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Committee

Report of the Working Group on Homarus Stocks

Bergen, Norway 3-6 May 1977

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Recommendation 2:37 of ICES CM 1976 Shellfish and Benthos Committee: the Working Group on Lobster Stocks should reconvene .... to consider and report on the significant progress in lobster research and development made since the first meeting in 1975 (ICES CM 1975/K:38).

CONTENTS

1. REVIEW OF LOBSTER FISHERIES

1.1. EUROPE

The catches of the european lobster Homarus gammarus (Table 1) have continued to decline in the traditional fisheries of Sweden, W Norway, E Scotland and Wales. In England and France catches have been maintained at recent levels, which are below average. Catch-per-unit-effort (cpue) is low and falling in many areas. Fishermen are attempting to compensate for falls in cpue by increasing the number of traps fished. Catches and cpue have increased in the

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inner Skagerrak in Norway, Ireland and W-Scotland, the latter partly as a result of French, English and Channel Island vessels fishing previously unexploited stocks. Part-time fishermen continue to increase in many areas. In Sweden it is estimated that only 40% of the total catch is landed by full-time fishermen. The value per kg of lobsters has increased considerably in all fisheries.

1.2. NORTH AMERICA

Landings of the American lobster (*Homarus americanus*) in recent years by Canada and the United States have been valued in excess of $80 million, making this fishery one of the most valuable in the Northwest Atlantic. The USA currently (1975-76) lands about 13 000 tonnes annually (Table 2a). About 20% of the catch now comes from the offshore fishery. There has been a slow decline in landings and cpue while the fishing effort (number of traps) has more than doubled. Stocks appear to be fully utilised.

Landings in the Canadian fishery (Table 2b) over the last decade have fluctuated from year to year with a slight downward trend, to the present level of 16 000-17 000 tonnes per annum. Within the overall landing figures, trends have been evident from area to area along the Canadian Atlantic Coast. While Newfoundland and Quebec landings have increased over the last 3 years, there have been declines in Martimes inshore catches. These declines have not been totally offset by an offshore trap fishery from South Nova Scotia to the Gulf of Maine, which began in 1972, and has made an increasing contribution to Maritime landings up to a plateau of 500-600 tonnes over the last few years. Other events in the fishery which have followed from the high fishing intensity in most areas, have been a limitation on numbers of traps per boat and numbers of licences in the fishery in the late 1960's; more recently, buy-back schemes are being introduced in some areas, as a first attempt to reduce existing effort levels. Another significant event has been the increasing use of large traps with wider entrance holes to exploit the small proportion of the population growing through the size range that can enter the 4-5 inch (10-13 cm) diameter entrance rings of the conventional inshore traps. Taken together with the generally low size limits (below the size at first female maturity in most areas), and the high exploitation rates, this development may have disturbing implications for future recruitment to the stocks.

2. RESEARCH AND DEVELOPMENT - 1975-76

2.1. EUROPE

England and Wales

Monitoring of population structure and catch and effort ~~trends~~ have continued in all the major fisheries. To estimate growth and mortality rates and migrations a tagging programme commenced in 1976 on the E and NE coasts of England. Biological studies have included work on larval recruitment, juvenile ecology and moult staging.

France

Studies have continued on the size composition and catch rates of lobster stocks resulting from the prohibition of fishing and release of juvenile lobsters into sanctuary areas. Comparisons are being made in the laboratory of the growth rates of *H. gammarus* and *H. americanus* and hybrids.

Ireland

Monitoring of size frequencies and catch and effort (boat-trap census) has continued with comparisons of the carapace length/total length ratio on the Atlantic and Irish Sea coasts. Branded lobsters were released in 1974. Only small movements of recaptures were recorded. Exploratory fishing in 40-70 fathoms (72-126 m) 50 miles (80 km) offshore proved unsuccessful.

Norway

Catch/effort and size composition data collected over a number of years has been analysed for a yield assessment. Tagged lobsters continue to be returned.

Scotland and Sweden

Monitoring of catch, effort and population structure continued.

2.2. NORTH AMERICA

Canada

Research effort is at present expanding. Size frequency, moult stages and fishing effort are sampled at key ports. Historical data is being prepared for analysis. The need for increased size limits is being considered. Escape gap studies have been completed on crabs (*Cancer irroratus*) and lobsters. Tagging studies to estimate growth, mortality rates, movements, standing stock, recruitment etc are continuing in a number of areas. First estimates of population parameters suggest that in addition to yield/recruit considerations, present fishing strategy may be adversely affecting recruitment potential.

Tagging studies in Canadian waters have so far shown few movements >10 miles although there appear to be seasonal vertical movements in some areas which may also result in horizontal displacements on a seasonal basis.

United States.

A State-Federal Scientific Committee, consisting of scientists from 11 coastal states (Maine to North Carolina) and the National Marine Fisheries Service (NMFS), has been established to organise and conduct the necessary research to allow the formulation of lobster management plans. Every lobster-producing state has now initiated or intensified its own lobster R & D. The Lobster Scientific Committee has conducted a preliminary assessment of lobster growth and mortality to determine levels of yield-per-recruit for various levels of minimum sizes and fishing mortality, and to identify research priorities.

3. RECENT OR IMMINENT CHANGES IN MANAGEMENT STRATEGY

3.1. EUROPE

England, Wales and Scotland in 1976 introduced carapace length for the measurement of minimum landing size at 80 mm, equivalent to the previous total length measurement of 9 inches (229 mm). France, Norway and Sweden still use total length. Sweden has recently extended the summer closed season in an attempt to reduce the fishing activity of part-time fishermen, and to protect moulting lobsters. Ireland is in the process of introducing a licensing system for lobster boats, sellers and buyers, designed to control fishing effort, particularly of part-time fishermen.

3.2. NORTH AMERICA

Efforts to develop a unified management programme in the United States resulted in the establishment of a Policy Committee, composed of state fishery administrators and the Regional Director of NMFS, which provides overall programme guidance and facilitates implementation of decisions through existing legal and institutional channels. It is intended to increase the present size limits of 3 1/16 in (78 mm), 3 1/8 in (79 mm) and 3 3/16 in (81 mm) to a uniform 3½ in (89 mm) in the United States. Escape gaps are being introduced in various states.

Canada hopes to increase the size limits in some areas over the next few years. In an attempt to reduce fishing effort a licence buy-back scheme is being introduced. A closed season may be introduced for the offshore fishery. The management strategy ~~favours full-time fishermen.~~

4. GROWTH AND MORTALITY RATES

Discontinuous growth (made up of two components, moult increment and moult frequency), the apparent lack of ageing structures, the difficulty of distinguishing the modes of a size frequency distribution which might indicate year-classes or moult-classes, and the need for special tagging techniques which ensure that tags are not lost at ecdysis are the inherent problems associated with the estimation of annual growth rates of large decapod Crustacea, such as *Homarus*. The von Bertalanffy growth equation has been extensively used to describe the growth of fin-fish. While this equation is not ideally suited to the discontinuous growth pattern of lobsters it is a useful approximation which allows the use of the Beverton and Holt dynamic pool model for yield-per-recruit assessment. This is especially so when lobsters are moulting once each year over the size range considered for an assessment.

Analysis of polymodal size frequency data has provided some estimates of annual growth. The use of tagging data has provided good estimates of moult increments which have been coupled with sparse data on moult frequency. Von Bertalanffy growth equations from a number of *Homarus* stocks were examined (Table 3, Figure 1). It is readily apparent that there is considerable variation in the growth curves (Figure 1) with the slowest growth from Norway females (*H. gammarus*) and the fastest from southern New England, USA (*H. americanus*). K values ranged from 0.10 for the Norway females to 0.39 for Newfoundland males. There was also a wide range in L_∞ from 105 mm CL for Newfoundland males to 267 mm CL for Maine, USA lobsters. Much of this variability in growth rates is due to variable moult frequencies - the parameter which is the most difficult to estimate accurately!

Fishing mortality (F) rates from various sources have been calculated from tag return data and/or size composition data. The values obtained (Table 3) range from F = >0.67 (last available estimate of 0.67 in 1971) for the American offshore fishery to F = 2.30 in the Maine fishery. Generally F values exceed 1.0 and are frequently as high as 2.0.

There are no direct estimates of natural mortality (M) and the best available estimates range from M = 0.1 to 0.25 with a general consensus from the Working Group that such a slow-growing long-lived animal has few predators and that therefore natural mortality can be expected to be low - say M = <0.1.

5. YIELD ASSESSMENT

At the present time it is obvious that some of the ~~estimates for the~~ parameter inputs for a yield assessment are not wholly reliable. However, the examination of the available data for a range of stocks from both Europe and North America does enable a preliminary assessment to be made utilising a range of probable values for growth, fishing and natural mortality rates. The choice of a suitable yield model is not critical at this stage. For convenience, the Beverton and Holt (1959) dynamic pool model was chosen. This model incorporates the von Bertalanffy growth equation, which as already discussed may not be an ideal description of the discontinuous growth of lobsters. (A yield-per-recruit analysis using a discontinuous growth curve was briefly examined at the meeting and found to give similar results to those obtained by the Working Group). Isometric growth is also assumed by the model and although male lobsters show allometric growth of the chelae this model is a suitable approximation. The dynamic pool model also assumes constant mortality rates for various ages: this assumption may not be valid but the available data on mortality rates is not comprehensive enough to reject this assumption. Despite these reservations, the Group felt that useful management advice could be obtained from a yield-per-recruit assessment using this dynamic pool model with the parameter inputs at present available.

Three stocks were chosen for yield-per-recruit assessment incorporating a range of K values from 0.10 to 0.39 (Table 4). Two values of M were chosen M = 0.1, thought to be the more realistic value, and M = 0.3 to observe the effect of incorporating a higher M value. Fishing mortality (F) ranged from 0.1 to 1.5 and age at first capture - assuming knife-edged selection - from 4 to 15 years (Table 4).

5.1. YIELD-PER-RECRUIT RESULTS

Newfoundland Males

The maximum yield in weight per recruit $(Y_W/R)_{max}$ of 552 kg/1000 when M = 0.1 occurs at a high fishing mortality (F_{max} = 1.5) and an age (size) at first capture $(t_c)_{max}$ of 7 yr (96 mm CL) (Table 5, Figure 2). If M = 0.3 the $(Y_W/R)_{max}$ is reduced to 372 kg/1000 at an $(F)_{max}$ of 1.5 and a $(t_c)_{max}$ of 4 yr (Table 5, Figure 2). Although the $(Y_W/R)_{max}$ occurs at quite high values of $(F)_{max}$ the low growth rates produce flat-topped yield-per-recruit curves in which, above fairly low levels of fishing mortality, further increases in F produce only small gains in yield-per-recruit. For example, if M = 0.1 and t_c = 7 yr, the Y_W/R at F = 0.5 is 519 kg/1000, only 6% less than the Y_W/R at $(F)_{max}$ = 1.5, at

$F = 0.3$ the Y_W/R is only 13% less than at $(F)_{max}$.

Norway Males

If $M = 0.1$ the $(Y_W/R)_{max}$ of 564 kg/1000 occurs at $(F)_{max} = 1.5$ and $(t_c)_{max}$ of 9 yr (106 mm CL) (Table 5, Figure 3). The $(Y_W/R)_{max}$ is reduced to 277 kg/1000 at $(F)_{max} = 1.5$ and $(t_c)_{max} = 5$ yr if $M = 0.3$. As with the Newfoundland males, the yield-per-recruit curves are flat-topped. A reduction from $(F)_{max} = 1.5$ to $F = 0.3$ at $t_c = 9$ and $M = 0.1$ results in only a 9% loss in Y_W/R. If $M = 0.3$ at $t_c = 5$ the loss is 20%.

Norway Females

Although the growth rate is low ($K = 0.1$, Table 4) the W_∞ is higher (2.448 kg) than for the other two assessments. This results in quite high $(t_c)_{max}$ values when $M = 0.1$, the $(Y_W/R)_{max}$ of 371 kg/1000 occurs at $(F)_{max} = 1.5$ and $(t_c)_{max} = 14$ yr (Table 5, Figure 4). Of course if M is higher ($M = 0.3$) $(t_c)_{max}$ is reduced to 7 yr, although $(F)_{max}$ remains high at 1.5. As with the other assessments a considerable reduction in F has little effect on Y_W/R values. For example, if $M = 0.1$ and $t_c = 14$ a reduction from $(F)_{max} = 1.5$ to $F = 0.3$ results in only a 19% drop in Y_W/R to 300 kg/1000.

6. MANAGEMENT RECOMMENDATIONS

6.1. YIELD-PER-RECRUIT

The three assessments carried out have been used to show general conclusions regarding the relationships between Y_W/R and M, F and t_c. The model is obviously sensitive to M, the parameter which in most cases is estimated roughly. However, the general consensus is that M is low and probably less than 0.1. It is probably safe, therefore, to consider the assessments utilising $M = 0.1$ as closer to reality than those with $M = 0.3$. Although the $(F)_{max}$ values were quite high ~ 1.5, it is clear that a considerable reduction in F would result in relatively small losses in Y_W/R. This would of course increase the economic efficiency of a fishery as cpue would be expected to increase (see 6.2 also). The present calculated or estimated values of F (Table 3) generally exceed $F = 1.0$. These yield-per-recruit assessments clearly show that F values of the order of 0.3 - 0.5 would be more suitable.

The present l_c values in most fisheries are around 80 mm CL, although in one area in Canada, the southern Gulf of St Lawrence, the l_c is as low as 64 mm CL. If $M = 0.1$ the $(l_c)_{max}$ values at $(F)_{max}$ range from 96 to 117 mm CL ($t_c = 7$ to 14 yr). At the suggested level of $F \sim 0.5$ the l_c values range from 91 to 108 mm CL (t_c = 6 to 12 yr) - still well above the present size (age) at first capture. An increase in l_c would increase the yield-per-recruit from all these fisheries.

The conclusion from these preliminary assessments is clear - the present levels of fishing mortality are too high and the size (age) at first capture too low.

6.2. RECRUITMENT

Little is known about the behaviour and ecology of larval and juvenile lobsters. The source of recruitment to many fisheries is not known and little is known of the stock-recruitment relationship. Despite these unknowns, it is clear that with the present situation where exploitation rates are high and the size (age) at first capture is often below the size (age) at first maturity, many of the lobster stocks on both sides of the Atlantic are heading for recruitment failure. The proposed reduction in fishing mortality and increases in size (age) at first capture would alleviate this situation. The reduced catch rates in recent years indicate a reduction in stock abundance. Although the stock-recruitment relationship is unknown, at some low level of spawning stock an increase in stock size (resulting from a reduction in F and increase in l_c) will certainly increase recruitment.

6.3. SUMMARY OF MANAGEMENT RECOMMENDATIONS

To improve yield-per-recruit and to ensure an adequate breeding stock it is essential in most European and North American *Homarus* stocks to reduce fishing mortality significantly from the present level in excess of F = 1.0 to an optimum level within the range F = 0.3 - 0.5. At the same time the present size (age) at first capture (minimum landing size) is too low and should be raised, at least above the size (age) at first maturity for each stock.

If these management recommendations are not implemented in the near future recruitment failure in several *Homarus* fisheries can be expected and other stocks will continue to decline.

For obvious reasons, the considerable reductions in fishing mortality proposed and the immediate losses in catches resulting from increases in minimum landing sizes will be difficult to accept in socio-economic terms. The changes proposed will inevitably have to take place in measured steps. It is thus essential that the first steps in the right direction for the future management policy of

Homarus stocks to be taken immediately. Further delay only makes the inevitable proposed action more difficult to implement.

7. FUTURE RESEARCH

Although the preliminary assessments made by the Working Group used data which in many cases should be improved, clear management recommendations have been justifiably produced. Future research must concentrate on improving the parameter inputs for a yield assessment together with the additional information on the biology, particularly reproduction and recruitment, necessary to evaluate yield assessments and make valid management conclusions.

The Group felt that a considerable amount of data both published and unpublished existed which should be collated in such a way as to benefit those whose task it is to manage the Homarus stocks. In particular it was felt that a review of the growth data available and a consideration of the modelling of growth in homarids was essential. There is an obvious need to re-examine data and make better estimates of mortality parameters. Data on size and age at maturity together with information on recruitment is necessary, particularly in the light of the likelihood of recruitment failure in a number of stocks. The assessments in this report can only be regarded as preliminary. The Group believes that many of the necessary data are available for more accurate assessments to be made of many stocks other than those considered here.

REFERENCES

BERTALANFFY, von.L. 1938. A quantitative theory of organic growth. Hum. Biol. 10 (2) : 181-213.

BEVERTON, R.J.H. and S.J. HOLT. 1957. On the dynamics of exploited fish populations. Fishery Invest., Lond., Ser. 2, 19 : 533 pp.

TABLE 1

EUROPEAN LOBSTER LANDINGS (tonnes) SOURCE: BULLETIN STATISTIQUE - ICES (*Approximate or estimated as available)

	DENMARK	E & W	FRANCE	IRELAND	NORWAY	SCOTLAND	SPAIN	SWEDEN	ALL EUROPEAN COUNTRIES
1950	216	352*	304	170	969	784	19	215	3 074
51	157	346	368	139	862	643	29	252	2 833
52	186	331	449	164	712	635	32	210	2 751
53	145	403	485	200	848	635	37	216	3 006
54	124	450	499	189	648	597	34	188	2 765
55	108	506	497	253	632	662	34	167	2 889
56	101	492	537	308	708	688	32	178	3 074
57	74	528	568	270	655	728	53	148	3 059
58	75	495	625	300	714	704	68	164	3 174
59	72	489	401	347	684	819	57	160	4 159
1960	85	465	497	267	787	890	37	168	3 226
61	76	565	509	180	681	991	26	147	3 211
62	67	469	437	167	551	898	24	120	2 767
63	71	480	318	153	498	805	5	105	2 470
64	50	477	388	217	353	793	23	92	2 443
65	35	398	426	205	350	643	20	86	2 194
66	30	420	446	278	248	586	20	78	2 325
67	30	387	422	279	239	567	161	64	2 411
68	24	371	361	287	276	616	99	66	2 358
69	25	383	340	298	218	568	17	66	1 954
1970	22	491	324	277	202	602	47	71	2 108
71	15	451	310	285	133	678	20	50	1 952
72	16	429	373	221	161	585	16	43	1 893
73	13	457	420	258	150	545	13	42	1 898
74	11	377	400*	253	139	600	12	38	1 830*
75	14	342	400*	332	128	503	-	43	1 762*
76	12	348	400*	370	116	531	-	33	1 810*
Averages 1950-59	126	439	573	234	743	690	40	190	3 078
1960-69	49	442	414	233	420	736	43	99	2 536
1970-76	15	414	357*	285	147	578	22*	46*	1 893*

Table 2a. Lobster landings (tonnes) from the United States inshore and offshore (traps and trawls) fisheries for 1965-75. *Includes scuba diving and fish pots.

Year	Inshore Traps	Offshore Traps	Offshore Trawls	Other*	Total
1965	11 218	0	2 481	20	13 719
1966	11 609	0	1 776	15	13 400
1967	10 068	0	2 048	15	12 131
1968	12 253	0	2 490	25	14 768
1969	12 165	52	3 086	22	15 325
1970	11 604	666	3 199	23	15 492
1971	11 308	1 480	2 477	16	15 281
1972	10 626	2 890	1 093	17	14 626
1973	10 518	1 945	671	16	13 150
1974	10 398	1 749	940	-	13 087
1975	10 476	1 939	726	-	13 141
1976	11 708	1 914	598	-	14 220

Table 2b. Lobster landings (tonnes) in Canada.

	Maritimes					
Year	Inshore	Offshore (trap)	Total	P.Q.	Nfld	Canada
1965	15 193	-	15 193	1 494	1 695	18 382
1966	13 584	-	13 584	1 773	1 580	16 937
1967	12 926	-	12 926	1 501	1 414	15 841
1968	13 842	-	13 842	1 274	1 808	16 924
1969	15 406	-	15 406	1 083	1 730	18 219
1970	13 937	-	13 937	1 195	1 463	16 595
1971	14 720	100	14 820	1 108	1 381	17 309
1972	12 471	334	12 805	1 009	1 237	15 051
1973	13 422	481	13 903	981	1 263	16 147
1974	11 496	410	11 906	1 005	1 326	14 237
1975	14 040	547	14 587	1 204	1 697	17 488
1976	11 669	636	12 305	1 247	2 229	15 781

Table 3. Calculated or estimated von Bertalanffy growth constants, fishing and natural mortality, minimum landing size and size at maturity for a number of *H. gammarus* and *H. americanus* stocks.

COUNTRY	SEX	K	L_∞ (mm)	W_∞ (kg)	t_o	F	M	Present l_c (mm)	Size at 1st Maturity	Size at 50% Maturity
H. gammarus										
ENGLAND	♂	0.12	196	6.55		1.17	0.25	80		
	♀	0.17	160	2.59		1.17	0.25	80	77	85+
IRELAND	♂	0.121	174		0.34	0.8	0.06	83	76 - 83	
NORWAY	♂	0.20	129	1.65	(0.34)	1.5	<0.1	78		
	♀	0.10	157	2.45	(0.34)	1.5	<0.1	78		
H. americanus										
CANADA	♂	0.390	105	0.99	0.796	1.77	0.11	81		
(Newfoundland)	♀	0.240	112	1.06	0.689	1.77	0.11	81	67	75
USA										
Maine	⚥	0.048	267	12.2	-0.772	2.30	0.1-0.2	81	83	
S New England	♂	0.115	253	11.2	-0.140	>0.67	0.1-0.2	81		

Table 4. Input parameters for the Beverton and Holt (1959) yield-per-recruit equation for the Newfoundland male, and Norway male and female *Homarus* stocks.

Input	Newfoundland ♂	Norway ♂	Norway ♀
K	0.39	0.20	0.10
W_∞ (kg)	0.992	1.654	2.448
(L_∞ mm CL)	(105)	(129)	(157)
t_o (yr)	0.8	0.34	0.34
t_λ (yr)	20	20	20
t_r (yr)	4	4	4
R	1000	1000	1000
M	0.1/0.3	0.1/0.3	0.1/0.3
F_{min}	0.1	0.1	0.1
F_{max}	1.5	1.5	1.5
F_{inc}	0.1	0.1	0.1
$t_{c\ min}$ (yr)	4	4	4
$t_{c\ max}$ (yr)	15	15	15
$t_{c\ inc}$ (yr)	1	1	1

Table 5. Calculated age (size) at first capture $(t_c)_{max}$ $((l_c)_{max})$ giving maximum yield $(Y_W/R)_{max}$ for selected values of M and F, and fishing mortality $(F)_{max}$ giving $(Y_W/R)_{max}$ for selected values of M and t_c (l_c) for three *Homarus* stocks.

COUNTRY	SEX	M	F	$(t_c)_{max}$	$(l_c)_{max}$	$(Y_W/R)_{max}$	t_c	l_c	$(F)_{max}$	$(Y_W/R)_{max}$
Newfoundland	♂	0.1	0.2	5	85	458	4	75	0.4	480
			0.5	6	91	529	5	84	0.6	520
			1.5	7	96	552	6	91	>1.0	545
Newfoundland	♂	0.3	0.2	4	75	>240	4	75	>1.4	>372
			0.5	4	75	>333	5	85	>1.5	>365
			1.5	4	75	>372	6	91	>1.5	>322
Norway	♂	0.1	0.2	7	93	481	5	78	0.3	469
			0.5	8	101	547	6	87	0.4	505
			1.5	9	106	564	7	93	0.6	533
Norway	♂	0.3	0.2	4	60	>201	5	78	>1.5	>277
			0.5	4	60	253	6	87	>1.5	>272
			1.5	<5	<78	277	7	93	>1.5	>249
Norway	♀	0.1	0.2	10	97	306	7	76	0.3	290
			0.5	12	108	359	10	97	0.5	346
			1.5	14	117	371	12	108	1.0	366
Norway	♀	0.3	0.2	5	58	87	7	76	>1.5	>113
			0.5	6	68	106	10	97	>1.5	> 88
			1.5	7	76	113	12	108	>1.5	> 65

Figure 1. Lobster growth curves (von Bertalanffy) for various stocks of *H. gammarus* and *H. americanus*.

Figure 2. Yield-per-recruit (kg/1000) isopleths for a range of fishing mortalities (F) and age at first capture (t_c) for Newfoundland, Canada, male *H. americanus*: (top) natural mortality (M) = 0.3, (bottom) M = 0.1.

Figure 3. Yield-per-recruit (kg/1000) isopleths for a range of fishing mortalities (F) and age at first capture (t_c) for Norwegian male *H. gammarus*: (top) natural mortality (M) = 0.3, (bottom) M = 0.1.

Figure 4. Yield-per-recruit (kg/1000) isopleths for a range of fishing mortalities (F) and age at first capture (t_c) for Norwegian female *H. gammarus*: (top) natural mortality (M) = 0.3, (bottom) M = 0.1.

FIGURE 1.

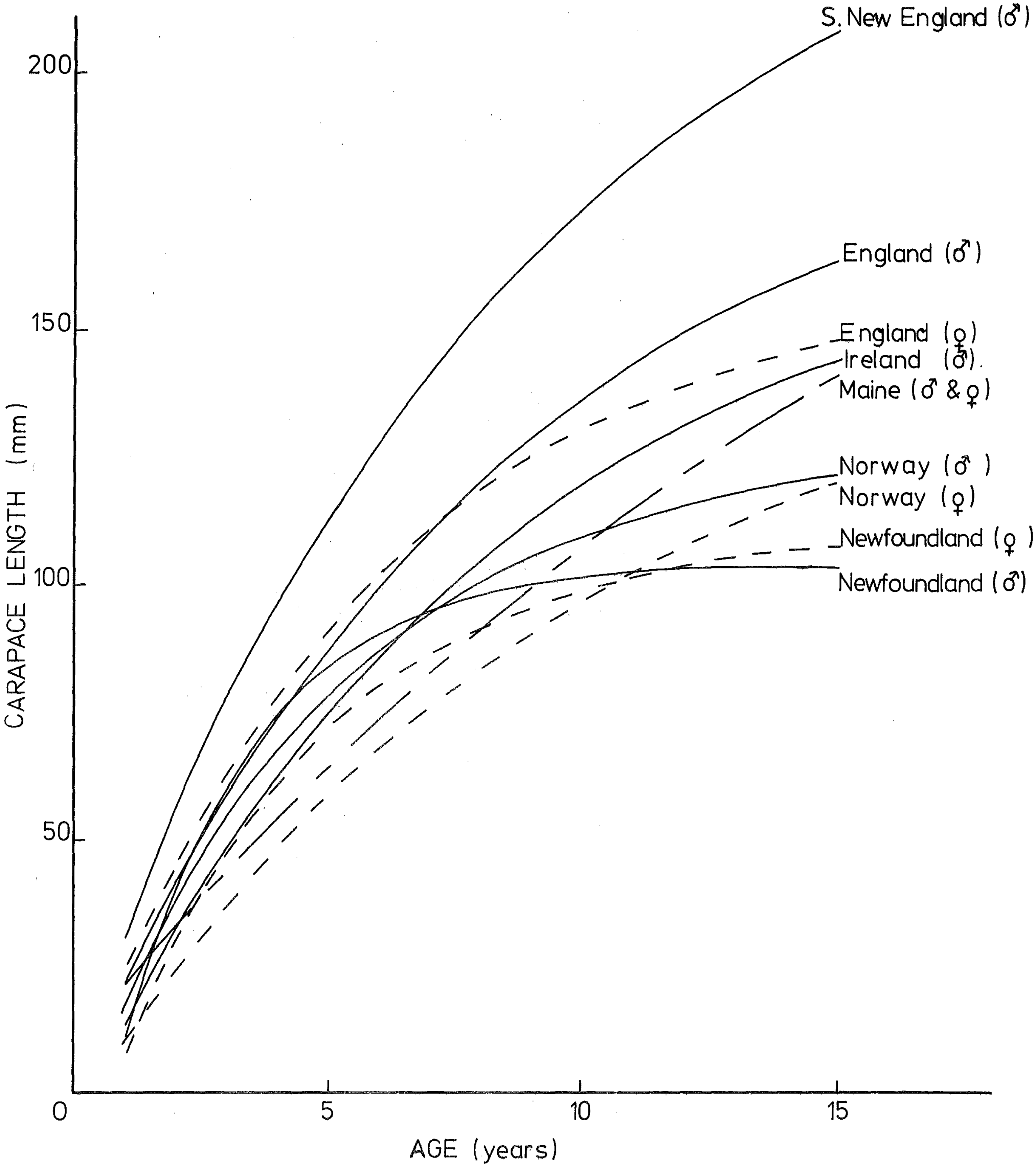
S. New England (♂)
England (♂)
England (♀)
Ireland (♂).
Maine (♂ & ♀)
Norway (♂)
Norway (♀)
Newfoundland (♀)
Newfoundland (♂)
CARAPACE LENGTH (mm)
200
150
100
50
0
5
10
15
AGE (years)

FIGURE 2.

t_c																
15	8	13	17	20	22	24	25	26	27	28	28	29	29	30	30	25
14	11	18	24	27	30	32	34	35	36	37	38	39	39	40	40	50
13	15	25	32	37	41	43	46	47	49	50	51	52	53	54	54	
12	21	34	43	50	54	58	61	64	65	67	69	70	71	72	73	
11	29	46	58	67	73	78	82	85	87	89	91	93	94	95	97	100
10	38	62	78	89	97	103	108	112	115	118	121	123	124	126	127	
9	81	82	102	117	127	135	142	147	151	155	158	160	163	165	166	
8	67	107	133	152	165	175	182	189	195	199	203	206	209	212	214	200
7	87	138	171	193	210	222	232	239	246	251	255	259	262	265	268	
6	110	173	213	239	258	273	283	292	299	305	309	313	317	320	322	300
5	136	210	255	284	304	319	330	338	344	349	354	357	360	362	365	
4	159	240	286	314	333	345	353	359	363	366	368	370	371	372	372	
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	F

t_c																
15	104	170	212	240	259	272	281	288	293	296	299	301	303	305	306	300
14	126	201	246	274	293	305	313	319	323	327	330	332	334	336	227	
13	150	233	280	308	326	337	345	351	356	359	362	365	367	369	370	
12	175	265	314	342	360	371	379	385	390	394	397	399	402	403	405	400
11	201	298	349	377	395	406	415	421	425	429	433	435	438	439	441	
10	228	332	384	412	430	442	450	456	461	465	468	471	473	475	477	
9	255	365	418	447	464	476	484	490	495	498	502	505	507	509	510	500
8	282	398	451	479	495	506	514	520	524	527	530	532	534	536	537	
7	309	426	478	504	519	529	535	539	543	545	547	549	550	551	552	
6	331	448	495	518	529	536	540	542	544	545	545	545	545	545	545	
5	347	458	497	513	518	520	520	519	517	516	514	512	511	510	507	
4	354	450	476	480	477	472	466	450	454	448	444	439	435	431	428	
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	F

FIGURE 3.

t_c	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5
15	12	20	26	30	33	35	37	38	40	41	41	42	43	43	44
14	16	27	34	40	43	46	49	50	52	53	54	55	56	57	57
13	22	36	45	52	57	60	63	66	67	69	70	72	73	73	74
12	29	47	59	68	73	78	82	84	87	89	90	92	93	94	95
11	38	61	76	87	94	99	104	107	110	113	115	116	118	119	120
10	49	78	97	109	118	125	130	135	138	141	143	145	147	149	150
9	63	98	121	136	146	154	161	165	169	173	175	178	180	181	183
8	78	121	147	165	177	186	193	198	203	206	209	212	214	216	217
7	95	145	175	195	208	218	225	231	235	238	241	244	246	248	249
6	112	169	202	222	235	245	251	257	260	263	266	268	269	271	272
5	128	189	222	241	253	260	266	269	272	273	275	276	276	277	277
4	140	201	230	245	253	257	259	260	260	260	259	258	258	257	256
F	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5

50 100 200 250

t_c	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5
15	156	254	317	358	384	402	414	423	429	434	438	440	443	445	446
14	187	296	360	399	423	439	449	457	462	466	469	472	474	476	477
13	218	335	399	436	458	472	481	488	492	496	499	501	503	505	506
12	248	371	435	469	489	502	510	515	519	523	525	527	529	530	532
11	277	405	466	498	516	526	533	538	541	544	546	548	549	551	552
10	305	434	492	520	536	544	550	554	556	558	560	561	562	563	563
9	330	458	511	535	547	553	557	559	561	562	563	563	563	564	564
8	350	474	520	539	547	550	552	552	552	552	552	551	550	550	549
7	366	481	518	530	533	533	531	529	527	525	523	521	520	518	517
6	375	476	502	505	502	497	492	487	482	478	475	472	469	466	464
5	375	458	469	463	452	442	432	424	417	411	406	401	397	393	390
4	365	426	420	402	384	368	354	343	333	325	318	312	306	301	297
F	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5

400 500 550

FIGURE 4.

t_c	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5 F	
15	10	17	22	25	28	30	31	32	33	34	34	35	35	36	36	
14	14	22	28	32	35	37	39	40	41	42	42	43	43	44	44	50
13	18	28	35	40	43	46	47	49	50	51	52	52	53	54	54	
12	22	35	43	49	53	55	57	59	60	61	62	63	64	64	65	
11	28	43	53	59	63	66	68	70	72	73	74	75	75	76	77	75
10	34	52	62	69	74	77	80	82	83	85	86	86	87	88	88	
9	40	61	73	80	85	88	91	93	94	96	97	98	98	99	99	100
8	47	70	82	90	95	98	101	103	104	105	106	107	107	109	108	
7	53	78	91	98	103	106	108	109	110	111	112	112	112	113	113	
6	59	84	96	103	106	108	110	111	111	111	112	112	112	112	112	
5	63	87	98	102	104	105	105	105	105	105	104	104	103	103	103	
4	65	86	94	96	95	94	93	92	91	90	88	87	87	86	85	

t_c	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5 F	
15	138	223	275	308	329	342	350	356	359	362	363	364	365	366	366	
14	160	248	300	329	346	355	361	365	367	368	369	370	370	371	371	
13	180	272	319	343	356	362	366	268	367	370	370	370	370	370	370	
12	198	288	330	350	359	363	365	365	366	366	366	365	365	365	365	
11	212	300	336	350	356	357	358	357	356	356	355	354	354	353	353	350
10	224	306	334	344	346	345	344	342	341	339	338	337	336	335	334	
9	231	305	327	330	329	326	323	320	318	316	314	312	311	309	308	300
8	235	299	312	310	306	300	296	292	288	285	283	281	279	277	276	
7	234	286	290	284	275	268	262	256	252	248	245	243	240	238	236	
6	230	268	263	251	239	230	222	216	210	206	202	199	197	194	192	200
5	221	244	230	213	199	187	178	171	165	161	157	153	150	148	146	
4	209	216	194	173	156	143	134	126	120	115	111	107	105	102	100	