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Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland II: fecundity and size at onset of sexual maturity

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The fecundity and size at onset of sexual maturity of *Nephrops norvegicus* was estimated at different locations within the Firth of Clyde, S.W. Scotland. The "potential" fecundity was estimated from oocyte counts in mature ovaries, while estimates of "actual" fecundity were made from counts of the eggs attached to the pleopods of ovigerous females. Size at onset of maturity of *Nephrops norvegicus* was estimated from the study of primary (ovary maturity and eggs on pleopods) and secondary (allometric) sexual characteristics.

Relationships between potential fecundity and female carapace length were found to conform to a power function ($F=aL^b$). Comparison of the logarithmic formulations of the relationships for seven locations revealed no differences in power terms, but there were significant differences in the constants. Results suggested that differences in fecundity mainly reflected a geographical variation in oocyte volume (expressed in terms of mean dry weight) which appeared to be related to growth. Where growth rate was characterized by a low value for the asymptotic length of the carapace (L_∞), females appeared to have smaller oocytes and larger size-specific fecundity.

Estimates of size at onset of sexual maturity varied over small geographic scales (tens of km) and ranged between 21–34 mm carapace length for females and 29–46 mm for males, the estimate obtained from the different approaches being similar. Size at onset of maturity was positively related to L_∞ ($p<0.05$) and negatively related to adult density ($p<0.05$). Age at onset of maturity appeared relatively constant geographically but varied between the sexes (males, 4–4.5 years; females, 3–3.5 years).

Key words: *Nephrops norvegicus*, fecundity, size at onset of maturity.

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Introduction

The fecundity of female *Nephrops norvegicus* has been examined throughout its geographical distribution (Eiriksson, 1970; Chapman and Ballantyne, 1980; Morizur *et al.*, 1981; Orsi Relini and Relini, 1989). Two aspects of this subject are of major interest. The first, noted by several authors (e.g. Thomas, 1964; Farmer, 1975; Chapman and Ballantyne, 1980; Bailey *et al.*, 1986; Smith, 1987), is the occurrence of large variations in fecundity between different populations, and perhaps even between different parts of the same population. Smith (1987), for example, suggested that local variability in fecundity could exist within the Firth of Clyde. As far as we are aware, no work has been done on the possible genetic basis of fecundity variability, but there have been suggestions of a link with other parameters such as growth and size at maturity. Variations in these parameters are thought to be related to environmental factors (Bailey *et al.*, 1986; Chapman and Bailey, 1987; Chapman and Howard, 1988; Tuck *et al.*, 1997a). In contrast, Sarda (1995) concluded that variability in *Nephrops* fecundity could not be attributed to local area or population effects, but was more likely to have arisen from other factors, such as the variety of methods used and egg loss. We define potential fecundity as the number of oocytes in the ovary, actual fecundity as the number of eggs on the pleopods at the time of capture,

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Table 1. Firth of Clyde station positions and equation parameters for relationships of potential fecundity based on oocyte counts $F = a \times CL^b$ where F is potential fecundity, CL is carapace length, and a and b are constants. Parameters are given for the best fits to individual data sets. Intercepts for pooled slope (2.697) followed by same letter are not significantly different ($p > 0.05$).

Trawl station	Lat. and long. start	Lat. and long. finish	No. of obs	Parameters for equation $F = a \times CL^b$		Pooled slope intercept
				(a)	(b)	
1	55°23.86′N 04°57.82′W	55°22.45′N 04°57.65′W	24	0.1928	2.699	0.1947[a,d]
2	55°14.76′N 05°02.41′W	55°14.78′N 05°04.72′W	17	0.0981	2.821	0.1501[b]
3	55°10.41′N 05°13.05′W	55°09.03′N 05°13.12′W	34	0.2353	2.647	0.2001[c,d]
4	55°08.82′N 05°16.89′W	55°10.15′N 05°17.72′W	29	0.4835	2.417	0.1897[a,d]
5	55°19.52′N 55°19.44′W	55°20.73′N 05°18.66′W	26	0.3052	2.539	0.1782[a,d]
6	55°20.94′N 05°15.69′W	55°21.67′N 05°13.86′W	25	0.0287	3.180	0.1543[b]
7	55°41.62′N 04°56.86′W	55°40.98′N 04°58.10′W	32	0.2052	2.654	0.1765[a,d]

and effective fecundity as the estimated number of eggs on the pleopods at the time of hatching.

The loss of eggs from the abdomen during incubation is another important aspect of fecundity in *Nephrops* (Froglia and Gramitto, 1979; Chapman and Ballantyne, 1980; Figueiredo *et al.*, 1982; Gramitto and Froglia, 1980; Morizur, 1981; Smith, 1987). Information on this aspect is essential when fecundity is used in conjunction with *Nephrops* larval surveys for estimating spawning stock size (e.g. Nichols and Thompson, 1988; Tuck *et al.*, 1997b).

Wenner *et al.* (1974) considered the size at which crustaceans become sexually mature to be a very useful gauge in the study of environmental effects on field populations. Size at the onset of maturity (SOM) in female *Nephrops* has been studied by measurement of the smallest ovigerous female (for review, see Farmer, 1974a) and estimation of 50% maturity from ovary examination (Bailey, 1984). In reviewing the literature, Farmer (1974a) found considerable geographic variation in the size of the smallest ovigerous female (18–36 mm). Thomas (1964) found variations in the size at first maturity around the Scottish coast, and Bailey (1984) recorded variations in size at 50% maturity over relatively small geographic ranges. No reliable external index of maturity has been described for male *Nephrops* (Figueiredo and Thomas, 1967) and the SOM has not been successfully examined through study of the development of the testes (Farmer, 1974a). Tessier (1960), however, found that changes in the relative growth of various body proportions (allometry) occur at sexual maturity and Farmer (1974b) successfully examined the relative growth of *Nephrops* in the Irish Sea using chela propodal length (males) and abdomen width (females). Variations in SOM over small geographic scales could have important implications for fisheries management, particularly if mesh sizes are set to avoid the capture of immature individuals.

The present paper investigates the geographic variability in potential fecundity and SOM in the Firth of Clyde, comparing the results of a number of different techniques. Observations are also made on egg loss during incubation.

Materials and methods

Potential fecundity

During August and October 1991, non-ovigerous females with mature, dark green, ovaries (stage 4; Bailey, 1984), were caught during a trawling survey of *Nephrops* grounds in the Firth of Clyde by R.V. "Aora". Samples were collected from six stations in the Outer Firth, south of the Island of Arran, and from one station further north, near the Island of Little Cumbrae (see Table 1). The latter station (No. 7 in Table 1) was selected to be reasonably close (within 1.7 km) to the Firth of Clyde position sampled previously by Smith (1987). Water depth varied from 47–80 m and the distances between the six southerly stations ranged from 4–32 km. The northerly station was between 30–60 km from the other stations.

Whole mature females were frozen on board the research vessel and returned to the laboratory for analysis. They were fixed in 4% buffered formalin for 24 h, then transferred to 70% alcohol. The use of both these

preservatives hardened the oocytes and facilitated the dissection of the intact ovary (Figueiredo and Nunes, 1965).

The carapace length (CL) of each female was measured to the 0.1 mm below, using callipers. The dissected ovaries were dried to constant weight at 100°C for 24 h. The weighing was performed on a digital balance to an accuracy of 0.001 g. Figueiredo *et al.* (1982) found no variation in oocyte weight in different parts of the ovary, so for each female, a single sub-sample of the oocytes was counted, dried again, weighed, and then raised to the dry weight of the whole ovary to calculate the total number of eggs. The size of the sub-sample varied with female size, from over half the weight of the whole ovary in small females to over 1000 ova in larger lobsters. Smith (1987), using similar techniques, found the maximum error in oocyte counts was less than 3%.

The fecundity estimates were analyzed in relation to female size by regressions on $\log_{10}$-$\log_{10}$ (allometric) plots, since this gave a better fit than untransformed data. Most previous studies in size-specific fecundity in *Nephrops* have also used this method. The allometric model has a theoretical slope of 3.0, implying that fecundity is a simple volumetric function of female size (Somers, 1991).

Actual fecundity

Additional trawling in the Outer Firth of Clyde was carried out at various times, between November 1990 and February 1992, during which ovigerous females were removed from the catch, frozen individually in labelled polythene bags and returned to the laboratory. All the eggs in each brood were carefully removed from the pleopods and counted. Although a high proportion of eggs sometimes failed to adhere to the pleopods (Smith, 1987), all observations were included.

Size at onset of sexual maturity

During August 1991, the carapaces of a sample of non-ovigerous female *Nephrops* from each trawling station were cut open and the ovaries were staged by colour and shape according to the method by Bailey (1984). Spawning occurs in September or October in the Clyde Sea area, and SOM estimates based on ovary maturity are known to show temporal variability in relation to this (Anon., 1994). By sampling in August we aimed to estimate SOM at the time of peak abundance of females with mature ovaries. SOM was estimated by fitting the logistic model to data on the percentage of mature females for each mm size class and estimating the CL at which 50% had ovaries in advanced stages of development (pale or dark green in colour; stages 2–4, Bailey, 1984). The CL of the smallest ovigerous female from each station was also taken as a measure of SOM (Bailey, 1984).

Samples of male and female *Nephrops* were taken from the catches in August and October 1991, frozen on board and returned to the laboratory where biometric measurements were taken. Additional samples were also collected in January 1994. The measurements taken included CL, abdomen width (at the second abdominal somite) and the propodal length of the crusher claw. *Nephrops* are usually heterochelous, one chela being shorter and stouter with coarse blunt teeth (crusher), while the longer more slender chela has only short fine teeth (cutter) (Holthuis, 1950). The chela measurement was not taken when limb regeneration was suspected.

The indicator of body size was chosen to be CL (Farmer, 1974b), with the other measurements being examined in relation to this. Analysis of the allometric data was carried out using the methods of Farmer (1974b) (least analysis regression [LSR] with log-transformed [claw length] or untransformed data [abdomen width]) and Lovett and Felder (1989) (by reduced major axis [RMA] with untransformed data). For the LSR, the data for males and females were initially analyzed separately, with parts or all of the data sets being grouped together later if there were no significant differences between them. Regression lines were calculated for upper and lower size ranges of animals where inflexions were noted in the relationship on arithmetic coordinates. Individual points around the point of inflexion were assigned to the upper or lower regression by minimization of the sum of squares of the residuals of the regressions. Differences between these regressions were examined by analysis of variance (ANOVA) and analysis of covariance (ANCOVA). Where no inflexion was noted over the size range examined, a combined regression equation was obtained. For the RMA, the sexes were analyzed separately throughout. For each data set, data were repetitively split into two groups, with CL < and > a hypothesized transition point. A separate regression function was calculated for each of the two groups after each relocation of the transition point, such calculations being performed iteratively with successive relocation of the transition point at 0.5 mm intervals across the range of CL. The CL at which the relative growth changed most precipitously (point of inflexion) was defined as the transition point for which the regression functions of the two groups best fit the combined data set. This point was selected empirically as that which produced the highest probability of random residuals for the two groups. Lovett and Felder (1989) provide full details of this technique. For both techniques, SOM was taken as the point of inflexion in the data, and the estimates from each technique were compared.

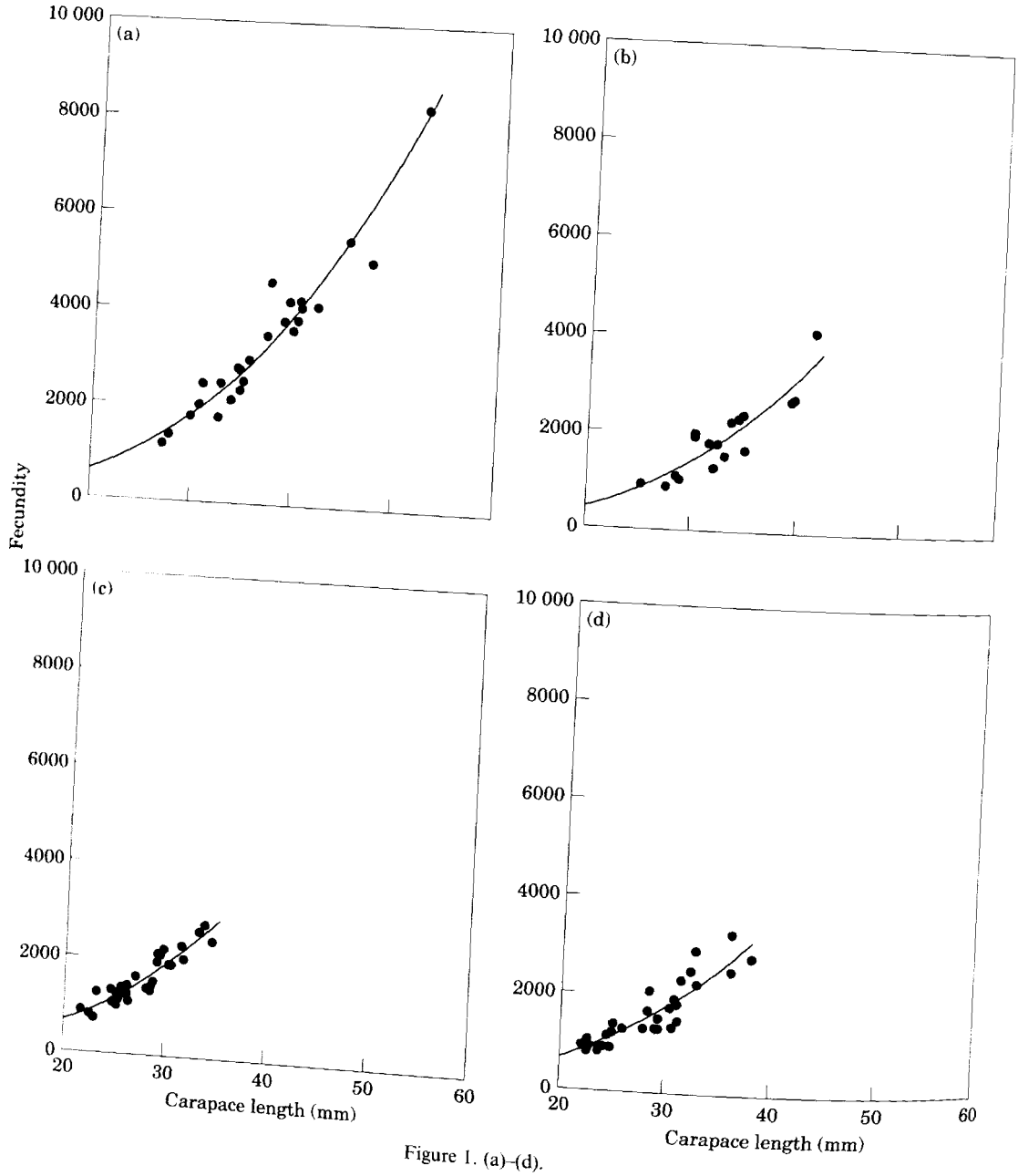

Figure 1. (a)–(d).

Results

Estimates of potential fecundity from oocyte counts

Relationships between potential fecundity and CL for females caught at each of the trawl stations were curvilinear (Fig. 1). The size range of individuals measured varied between stations (Fig. 1), reflecting the considerable spatial variability in growth rate known to exist in the Firth of Clyde (Tuck *et al.*, 1997a). The slopes of the original equations (Table 1) were found to be significantly different from the theoretical slope of 3.0 (t-test, $p<0.05$), the value which implied that potential fecundity was a simple volumetric function of female size (Somers, 1991). ANOVA results for the seven biometric relationships revealed no significant difference in their slopes but significant differences in intercepts (Table 2). A pooled slope was therefore calculated (2.697, with standard error of ± 0.076) and the intercepts were re-calculated using this slope (Table 1). The difference

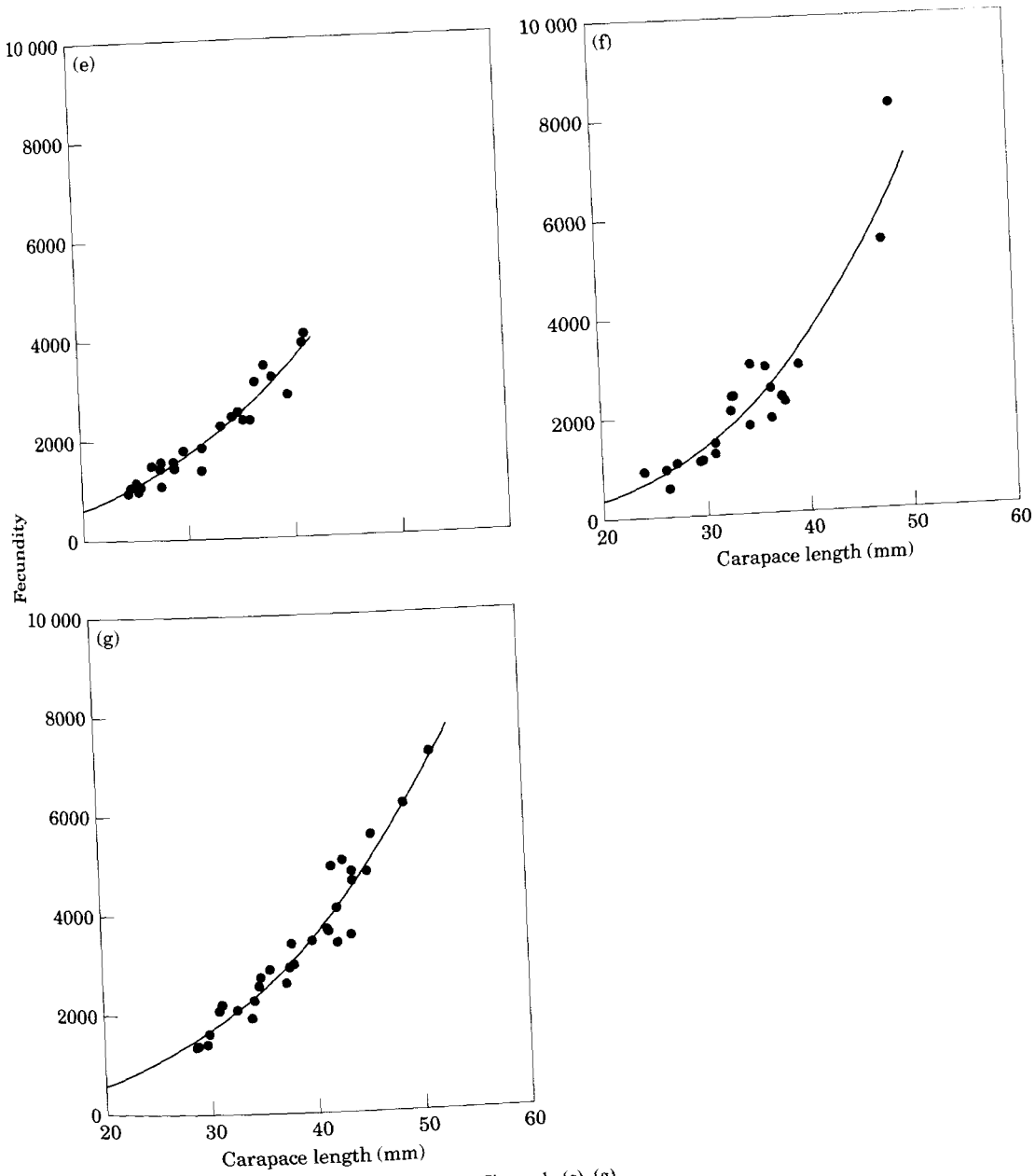

Figure 1. (e)–(g).

Figure 1. Scatterplots of potential fecundity against carapace length for stations 1 (a), 2 (b), 3 (c), 4 (d), 5 (e), 6 (f), and 7 (g). Lines represent best fit to equation Fecundity=a.CL^b, with parameters given in Table 1.

between these intercepts represented variation in potential fecundity between stations. A pairwise comparison between intercepts, using the Tukey HSD test suggested that the fecundity data could be broadly divided into two groups of stations (Table 1). The intercept values for females at stations 2 and 6 did not differ significantly from each other but both were significantly smaller than at all the remaining stations. Among the remaining stations the intercept values did not differ significantly, with the exception of those for stations 3 and 7.

Fecundity was a function of ovary and oocyte volumes, and hence was likely to be related to ovary and oocyte dry weight. Indeed, the method of fecundity determination adopted in this study was based on the measurement of both of these weight parameters. The above variations in fecundity could reflect differences in

Table 2. Analysis of variance tables for comparison of potential fecundity regressions.

	Sum of squares	d.f.	Mean square	F value	p
Test for homogeneity of slopes					
Station	0.230	6	0.038	1.576	0.157
Log (CL)	27.511	1	27.511	1130.810	>0.001
Interaction	0.188	6	0.031	1.287	0.265
	4.209	173	0.024		
ANCOVA test of intercepts					
Station	1.881	6	0.313	12.761	>0.001
Log (CL)	30.153	1	30.153	1227.588	>0.001
	4.397	179	0.025		

ovary and/or mean oocyte weights. At each station, there was a significant positive relationship between the log total dry weight of the mature ovary and female CL. When these relationships were analyzed by ANCOVA, that for station 2 was found to differ significantly from the others in intercept, but not in slope. The relationships for the other six stations did not differ significantly from each other. When a pooled slope was adopted (0.0378) and the intercepts recalculated, the value obtained for station 2 was significantly smaller than for stations 1 and 7. The intercepts for all the other stations did not differ significantly.

A similar analysis of the mean dry weight of oocytes from the ovary found no significant relationships with female CL at any of the individual stations. The mean oocyte dry weights, averaged for all females from each station, ranged from 0.2118 mg (station 3) - 0.3228 mg (station 7). Significant differences were found in mean oocyte dry weight between stations (ANOVA, $p<0.001$). A pairwise comparison of the data showed the mean at station 3 was significantly smaller than the means at stations 1, 5 and 7, which did not differ from each other. The mean for station 7 was also significantly different from the means at stations 2, 4 and 6. All other stations means did not differ significantly from each other. Since all the ovaries examined were at a similarly late stage of maturation, variation in mean dry weight of the oocytes was unlikely to be related to differences in development stage of the ovaries.

The method used for *Nephrops* fecundity estimation in the present study was essentially based on determining the dry weight of the ovary and a portion of the oocytes. Therefore, fecundity variability needs to take account of possible geographical variation in ovary and mean oocyte weight. Figure 2 showed the variation in all three parameters between stations, arranged in ascending order of fecundity intercept values (Fig. 2a). The fecundity intercept values at stations 2 and 6 (Fig. 2a) were significantly smaller than at the other stations (Table 1) reflecting a smaller ovary dry weight (assumed to be proportional to ovary volume) (Fig. 2b), and to a lesser extent, a relatively small oocyte dry weight (Fig. 2c). There was relatively little variation in log ovary dry weight between the remaining stations (7, 5, 4, 1, and 3) (Fig. 2b). For the latter group of stations, fecundity may have been inversely related to the mean dry weight of the oocytes (assumed proportional to oocyte volume) (Fig. 2c).

Actual fecundity

The numbers of eggs on pleopods ranged from 140 to over 4000 per female, showing a general increase with

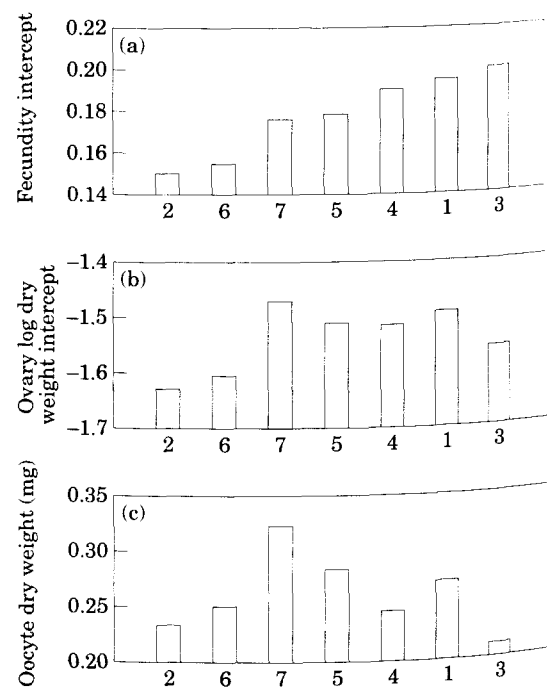

Figure 2. Summary of (a) potential fecundity intercept, (b) ovary log dry weight intercept and (c) mean oocyte dry weight (mg) values for mature females at each station. Bars representing each station are arranged in increasing order of their fecundity intercept value.

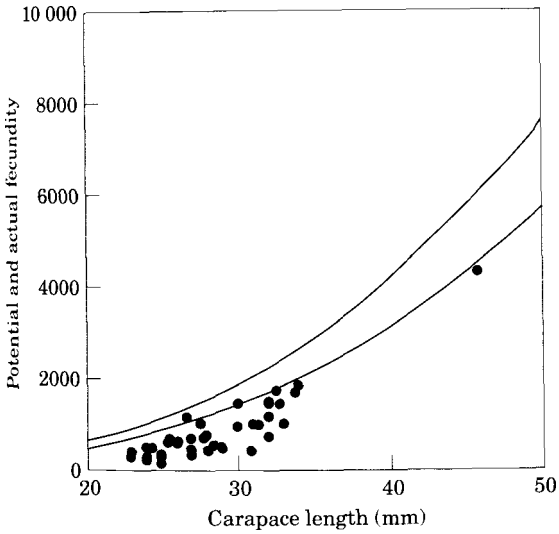

Figure 3. Range of potential fecundity measured in the Firth of Clyde (solid lines), and actual fecundity (●) of trawl caught animals.

female (Fig. 3). Actual fecundity also varied considerably for a given CL, with egg counts for 27 mm CL females, for example, ranging from 347 to 1050. The actual fecundity was compared with the potential fecundity range for the Firth of Clyde (Table 1), and indicated a considerable egg loss for some individuals (Fig. 3).

Size at onset of sexual maturity

The estimates of SOM of *Nephrops* for each sex at each station, as assessed by each method, are shown in Table 3. The parameters for the LSR analysis are shown in Tables 4a and b, with a summary of their further analysis in Table 5. The parameters for the RMA analysis are shown in Tables 6a & b. It was not possible to obtain estimates for all stations using each technique. No inflexion was identified in the crusher length relationship for males at station 1 using the LSR technique. The RMA technique provided estimates with the highst probability of random residuals, but these probabilities were not significant for females at stations 1, 2 and 7, and for males at stations 2 and 5. In examining relationships between SOM parameters, these non-significant estimates were not included.

The estimates of female SOM varied considerably between stations (ranging from 21–32 mm; Table 3), but did not vary significantly between techniques (Wilcoxon signed rank test). A similar pattern was also shown by the male estimates, which did not vary significantly between techniques. Significant differences were identified between sexes, with estimates of male SOM significantly greater than the female estimates ($p<0.05$) in all but one case (RMA analysis of males vs. smallest ovigerous female; $p=0.075$).

Similar trends were shown between stations, and the estimates from each technique were positively correlated, although not all significantly so. For females, Spearman rank correlation showed that estimates from ovary maturity and both allometric approaches were significantly correlated ($r_s>0.94$, $p<0.05$). Neither the correlation coefficients between techniques for males ($r_s=0.700$) or between sexes (r_s 0.493 0.949) were significant given the small sample sizes.

The strong positive correlation between the estimates from different techniques results in each set of estimates showing similar relationships with population parameters. These relationships are summarized by describing the analysis for females based on ovary maturity and males based on crusher length (LSR and RMA

Table 3. Estimates of size at onset of maturity for each of the trawling stations, using primary sexual characteristics and least squares regression (LSR) and reduced major axis (RMA) allometric techniques.

	Females (mm)				Males (mm)	
			Abdomen width		Crusher length	
Station	50% Maturity	Smallest ovigerous female	LSR	RMA	LSR	RMA
1	29.5	32	28.7	30.6†	–	34.0
2	27.2	26	28.7	28.9†	32.7	32.0†
3	22.6	22	21.4	21.3 and 25.8*	29.1	30.9
4	23.3	24	23.6	22.4	29.0	29.9
5	27.0	27	24.1	24.1	31.0	24.0†
6	27.7	27	25.2	25.7	34.0	32.3
7	33.5	31	34.6	45.0†	46.3	46.3

†Probability of random residuals for the two subsets not significant at 5% level.
*Two equally significant values produced for this station.

Table 4a. Regression parameters for claw propodus analysis.

Station	Grouping†	Coefficients and parameters for equation: $\log_{10}$(claw length) = a × $\log_{10}$(CL) + b. All p<0.001			
		a	b	r	n
1	All ♂	1.200	0.757	0.990	37
	All ♀	1.047	1.208	0.994	42
2	Imm ♂	1.013	1.432	0.901	12
	Mat ♂	1.499	0.698	0.976	15
	All ♀	0.912	1.875	0.967	14
3	Imm ♂	1.091	1.086	0.982	25
	Mat ♂	1.475	0.323	0.931	13
	All ♀	1.058	1.159	0.958	22
4	Imm ♂	1.184	0.813	0.994	24
	Mat ♂	1.472	0.318	0.977	23
	All ♀	1.025	1.503	0.974	21
5	Imm ♂	0.972	1.585	0.985	20
	Mat ♂	1.131	0.998	0.954	20
	All ♀	1.018	1.312	0.993	24
6	Imm ♂ and All ♀	1.009	1.374	0.991	67
	Mat ♂	0.958	1.866	0.907	11
7	Imm ♂	1.193	0.774	0.953	115
	Mat ♂	1.329	0.501	0.893	17
	All ♀	0.979	1.531	0.940	123

†Grouping as follows (Imm, immature individuals; Mat, mature individuals; All, all individuals).

Table 4b. Regression parameters for abdomen width analysis.

Station	Grouping†	Coefficients and parameters for equation: abdomen width = a × CL + b				
		a	b	p	r	n
1	All ♂	0.507	−0.714	<0.001	0.980	41
	Imm ♀	0.551	−1.001	<0.001	0.984	26
	Mat ♀	0.583	−1.000	<0.001	0.981	42
2	All ♂	0.512	−0.682	<0.001	0.989	34
	Imm ♀	0.544	−0.744	<0.05	0.957	7
	Mat ♀	0.582	−0.805	<0.001	0.984	11
3	All ♂	0.514	−0.942	<0.001	0.995	44
	Imm ♀	0.475	0.225	<0.001	0.983	12
	Mat ♀	0.584	−1.309	<0.001	0.968	62
4	All ♂ and Imm ♀	0.516	−0.697	<0.001	0.992	66
	Mat ♀	0.618	−2.167	<0.001	0.981	46
5	All ♂ and Imm ♀	0.500	−0.302	<0.001	0.987	50
	Mat ♀	0.604	−1.738	<0.001	0.984	49
6	All ♂	0.542	−1.643	<0.001	0.994	42
	Imm ♀	0.570	−1.545	<0.001	0.981	23
	Mat ♀	0.574	−0.769	<0.001	0.989	44
7	All ♂	0.513	−0.485	<0.001	0.972	163
	Imm ♀	0.607	−2.244	<0.001	0.821	88
	Mat ♀	0.511	1.686	<0.001	0.826	80

†Grouping as follows (Imm, immature individuals; Mat, mature individuals; All, all individuals).

averaged, where both techniques provided a significant result).

Both male and female SOM estimates were positively related to the male L_x values estimated by Tuck *et al.*, (1997a) ($p<0.05$ and 0.001 for males and females, respectively), and the mean CL of animals in the catches ($p<0.05$ and 0.05 for males and females, respectively), and negatively related to *Nephrops* catch rate ($p<0.05$), and burrow density ($p<0.01$ and $p=0.056$ for males and females, respectively) (Tuck *et al.*, 1997a). Given the

Table 5. Statistical comparison of relative growth relationships based on homogeneity of slopes and analysis of covariance. The figures given are probabilities (n.s.=not significant at the 5% level). ANCOVA only carried out where slopes not significantly different from parallel.

	Crusher length				Abdomen width			
	Imm ♂ vs. Mat ♂		Imm ♂ vs. All ♀		Imm ♀ vs. Mat ♀		Imm ♀ vs. All ♂	
Station	h.s.	ANCOVA	h.s.	ANCOVA	h.s.	ANCOVA	h.s.	ANCOVA
1	—	—	<0.001†		n.s.	<0.001	n.s.	<0.001
2	<0.02		n.s.	<0.002	n.s.	<0.005	n.s.	<0.005
3	<0.02		n.s.	<0.002	n.s.	<0.05	n.s.	<0.005
4	<0.01		<0.05		<0.001‡		n.s.	n.s.
5	n.s.	<0.001	n.s.	<0.001	<0.001‡		n.s.	n.s.
6	n.s.*	<0.001*	n.s.	n.s.	n.s.	<0.001	<0.005	
7	n.s.	<0.001	<0.001		<0.05		<0.001	

h.s., homogeneity of slopes (parallelism).
†Tests carried out between all males and all females.
‡Tests carried out between mature females and immature females with all males.
*Tests carried out between mature males and immature males with all females.

Table 6a. Summary of reduced major axis regression analysis of female abdomen width allometric data.

Station	Lower group		Upper group		F	N	p
1	0.6078	−2.2212	0.5957	−1.5032	2.2911	69	n.s.
2	0.6628	−3.8789	0.5022	1.5009	3.3927	23	n.s.
3	0.7001	−3.9885	0.6818	−4.2363	4.1417	74	<0.05
	0.4829	6.8718	0.6037	−1.8353	3.7874	74	<0.05
4	0.5458	−1.2425	0.6275	−2.4887	3.4349	62	<0.05
5	0.3857	2.2671	0.6139	−2.0317	6.0456	57	<0.005
6	0.5987	−2.1065	0.5988	−1.6029	3.2046	68	<0.05
7	0.6297	−2.9363	0.3731	8.9119	1.7936	168	n.s.

Table 6b. Summary of reduced major axis regression analysis of male crusher claw allometric data.

Station	Lower group		Upper group		F	N	p
1	1.7211	−7.1051	1.5344	1.3676	3.7607	37	<0.05
2	1.7016	−5.8580	2.6554	−36.7980	3.2715	27	n.s.
3	1.6421	−4.3017	2.6303	−30.5173	9.0898	38	<0.001
4	1.7559	−6.9684	2.3899	−24.3657	6.8243	47	<0.005
5	1.4824	−0.6249	2.0046	−14.7676	1.7261	40	n.s.
6	1.4717	−1.0159	1.9604	−13.3242	6.4311	37	<0.005
7	1.9229	−13.2512	2.5763	−37.6827	26.8017	132	<0.0001

positive relationship between mean oocyte dry weight and L_∞ (see Fig. 4), it was not surprising to find a similar relationship between oocyte dry weight and SOM (females, $p<0.05$).

The age at maturity at each of the stations was estimated from the growth parameters previously calculated for each station (Tuck *et al.*, 1997a). Although the growth parameters were only calculated for males, up to maturity, both sexes can be assumed to grow at the same rate (Anon., 1997) and so estimates of the age of the females at maturity can be made from the male growth data. The estimates for age at maturity are shown in Table 7. For the females, maturity generally occurred between the ages of 3 and 3.5, while for males maturity occurred between about 4 and 4.5 yr for most of the stations. The age at maturity for males at stations 3 and 4 were consistently higher than the other stations (5–5.5 yr).

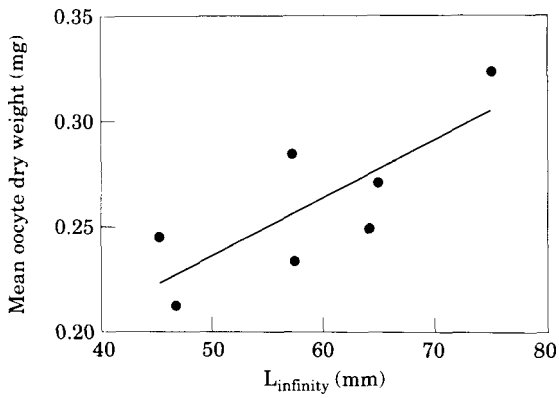

Figure 4. Linear relationship between mean oocyte dry weight (mg) for females at each station and the growth parameter L_∞ (mm) for corresponding males. The equation of the fitted line is: Weight=0.0027 L_∞ +0.1002 ($r=0.786$, $p<0.05$).

Discussion

Geographical variation in fecundity

The results from the present work show that the fecundity of female *Nephrops* is extremely variable, even within the same population. In log-log plots relating fecundity to female CL, differences in intercept values, rather than the slopes, were identified as the main variant. This appears to be a general feature in fecundity relationships of *Nephrops* (Thomas, 1964; Smith, 1987) and other crustaceans (France, 1992).

In our study, the maximum difference between the lowest (station 2) and highest (station 3) fecundity estimate was about 33%. This range of variation within the Firth of Clyde population is comparable to the variability evident in the data by Thomas (1964) for different Scottish populations (Table 8). No details on trawling positions were given in Thomas's (1964) paper, but we have been able to locate his original data. His rather low fecundity estimate for the Firth of Clyde was mainly based on one trawl haul in July 1961, roughly 5.2 km SE of our station 6. Whether the low fecundity estimated by Thomas (1964) at his Clyde station represents an extension to the range of spatial variability we have identified, or whether there may have been a shift in fecundity with time is unclear. Changes in fecundity might be brought about by temporal variations in food supply and/or growth rate (see below). Beyers and Goosen (1987) found a significant difference in fecundity of the rock lobster, *Jasus lalandii*, between successive years at one site, which they postulated might be related to temporal differences in food availability. On the other hand, Annala (1991) concluded that growth rate did not explain fecundity differences in *J. edwardsii*, but suggested that water temperature might be important.

Table 8 includes a comparison between present results and those of Smith (1987) for females caught in 1984, close to our station 7 and in the Sound of Jura. The fecundity estimate by Smith (1987) at the Clyde station was lower than we found during the present study. However, when compared with our data for all stations, Smith's results did not to differ significantly in slope. After applying a pooled slope to both sets of data, followed by a pairwise comparison of intercepts, we found no significant difference between Smith's intercept values and our own at station 7 ($p=0.17$).

This study showed that interpreting geographical differences in fecundity was difficult, unless fecundity was determined independently of other variables such as ovary and oocyte volumes (or as here, dry weights). We expected, for example, that fecundity in *Nephrops* would be significantly correlated with growth rate and/or size at sexual maturity (which itself appears to be a function of growth, see Bailey and Chapman, 1983), as reported for other lobsters (Beyers and Goosen, 1987; Annala, 1991; Pollock, 1995). Although there were indications of weak correlations between these variables and *Nephrops* fecundity, the relationships were not statistically

Table 7. Estimated ages at onset of maturity for each of the trawling stations. Ages calculated from sizes at onset of maturity (Table 3) and growth parameters estimated previously (Tuck *et al.*, 1997a).

	Females				Males	
Station	50% Maturity	Smallest ovigerous	LSR (abdomen)	RMA (abdomen)	LSR (crusher)	RMA (crusher)
1	3.7	4.1	3.5	3.8	—	4.5
2	2.8	2.7	3.1	3.1	3.8	3.7
3	3.4	3.2	3.1	3.0	4.9	5.5
4	3.6	3.8	3.7	3.4	5.2	5.5
5	3.2	3.4	2.9	2.9	4.2	2.9
6	2.9	2.9	2.7	2.8	4.2	3.9
7	2.8	2.5	2.9	4.4	4.6	4.6

Ages from 1st August in year of settlement.

Table 8. Comparison of fecundity of female *N. norvegicus* at selected CL sizes in Scottish waters based on oocyte counts from the present and previous studies.

Location (station no.)	Parameters for equation $F=a \times CL^b$ (a)	(b)	Estimated fecundity 30 mm	40 mm	Author
1	0.1947	2.697	1876	4075	Present study
2	0.1501	2.697	1446	3141	
3	0.2001	2.697	1928	4188	
4	0.1897	2.697	1828	3970	
5	0.1782	2.697	1717	3730	
6	0.1543	2.697	1486	3230	
7†	0.1765	2.697	1700	3694	
Firth of Clyde†	0.191	2.644	1537	3288	Smith (1987)
Sound of Jura	0.201	2.644	1620	3460	
Firth of Clyde	0.353	2.423	1339	2689	Thomas (1964)*
Minch	0.808	2.204	1455	2744	
Shetland	0.128	2.758	1517	3355	
Moray Firth	0.408	2.450	1697	3433	
Firth of Forth	0.803	2.269	1804	3466	

†Station 7 in the present study was close to the Clyde location sampled by Smith (1987).
*Although the author found no significant differences in slopes, and calculated a pooled slope (=2.350), he did not use it to recalculate the intercepts.

significant (Tuck, 1993). There was, however, a strong positive correlation between mean oocyte dry weight and L_∞ in the males at each station ($r=0.786$, $p<0.05$; Fig. 4). For most stations, no growth information was available for the females but we have assumed their pattern of growth variation between stations would be similar to the males. Growth information for the males was given by Tuck *et al.* (1997a) (stations 1–6) and Baily and Chapman (1983) (station 7).

Our observations indicated that geographic variability in female *Nephrops* potential fecundity mainly reflected growth related differences in oocyte volume, and to a lesser extent, the total ovary volume. Where growth was characterized by high L_∞, the mean oocyte volume was relatively large (Fig. 4) and size-specific fecundity tended to be low.

Actual fecundity and egg loss

Nephrops did not realise their full potential fecundity, mainly because many of eggs were lost from the pleopods between spawning and hatching. Egg loss appears to be a common occurrence in crabs, lobsters, shrimps and prawns (Malacostraca), and the causes have recently been reviewed by Kuris (1991). Losses are generally most marked at the time of oviposition (spawning) and during embryo development, and failure of eggs to adhere to the pleopods may be a major cause of egg loss (Kuris, 1991; Talbot, 1991). The earlier work of Smith (1987) in the northern Firth of Clyde and Chapman (unpublished data in Anon., 1984) in Loch Torridon indicated that 20 and 35% respectively, of creel-caught ovigerous females had abnormally low egg counts immediately after spawning. These losses were attributed to failure of the eggs to adhere to the pleopods during spawning.

In addition to possible losses at the time of spawning, egg losses from the pleopods during the long egg-development period are extremely high in *Nephrops*. Previous studies have reported high values, 68% off the Portuguese West coast (Figueiredo *et al.*, 1982), 66% in the Adriatic Sea (Froglia and Gramitto, 1981), 45–50% in the Bay of Biscay (Morizur *et al.*, 1981; Morizur, 1981), and 32–51% in the Moray Firth (Chapman and Ballantyne, 1980). The underlying causes of egg loss in *Nephrops* are poorly understood at present. Such high levels of egg loss led Kuris (1991) to suggest that predation was the most likely cause. Kuris's review gave many examples of predation and/or parasitization of eggs in crustaceans, including the well documented cause of egg mortality in *Homaraus americanus* caused by a species of nemertean (Campbell and Brattey, 1986). No evidence has been presented so far to indicate this phenomenon as a cause of egg loss in *Nephrops*.

Eggs may be lost due to abrasion during capture by trawl and to enforced swimming during capture (Newland, 1985). Based on fecundity comparisons between trawl and creel-caught ovigerous females in the Firth of Clyde and Sound of Jura, Chapman and Ballantyne (1980) suggested that trawling could cause 11–22% loss of eggs. There must be some doubt about this analysis, however, in the light of the present results, because of the geographical separation required between the trawling and creeling areas in order to avoid loss of

gear. Since the differences in fecundity, attributed to the effects of trawling by Chapman and Ballantyne (1980), are smaller than the 30% geographical variation reported here, we have concluded that the possible effects of trawl capture on egg loss estimates cannot be adequately quantified at present. The work of Chapman and Ballantyne (1980) needs to be repeated by creel and trawl sampling of ovigerous females at the same geographical location. This will undoubtedly prove difficult, however, due to the logistical difficulties of protecting creel gear from trawl damage.

Size at onset of sexual maturity

All four methods of assessing the SOM of females produced similar estimates, which showed positive relationships with the mean size of females and the L_∞ (for males) and negative relationships with adult density estimates. Similar trends between SOM, the mean size and maximum size have previously been identified for female *Nephrops* (Bailey and Chapman, 1983).

The SOM values for the males were higher than for the females, but showed a similar pattern between stations and similar relationships with the biological parameters measured. The results from the present study were therefore consistent with the suggestion that geographic variation in the SOM of *Nephrops* may be related to differences in growth (Bailey and Chapman, 1983).

Although significant differences were recorded between the estimates for the RMA analysis for females and the 50% maturity and smallest ovigerous estimates (paired t-tests), each of the sets of estimates showed similar trends between the stations. No significant differences were identified between the estimates of the two regression techniques within sexes (paired t-tests). For the data analyzed here, there was no difference in the accuracy of the estimates between the two techniques, although model II regression techniques such as RMA are more appropriate for allometric data (Lovett and Felder, 1989).

The variation in SOM of both sexes between stations and the relationships with the growth parameters suggest that maturity may be determined by some factor other than size. For the females, the age at the onset of maturity appeared to be between 3 and 3.5 yr for most of the combinations of station and method of SOM estimation. Previous research has estimated an age of between 2.5 and 3 yr for the age at the onset of maturity of female *Nephrops* (Morizur, 1983; Bailey, 1984). For the males, the age at the onset of maturity appeared to be between 4 and 4.5 yr for the faster growing populations (stations 1, 2, 5–7) and slightly higher at between 5 and 5.5 yr for the slower growing populations (stations 3 & 4). Morizur (1983) reported that the onset of maturity for females was occasionally delayed in years characterized by lower growth rate. This may be the case for the males at stations 3 and 4 in the present study, where the growth rate appears to be consistently low (data only available for station 4; Tuck, 1993). There may be a minimum size threshold for sexual maturity, below which males may be too small to reproduce. Using data from the Irish Sea, Farmer (1975) suggested males reach maturity one year older than females, a pattern followed by *Nephrops* at most of the stations in the present study. The ages at maturity recorded by Farmer (1975) were, however, younger than in the present study (2 and 3 yr for females and males, respectively).

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