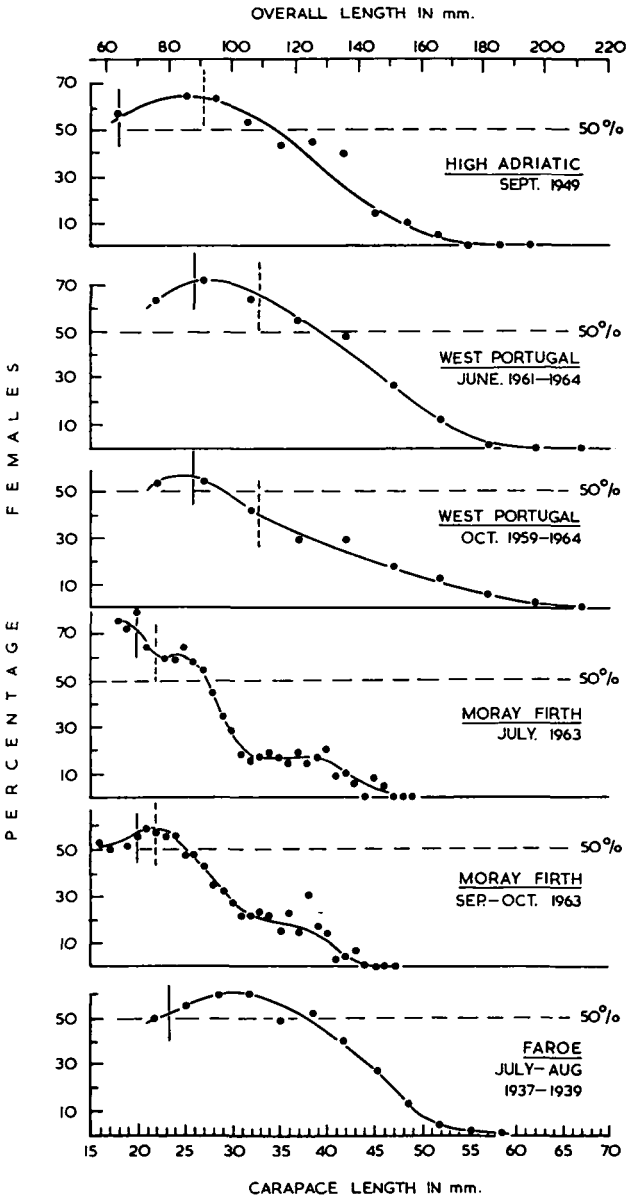

Figure 3. The percentage females of the total catch of Norway lobsters by size in stated seasons and areas. The lowest maturity size is shown by a solid vertical line and the 50% level by a broken line.

fishing. They are also important in all areas in interpreting catch data since sampling gives a biased estimate of the stock of females and the extent of the bias varies seasonally. Because of this, in the absence of a fuller understanding of the variation in catchability of females, the effects of fishing on the stocks are more readily interpreted by reference to the catch of males, which are not subject to seasonal variations in catchability.

Summary

1. The lowest mean size of male Norway lobster taken by research vessels was found in the Moray Firth whilst the highest was in the North Minch followed by the High Adriatic. The maximum recorded size is off Portugal followed by Iceland whilst the lowest is in the Irish Sea. The size of Norway lobster is not markedly related to latitude.

2. Whilst fishing intensity is a major factor influencing the size composition of the catch there is evidence that some biological factor, possibly food supply, is also important.

3. The 50% maturity size of female Norway lobsters is about 33 mm carapace length off Portugal as compared with 27 mm in the High Adriatic and 22 mm in the Moray Firth. Data on the lowest recorded size of a female carrying external eggs also support the conclusion that the maturity size is not markedly related to latitude.

4. Male Norway lobsters remain equally catchable at all seasons, whilst females are less readily caught when bearing external eggs. Consequently whilst the sex ratio in the catch remains constant at about 50% females in size groups below female maturity, in sizes above maturity the sex ratio varies seasonally, reflecting the main spawning and hatching seasons.

5. Seasonal variations in the sex ratio of the catch are more marked in Northern waters than in the Adriatic or Portugal owing to the greater catchability of egg-bearing females and to a lesser concentration of the egg-bearing period into a single season in southern latitudes.

6. The period of incubation during which females bear the eggs externally is about 30 weeks from June-July to January in the Adriatic, 28 weeks from August-September to March off Portugal and above 34 weeks from September to May around Scotland.

7. The growth rate of females relative to that of males decreases in sizes above female maturity. Consequently, the percentage of females in the catch (taken during the period when females are not bearing external eggs and are therefore fully represented) shows an initial increase in the length classes about the 50% level of female maturity thereafter decreasing rapidly in the higher length classes. The extent of this decrease in the percentage of females reflects not only the slower growth rate but also mortalities.

8. In general, mature female Norway lobsters spawn annually.

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