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# Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland – I: Growth and density

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The density, size composition and growth of *Nephrops norvegicus* were examined at six sites in part of the Firth of Clyde, SW Scotland, between 1990 and 1992. Sampling was carried out using small mesh trawls and by an underwater television camera. The growth of male *Nephrops* at each site was investigated by analysis of length–frequency distributions using the computer program "Multifan". Estimates of *Nephrops* density at each station were obtained from TV counts of burrows and from relative trawl catch rates. Both density measures were correlated and showed a similar pattern between stations, although burrow counts exceeded trawl catches by roughly two orders of magnitude. Marked geographical variations were recorded in both the growth ($L_\infty$ and K) and density parameters, and $L_\infty$ was found to be inversely correlated with burrow density, suggesting that growth may be density-dependent. The weighted annual mean carapace length of *Nephrops* in trawl samples was significantly correlated with $L_\infty$, suggesting that mean size data may provide a useful indicator of growth variability within and between populations. On the other hand, the maximum carapace length ($L_{max}$) of *Nephrops* in samples was found to provide an unreliable estimate of $L_\infty$. The results are discussed in relation to possible environmental influences on growth and population density.

Key words: *Nephrops norvegicus*, growth, density.

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## Introduction

Some early fishery investigations on the mud-burrowing Norway lobster, *Nephrops norvegicus*, revealed marked geographical variations in the size composition and abundance in trawl catches (Cole, 1965; Thomas, 1965). Thomas (1965) explained the variation occurring around the Scottish coast mainly in terms of differing fishing pressures, although he recognised that other factors could be involved, since differences in size composition between some adjacent stocks were observed even before full commercial exploitation. Such geographic differences, reported 30 years ago, are still evident despite varying levels of exploitation during this period (Anon., 1988).

More recent studies on *Nephrops* have demonstrated geographic variability in several biological parameters, including population density, size composition and growth (Bailey and Chapman, 1983; Bailey *et al.*, 1986; Chapman and Bailey, 1987; Chapman and Howard, 1988; Tully and Hillis, 1995). It has been suggested that this variability could be associated in some way with the sedimentary environment, though the form of any relationship seemed likely to be complex (Chapman and Bailey, 1987; Anon., 1988).

In Scottish waters, Chapman and Bailey (1987) suggested that seabed sediments with a high silt and clay content tended to support low density populations of fast growing *Nephrops*, whereas the converse seemed to be true on coarser sandy-mud sediments. These ideas are tested further in this paper, which examines the range of variability in density, size composition and growth of *Nephrops* occurring in a region of the Firth of Clyde characterised by marked sediment heterogeneity. This paper is the first of a series dealing with the population biology of *Nephrops* in the Firth of Clyde.

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Table 1. Sediment characteristics and locations of each trawling station.

| Station | Lat. and Long. start | Lat. and Long. finish | Mean depth (m) | Benthic faunal biomass $(\mathrm{g \cdot m^{-2}})$ | % organic carbon | % silt and clay |
|---|---|---|---|---|---|---|
| 1 | 55°23.86′N<br>4°57.82′W | 55°22.45′N<br>4°57.65′W | 57 | 52.17 | 1.27 | 96.5 |
| 2 | 55°14.76′N<br>5°02.41′W | 55°14.78′N<br>5°04.72′W | 47 | 44.79 | 0.75 | 69 |
| 3 | 55°10.41′N<br>5°13.05′W | 55°09.03′N<br>5°13.12′W | 54 | 6.27 | 0.97 | 81 |
| 4 | 55°08.82′N<br>5°16.89′W | 55°10.15′N<br>5°17.72′W | 60 | 35.60 | 0.76 | 30 |
| 5 | 55°19.52′N<br>5°19.44′W | 55°20.73′N<br>5°18.66′W | 49 | 50.07 | 1.10 | 81 |
| 6 | 55°20.94′N<br>5°15.69′W | 55°21.67′N<br>5°13.86′W | 53 | 75.70 | 0.99 | 83 |

# Materials and methods

## Trawl sampling

The study was conducted in part of the Firth of Clyde, south of the Isle of Arran. A programme of trawl sampling was conducted to provide information on *Nephrops* growth, size composition and relative abundance at the six stations covering a range of different sediment types (Table 1). Each station was trawled on a bimonthly basis from the R.V. *Aora*, between December 1990 and February 1992. The trawl used was a 22 mm mesh experimental *Nephrops* trawl, fitted with a 12 mm mesh codend. The timing of each trawling cruise was arranged to coincide with neap tides, in an attempt to maximise catch sizes and ensure some uniformity in the availability of *Nephrops* to trawl capture (Chapman, 1980). Minimum trawling durations were usually 30 min, at an average towing speed of $1.29\ \mathrm{m\ s^{-1}}$ (approximately 2.5 knots), although longer repeat hauls were sometimes required to provide adequate samples. On four occasions, acoustic range measuring equipment (Scanmar Netsonde) was mounted at the wing ends of the trawl to record the width of the trawl mouth opening (average 21 m at a towing speed of $1.29\ \mathrm{m\ s^{-1}}$).

## Grab sampling

In August 1991 sediment samples were taken at each station with a van Veen grab ($0.1\ \mathrm{m^2}$) and analysed for particle size (Folk, 1974) and organic carbon. Three additional grab samples from each station were sorted through a 1 mm mesh sieve and the retained fauna was preserved for later identification and biomass estimation. Details of station positions, depth and main sediment characteristics are given in Table 1.

## Television observations

During July 1991 the density of *Nephrops* burrows was estimated by means of a TV camera (Hydro Products, TC-125-SDA) mounted on an epibenthic sledge (Chapman, 1985). The camera was mounted to view the seabed obliquely forwards of the sledge and illumination of the camera field was obtained from one or two quartz iodine lights (Hydro Products, HQ250). Video tape recordings were made using a Panasonic recorder (type NV333, VHS format). The camera sledge was deployed from the R.V. *Aora*, the position and track of the vessel being recorded by a Racal-Decca Navigator (Mark 53), interfaced with a CVP 3500 plotter, and stored on computer disk. The area of seabed viewed by the camera was derived from the distance covered by the vessel (estimated from its speed over the ground, see Table 2) and the width of the camera field of view (estimated to be 1 m). Counts of *Nephrops* burrows were made from timed sections of tape and these counts were divided by the area to provide burrow density estimates.

## Analysis of trawling data

Following sorting and weighing of the catch, all *Nephrops*, or a weighed subsample, were measured to produce a carapace length (CL) frequency distribution for each sex. Measurements were taken to the mm below using vernier callipers. Where necessary, the number of individuals in subsamples were raised to the total catch weight. The catch data were first aggregated on a quarterly basis, expressed as mean numbers caught per half-hour tow, and examined for sex differences and seasonal effects. Catch rates were then averaged over the year to provide an index of relative abundance for comparison between stations.

The length–frequency distributions were further analysed to provide comparisons of mean CL and growth parameters of *Nephrops* between stations. Growth information was derived by splitting the length–frequency distributions into age classes and calculating the von Bertalanffy growth parameters (K and $L_{\infty}$) using the Otter Research software "Multifan" (Fournier *et al.*,

Table 2. *Nephrops* burrow density at each station estimated by towed TV camera.

| Station | Mean speed ($m\ s^{-1}$) | Time analysed (s) | Burrows counted | Area covered ($m^2$) | Burrow density: Estimate ($m^{-2}$) | Burrow density: S.E.M. |
|---|---|---|---|---|---|---|
| 1 | 0.75 | 1319 | 637 | 989.2 | 0.644 | 0.074 |
| 2 | 0.97 | 1295 | 1018 | 1256.1 | 0.810 | 0.104 |
| 3 | 0.83 | 1921 | 2327 | 1594.4 | 1.459 | 0.082 |
| 4 | 0.78 | 1932 | 2229 | 1507.0 | 1.479 | 0.091 |
| 5 | 1.04 | 880 | 1271 | 915.0 | 1.388 | 0.116 |
| 6 | 1.55 | 1350 | 963 | 2092.5 | 0.460 | 0.058 |

1990). The programme simultaneously analyses multiple length–frequency distributions. User input sets constraints on some of the mean lengths to ensure the model fits the obvious modes properly (Fournier *et al.*, 1990), and a log-likelihood function is used to produce maximum likelihood estimates for a mixture of normal distributions within a multinomial distribution. The main assumptions of the “Multifan” model are that lengths in each age class are normally distributed, mean lengths-at-age lie close to a von Bertalanffy growth curve and standard deviations of lengths-at-age are simple functions of their mean. The growth analysis was only carried out on males since behavioural changes while egg carrying resulted in relatively few mature females being caught throughout most of the year. Seasonal changes in their availability makes growth analysis of females from length–frequency data very difficult (Bailey and Chapman, 1983).

# Results

## Environmental conditions

The environmental conditions at each station are summarised in Table 1. Water depth varied from 47 to 60 m. Limited measurements suggested that mean annual water temperatures at the seabed were reasonably uniform between stations (within 0.5 deg C). The composition of the sediments, expressed in terms of the proportion of fine silt and clay particles ($<63\ \mu$ diameter) varied widely from 30 to 96.5%, with sand particles making up the remainder of each sediment. The organic carbon content of the sediment increased roughly in proportion to the silt and clay content (see also Chapman and Bailey, 1987). The biomass of benthic fauna in the sediment varied considerably between stations, from 6.27 (Station 3)–75.7 (Station 6) $g\ m^{-2}$, and the values showed no clear relationship with the sediment particle size composition. The fauna were dominated by polychaetes and small bivalves, all of which were considered suitable prey for *Nephrops*.

## Density of *Nephrops* burrows from TV observations

Counts of *Nephrops* burrows were based on examination of a large area of seabed at each station, in the range 915–1594 $m^2$ (Table 2). Estimates of *Nephrops* burrow density varied significantly between stations (Kruskal–Wallis one way ANOVA; $p<0.001$), from 0.46 (Station 6) to 1.48 burrows $m^{-2}$ (Station 4). Three stations (numbers 3, 4 and 5) had similarly high burrow densities (about 1.4 burrows $m^{-2}$) that were not significantly different (Kruskal–Wallis one way ANOVA; $p=0.645$).

## Relative abundance of *Nephrops* from trawl sampling

The relative abundance of *Nephrops* at each station, as shown by the mean number of each sex caught per half-hour tow, are given for each quarter in Table 3. Significant differences were identified in catch per half hour between station ($p<0.001$) and season ($p<0.05$), but not sex ($p=0.227$; Table 3). The number of individuals caught per half-hour tow at Station 4 was significantly higher than at Stations 1, 2, 5 and 6, while the numbers caught in the second quarter of the year (April–June) were significantly lower than in the first and fourth quarters. There was no significant interaction between the factors. The trawl sampling was over the period December 1990–February 1992, so that data for quarters 1 and 4 include catches from different years. Since a similar pattern of seasonal catches was shown at all but one station, we do not feel this introduces a problem. At Station 2, the catch reduced dramatically following the first cruise, in December 1990, and remained very low thereafter (Table 3). It is unclear why this occurred, but the catches at this station did not follow the general seasonal pattern, so parameter estimates may be less reliable than for the other stations.

Given that sampling was carried out throughout the year, the catches over the whole year were averaged to provide an overall index of abundance at each station, for both sexes separately and combined (Table 3). Mean

Table 3. Seasonal variation in numbers of *Nephrops* caught per half-hour tow at each station using experimental small mesh trawl and analysis of variance of mean catch with respect to sex, station and quarter.

| | Station 1 | | Station 2 | | Station 3 | | Station 4 | | Station 5 | | Station 6 | | Quarterly mean† |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quarter | M | F | M | F | M | F | M | F | M | F | M | F | |
| 1 Jan–Mar | 174 | 121 | 39 | 25 | 1267 | 836 | 1592 | 791 | 422 | 250 | 181 | 97 | 472 ± 107 |
| 2 Apr–Jun | 2 | 1 | 12 | 8 | 0 | 0 | 347 | 331 | 164 | 178 | 0 | 0 | 85 ± 97.4 |
| 3 Jul–Sep | 102 | 226 | 36 | 23 | 71 | 113 | 1000 | 700 | 328 | 295 | 253 | 232 | 275 ± 137.7 |
| 4 Oct–Dec | 71 | 53 | 223 | 200 | 762 | 567 | 1495 | 855 | 358 | 252 | 211 | 156 | 428 ± 92.2 |
| Mean† | 82 | 80 | 91 | 77 | 582 | 414 | 1130 | 670 | 316 | 237 | 150 | 108 | |
| Overall mean† | 162 ± 174 | | 168 ± 178 | | 996 ± 174 | | 1800 ± 174 | | 553 ± 174 | | 258 ± 174 | | |
| Catch density $m^{-2}$* | 0.0033 | | 0.0034 | | 0.020 | | 0.037 | | 0.011 | | 0.0053 | | |

M = male, F = female.

†Weighted mean catch per half hour for each sex. Overall mean and quarterly mean are the mean for both sexes combined, as predicted by model (± S.E.).

*Based on estimated total area swept by trawl of 48 650 $m^2$.

Analysis of variance table. The columns give degrees of freedom and mean square for each term, and the p-valve when an F-test is used to test for significance.

| Source of variation | d.f. | Mean square | F | p |
|---|---|---|---|---|
| Sex (A) | 1 | 342 720 | 1.51 | 0.227 |
| Station (B) | 5 | 1 416 294 | 6.24 | <0.001 |
| Season (C) | 3 | 802 636 | 3.54 | 0.024 |
| Interaction | | | | |
| A × B | 5 | 106 013 | 0.47 | 0.798 |
| A × C | 3 | 82 313 | 0.36 | 0.780 |
| B × C | 15 | 168 455 | 0.74 | 0.728 |
| A × B × C | 15 | 17 716 | 0.08 | 1 |
| Error | 38 | 259 130 | | |

total catch rates varied considerably between stations, from 162 (Station 1) to 1800 *Nephrops* per 30 min tow (Station 4).

The mean catch per unit time data in Table 3 were also converted to mean catch per unit area of seabed swept by the trawl. This conversion was based on the mean swept path width of 21 m, derived from "Scanmar" measurements, and the mean trawl path length of 2315 m (being the distance covered by the trawl in 30 min at the average towing speed of 1.29 m $s^{-1}$). These figures gave an average swept area of 48 650 $m^2$ which was assumed to apply to all hauls. The catch $m^{-2}$ values for each station (Table 3) are nearly two orders of magnitude lower than the burrow density estimates (Table 2), but the ranks of the two sets of data were positively correlated (Spearman rank order correlation coefficient = 0.829). The $\log_{10}$ total catch per half hour showed a significant positive correlation with burrow density ($r^2 = 0.700$, $p < 0.05$; see Fig. 1).

## Analysis of length composition data – mean size

Seasonal variations in the mean CL of male and female *Nephrops* at each station are shown in Table 4. Significant differences in mean size were found with season, station and sex ($p < 0.001$; Table 4). As is normally the case, males were significantly larger than females. The mean CL of *Nephrops* caught at Station 1 was significantly larger than at Stations 3, 4 and 5, while the mean CL of *Nephrops* in quarter 3 was significantly larger than during any other quarter. The interaction between season and sex was almost significant at the 5% level ($p = 0.057$; Table 4), almost certainly representing seasonal variations in the behaviour of mature egg-bearing (ovigerous) females. During this phase, females tend to remain in their burrows and are seldom caught (Chapman, 1980).

## Analysis of length composition data – growth parameters

Examples of the male CL distributions used in the "Multifan" analysis are given in Figure 2 for Stations 3 (Fig. 2a) and 5 (Fig. 2b). From the length–frequency distributions, prominent modes can be identified; for example, Figure 2a shows a prominent mode at a CL of approximately 20–21 mm in December, with the possibility of smaller peaks at larger sizes. The same mode

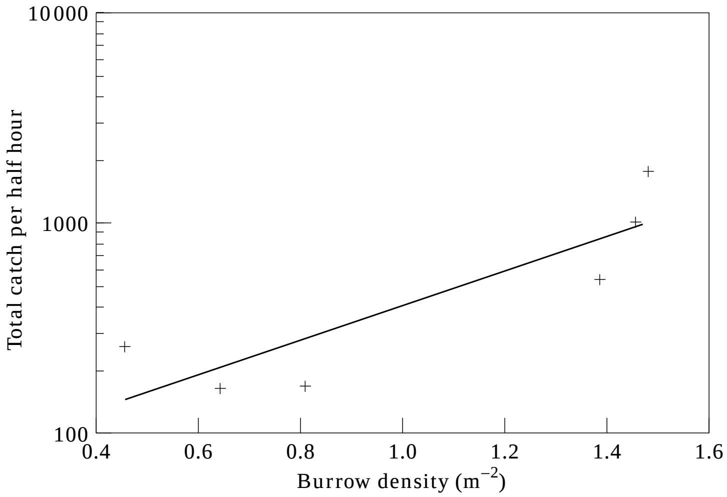

Figure 1. Relationship between the $\log_{10}$ of the total catch per half-hour tow and the burrow density. The best fit linear regression was $\log_{10} Y = 0.825X + 1.782$ ($r^2 = 0.700$, $p < 0.05$).

appears at a slightly larger CL in February and by August has reached a CL of about 23–25 mm. In August, new recruits to the small mesh trawl are evident, although the mode(s) are indistinct.

By October, the original mode is located around 27 mm CL and the new recruits appear at about 21–22 mm, equivalent to the previous year class first detected in December. Following the progression of modes in this way strongly suggests that they represent year classes or age-groups. Since August is taken to be the month of juvenile settlement on the seabed, the 23–25 mm mode in that month is assumed to represent three-year-old *Nephrops*. Modal progression can also be followed in CL frequency distributions from Station 5 (Fig. 2b), where it can be seen that equivalent CL modes tend to occur at slightly larger size than at Station 3 (Fig. 2a), indicating a faster growth rate at the former station.

Estimates of the von Bertalanffy growth parameters $L_\infty$ and K, obtained from the "Multifan" analysis, are summarised in Table 5. Estimates of the value of K varied between 0.16 (Station 1) and 0.214 (Station 2) and the values for $L_\infty$ ranged from 45.3 (Station 4) to 65.1 (Station 1). There was a very poor correlation between the estimates of $L_\infty$ and the maximum CL of *Nephrops* ($L_{max}$) in trawl samples from each station (Table 5). This may be due to poor selectivity of larger individuals by the small mesh trawl (N. Bailey, pers. comm.), but suggests that the common practice of using $L_{max}$ as an approximation to $L_\infty$ may be unreliable in some situations. Von Bertalanffy growth curves for *Nephrops* at each station are shown in Figure 3. These plots are derived from the parameter estimates in Table 5, using an assumed value for $t_0$ (the age at which CL=0). The value chosen for each station was $-0.115$ years (6 weeks), being the approximate period between hatching of the larvae and juvenile settlement (Tuck, 1993). On the basis of Figure 3, the growth curves appear to divide into two main groups of stations; the growth rates of *Nephrops* at Stations 3 and 4 were relatively slower than at the other four stations. Examination of the $L_\infty$ estimates and standard deviations (Table 5), confirms this division, and also splits the stations with faster growth rates (Stations 1 and 6 having significantly larger $L_\infty$ than Stations 2 and 5).

## Relationships between parameters

Figure 4 provides a summary of the main parameter estimates for *Nephrops* populations at each station. In Figure 4 the station data are arranged in ascending order of the percentage silt and clay content of the sediment (Fig. 4a). Organic carbon and burrow density data are not represented since they show very similar patterns to percentage silt and clay, and total catch per half hour, respectively. It can be seen that the relative abundance of *Nephrops*, expressed here in terms of the total catch per half hour, tends to decrease in proportion to the silt and clay content (Fig. 4b). The catch rate at Station 2, however, does not conform to the general pattern. It has already been mentioned that catches at Station 2 were very poor following the first cruise, and that parameters from this station may therefore be unreliable. Nevertheless, even with Station 2 included, total catch rate was negatively correlated with the sediment silt and clay content ($r^2 = 0.596$, $p < 0.05$).

From Figure 4c, there is an indication of a relationship between mean carapace length of both sexes and sediment composition, though its form may not be linear (see Discussion). Comparison of Figures 4c and 4b

Table 4. Seasonal variation in mean CL (mm) of male and female *Nephrops* in catch of small mesh trawl (BT 126 D) and analysis of variance of mean size with respect to sex, station and quarter.

| | Station 1 | | Station 2 | | Station 3 | | Station 4 | | Station 5 | | Station 6 | | Quarterly mean† | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Quarter | M | F | M | F | M | F | M | F | M | F | M | F | M | F |
| 1 Jan–Mar | 29.5 | 26.0 | 25.0 | 22.8 | 25.1 | 22.2 | 26.2 | 22.5 | 26.2 | 24.4 | 27.3 | 24.8 | 26.1 ± 0.407 | 22.9 ± 0.531 |
| 2 Apr–Jun | — | — | 27.0 | 22.6 | — | — | 22.7 | 21.1 | 24.0 | 23.2 | — | — | 23.7 ± 0.992 | 22.1 ± 1.055 |
| 3 Jul–Sep | 31.0 | 32.3 | 32.6 | 29.3 | 24.1 | 24.1 | 27.3 | 25.5 | 27.7 | 27.4 | 29.7 | 29.7 | 27.1 ± 0.952 | 26.2 ± 0.885 |
| 4 Oct–Dec | 28.4 | 25.3 | 24.3 | 22.0 | 23.1 | 20.4 | 24.0 | 20.6 | 25.6 | 22.9 | 26.6 | 23.2 | 24.4 ± 0.335 | 21.3 ± 0.413 |
| Mean† | 29.1 ± 1.176 | 26.4 ± 1.345 | 25.7 ± 1.895 | 23.3 ± 2.355 | 24.0 ± 0.545 | 21.6 ± 0.552 | 25.3 ± 0.300 | 22.0 ± 0.400 | 26.2 ± 0.58 | 24.0 ± 0.71 | 26.8 ± 0.881 | 24.7 ± 1.126 | | |

M = male, F = female.
†Weighted annual mean.

Analysis of variance table

| Source of variation | d.f. | Mean square | F-value | p |
|---|---|---|---|---|
| Season (A) | 3 | 19 143.4 | 27.10 | <0.001 |
| Sex (B) | 1 | 44 743.2 | 63.33 | <0.001 |
| Station (C) | 5 | 7034.5 | 9.96 | <0.001 |
| Interactions | | | | |
| A × B | 3 | 2064.9 | 2.92 | 0.057 |
| A × C | 12 | 325.9 | 0.46 | 0.917 |
| B × C | 5 | 416.4 | 0.59 | 0.708 |
| A × B × C | 12 | 169.9 | 0.24 | 0.993 |
| Error | 22 | | | |

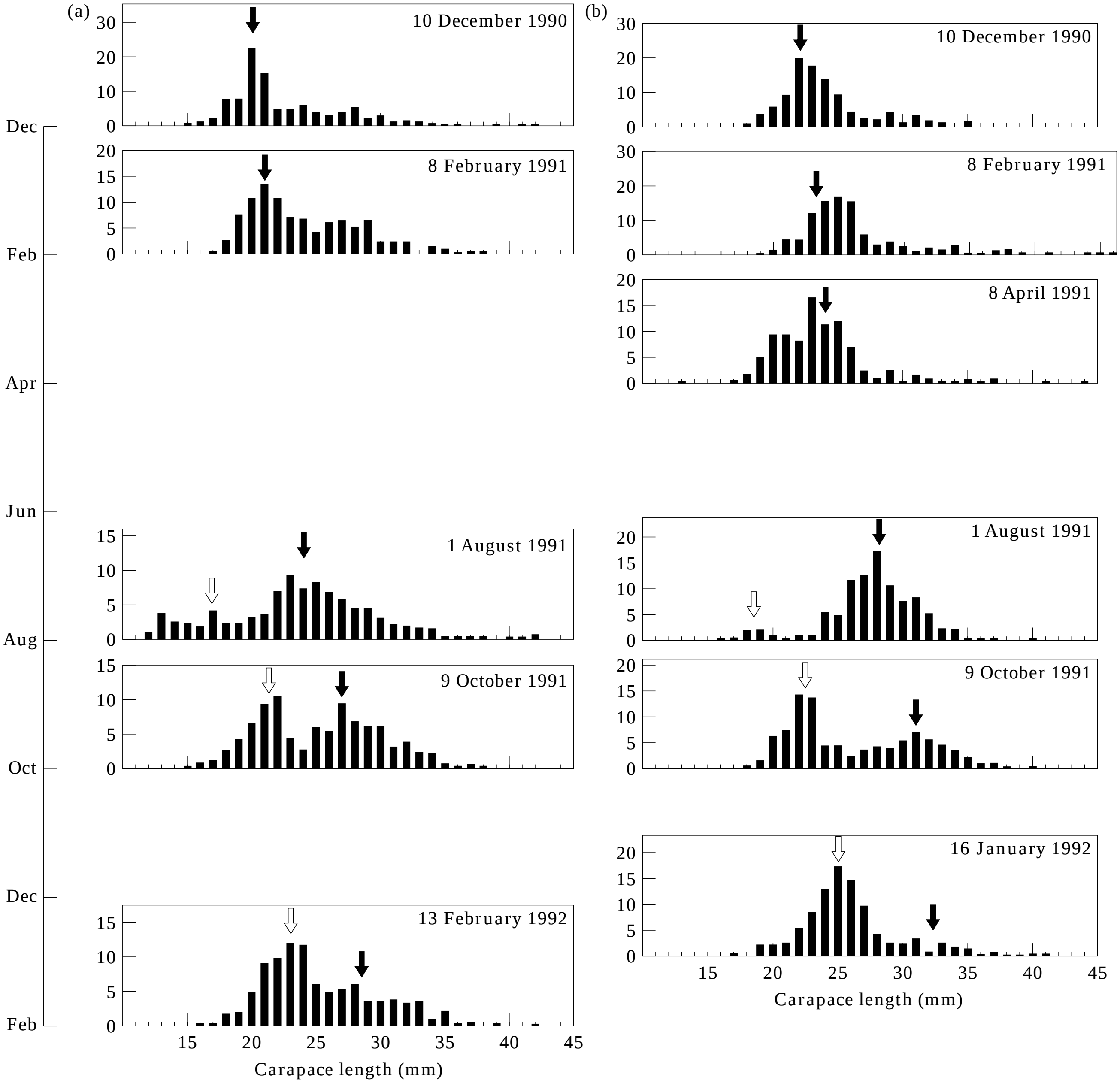

Figure 2. Male CL percentage frequency distributions for stated months at Stations 3 (a) and 5 (b). Arrows illustrate modal progression of some age groups (solid arrows, 1988 age class; hollow arrows, 1989 age class).

suggests an inverse relationship between mean CL of both sexes and total catch rate. Neither of these relationships were significantly correlated, however.

The growth parameters, K and $L_\infty$, for *Nephrops* at each station are plotted in Figure 4d. As expected the two parameters were inversely related (Beverton and Holt, 1959), although Station 2 again produced anomalous results. The negative correlation coefficient between the two growth parameters was statistically significant when Station 2 data were omitted from the analysis ($r^2=0.799$, $p<0.05$). Neither K nor $L_\infty$ were correlated with sediment composition, even when Station 2 data were omitted from the analysis.

A useful finding was that $L_\infty$ (but not K) was positively correlated with the mean CL of males ($r^2=0.626$, $p<0.05$). This suggests that mean CL, taken from a representative number of samples, spread throughout the year, could be used as an indicator of growth

Table 5. Von Bertalanffy growth parameters estimated using the 'Multifan' program for male *Nephrops* from each trawling station.

| Station | Estimate K | Estimate $L_\infty$ (mm) | St. Dev. K | St. Dev. $L_\infty$ (mm) | $L_{max}$ |
|---|---|---|---|---|---|
| 1 | 0.160 | 65.1 | 0.0008 | 0.408 | 47 |
| 2 | 0.214 | 57.5 | 0.0244 | 2.557 | 52 |
| 3 | 0.192 | 46.8 | 0.0013 | 0.232 | 42 |
| 4 | 0.192 | 45.3 | 0.0012 | 0.525 | 48 |
| 5 | 0.180 | 57.4 | 0.0008 | 0.245 | 46 |
| 6 | 0.175 | 64.4 | 0.0009 | 0.395 | 50 |

K and $L_\infty$—von Bertalanffy growth parameters.
$L_{max}$—maximum CL of *Nephrops* in trawl samples.

variability within a population. $L_\infty$ was found to be negatively correlated with burrow density (Fig. 5) and log catch rate ($r^2=0.715$, $p<0.05$; $r^2=0.742$, $p<0.05$ respectively), and was also positively correlated with the biomass of benthic fauna in the sediment ($r^2=0.584$, $p<0.05$).

## Discussion

The results from this study generally confirm earlier suggestions of a large degree of local variation in the density, size composition and growth of *Nephrops* (Bailey and Chapman, 1983; Chapman and Bailey, 1987; Chapman and Howard, 1988; Tully and Hillis, 1995). In a preliminary comparison of separate populations in the Firth of Clyde and Sound of Jura, Bailey and Chapman (1983) reported large differences in *Nephrops* density and growth rate. The latter investigation was limited to a single location within each population. The present study, on the other hand, examined six sites within a relatively small part of one, essentially continuous, *Nephrops* ground in the Firth of Clyde, and similar variations in population parameters were found.

Within our study area, we showed that the growth parameter $L_\infty$ was negatively correlated with burrow density, suggesting that growth could be density-dependent, as previously suggested (Bailey and Chapman, 1983; Chapman and Bailey, 1987). It is possible that at high population densities, competition for food could limit growth. The importance of available food supply was suggested in our study by the fact that $L_\infty$ was also found to be positively correlated with infaunal biomass. The growth of *Nephrops* may also be influenced at high densities through changes in social behaviour (Cobb *et al.*, 1982). In the Irish Sea, Tully and Hillis (1995) suggested that growth could vary because of spatial differences in sea-bed temperature and this could also be linked to changes in sediment composition (see below).

The underlying cause of local variation in *Nephrops* burrow density and abundance was considered previously by Bailey and Chapman (1983) and Chapman and Bailey (1987), without reaching firm conclusions. It was tentatively concluded that high densities probably resulted mainly from a high level of juvenile recruitment, though variation in the level of fishing effort was likely to be a contributory factor (Thomas, 1965; see also Tully and Hillis, 1995). It is well known from larval production studies (Nichols *et al.*, 1987; Nichols and Thompson, 1988; White *et al.*, 1988; Tuck, 1993) that *Nephrops* larvae are very patchy in their distribution, with abundance variations often associated with oceanographic gyres and frontal systems (Bailey *et al.*,

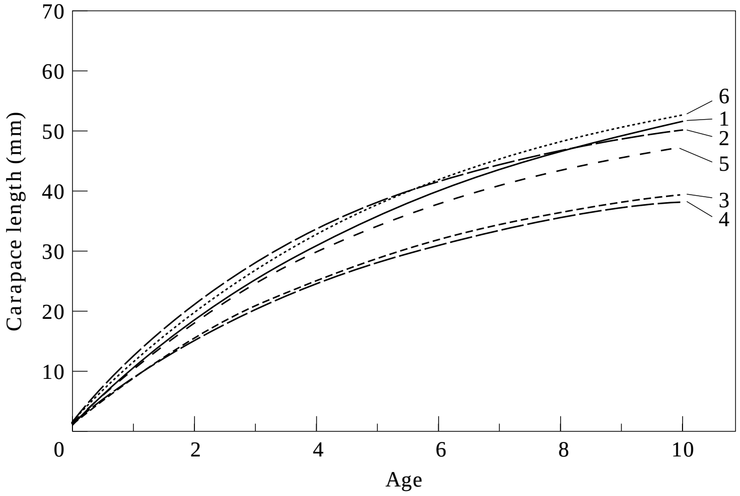

Figure 3. Comparison of growth curves of male *Nephrops* between stations (1–6), based on analysis of length frequency distributions by "Multifan" (Table 5).

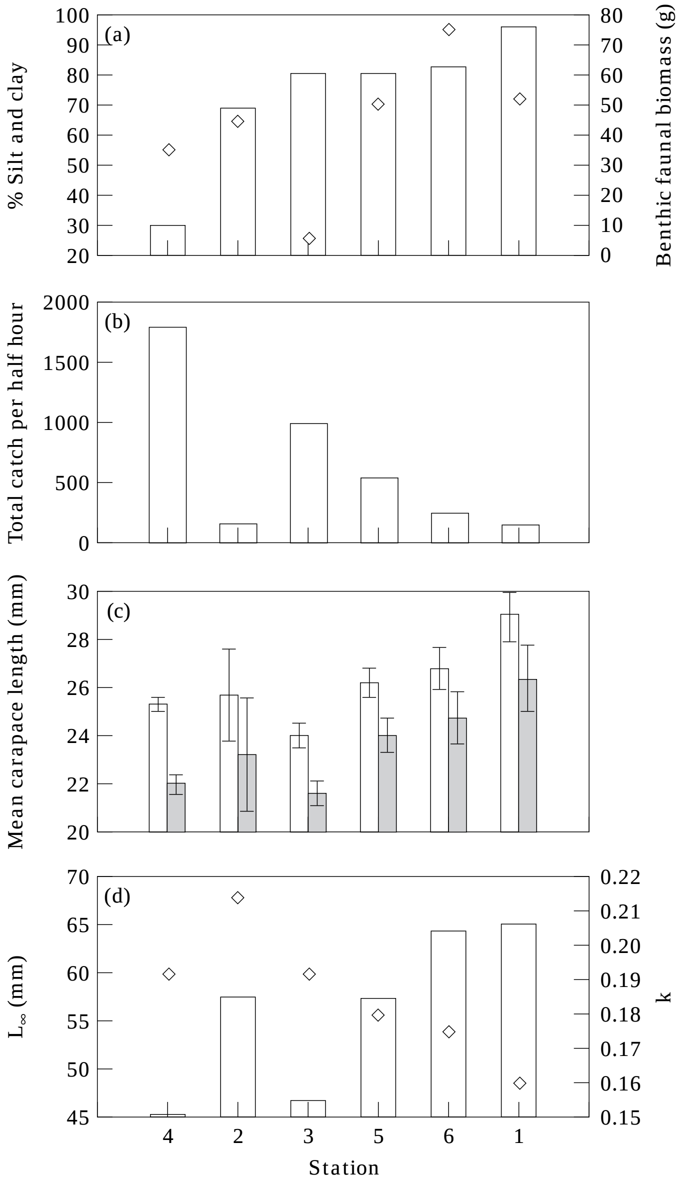

Figure 4. Summary of percentage silt and clay (a), relative density (b), mean CL ( ± S.E.) (c) and growth parameters (d) for each station. Bars representing each station are plotted in increasing order of their sediment percentage silt and clay content (a). In (a) the values of benthic faunal biomass are shown by ◇, in (d) the values of K are shown by ◇. In (c) ▨=females, ☐=males.

1995; Brown *et al.*, 1995). This patchiness may well be reflected later in juvenile settlement. It is thought likely that at the time of settlement, the juveniles initially occupy burrows linked to those of adults (Chapman, 1980; Tuck *et al.*, 1994), thus providing a mechanism for the maintenance of high burrow densities (Chapman and Howard, 1988).

It has also been postulated that burrow density (and by inference *Nephrops* growth and size composition) was in some way related to the particle size composition of the sedimentary environment. Chapman and Bailey (1987) suggested that in Scottish *Nephrops* populations, high burrow densities were usually found on coarse muds with a high proportion of sand particles mixed with silt and clay; conversely, low burrow densities were usually associated with fine muds with a low sand content. This idea is supported by the results of the present study which showed a significant negative correlation between catch rate and the percentage silt/clay content of the sediment (see Fig. 4a,b). Parallel studies in the Irish Sea (Anon., 1988; Hillis, 1988; Tully and Hillis, 1995) have found the converse of the Scottish situation,

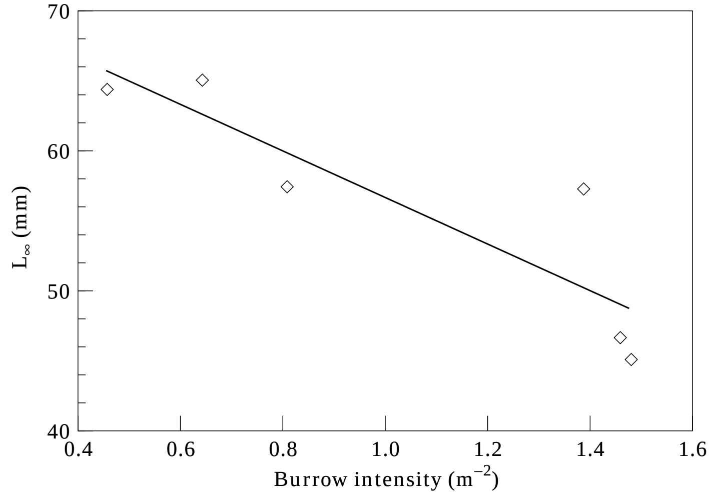

Figure 5. Relationship between $L_\infty$ and burrow density. The best fit linear regression was $Y=73.042-16.307X$ ($r^2=0.715$, $p<0.05$).

however, suggesting that any relationship between *Nephrops* density and granulometry is more complex than the simple linear relationship initially proposed by Chapman and Bailey (1987). This apparent discrepency appears to arise from the fact that the Irish Sea analysis was carried out over a much coarser range of sediments (4–49% silt/clay) than was the case in our studies (30–96%, see Table 1) and the earlier investigations in Scottish waters (Chapman and Bailey, 1987; Chapman and Howard, 1988). To reconcile the two sets of data, it has been suggested that burrow density is a non-linear function of sediment structure. A plot, combining the data from several areas showed that peak abundance (and smallest *Nephrops* size) occurred at intermediate sediment particle sizes (Anon., 1988), and further evidence for this was given recently by Bailey *et al.* (1995).

There has been much speculation about the mechanisms by which sediment composition could influence the population biology of *Nephrops*, but without any firm conclusions being reached (Bailey, 1986; Chapman and Bailey, 1987; Tuck, 1993; Tully and Hillis, 1995; Bailey *et al.* (1995). It is conceivable that a high silt and clay content is necessary for the sediment to support the burrows of large *Nephrops* (the largest *Nephrops*, albeit at low density, tend to occur on such sediments). At the other end of the sediment scale, some of the sediments in the Irish Sea, studied by Hillis (1988) and Tully and Hillis (1995) were extremely coarse, with a silt and clay content as low as 4%. Such sandy sediments are likely to be less suited to burrowing, so it is perhaps not surprising that *Nephrops* density tends to decline under these conditions. During scuba diving by one of us (C.J.C., unpublished), large *Nephrops* were occasionally observed foraging on coarse sand sediments adjacent to typical *Nephrops* ground, though no burrows were ever found on these coarse sediments.

While direct sediment affects on burrow density and size composition of *Nephrops* are certainly feasible at one extreme of the particle size range, it is more difficult to account for the peak in density on mixed sediments of sand, silt and clay and the decline in density on the finest silt and clay sediments. If, as suggested above, spatial variability in larval density and juvenile settlement is the main cause of variability in the density of adult *Nephrops*, then density may simply reflect general hydrographic conditions rather than sediment type directly (Chapman and Bailey, 1987; Chapman and Howard, 1988; Bailey *et al.*, 1995).

The results reported here have implications for the assessment and management of *Nephrops* stocks (Chapman and Howard, 1988). In most analytical models used for assessment purposes, it is assumed that the population is homogeneous in terms of its biological characteristics. This assumption is clearly invalidated in a population like the Firth of Clyde, where the population seems to consist of a mixture of sub-units, differing from each other in growth, size composition and density.

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## References

Anon. 1988. Report of the study group on *Nephrops*. ICES CM 1988/K:29.

Bailey, N. 1986. Why does the size of *Nephrops* vary? Scottish Fisheries Bulletin, 49: 31–36.

Bailey, N., and Chapman, C. J. 1983. A comparison of density, length composition and growth of two *Nephrops* populations off the west coast of Scotland. ICES CM 1983/K:42.

Bailey, N., Chapman, C. J., Afonso-Dias, M., and Turrell, W. 1995. The influence of hydrographic factors on *Nephrops* distribution and biology. ICES CM 1995/Q:17 Poster.

Bailey, N., Chapman, C. J., Kinnear, J., Bova, D., and Weetman, A. 1993. Estimation of *Nephrops* stock biomass on the Fladen Ground by TV survey. ICES CM 1993/K:34.

Bailey, N., Howard, F. G., and Chapman, C. J. 1986. Clyde *Nephrops*: biology and fisheries. Proceeding of the Royal Society of Edinburgh, 90(B): 501–518.

Beverton, R. J. H., and Holt, S. J. 1959. A review of lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. *In* Colloquia on aging (5). Ed. by G. Wolstenholme and M. O'Connor. CIBA Foundation.

Brown, J., Hill, A. E., Fernand, L., Bennett, D. B., and Nichols, J. H. 1995. A physical retention mechanism for *Nephrops norvegicus* larvae. ICES CM 1995/K:31.

Chapman, C. J. 1980. Ecology of juvenile and adult *Nephrops*. *In* The biology and management of lobsters (2), pp. 143–178. Ed. by J. S. Cobb and B. F. Phillips. Academic Press, London.

Chapman, C. J. 1985. Observing Norway lobster, *Nephrops norvegicus* (L.) by towed sledge fitted with photographic and television cameras. *In* Underwater photography and television for scientists, pp. 100–108. Ed. by J. D. George, G. I. Lythgoe, and J. N. Lythgoe. Clarendon Press, Oxford.

Chapman, C. J., and Bailey, N. 1987. Biological research on fish and shellfish stocks. Recent progress in Norway lobster research. *In* Developments in fisheries research in Scotland, pp. 99–111. Ed. by R. S. Bailey and B. B. Parrish. Fishing News Books Ltd, Farnham, England.

Chapman, C. J., and Howard, F. G. 1988. Environmental influences on the Norway lobster (*Nephrops norvegicus*) populations and their implications for fishery management. Symposium of the Zoological Society of London, 59: 343–353.

Cobb, J. S., Tamm, G. R., and Wang, D. 1982. Behavioural mechanisms influencing moult frequency in the American lobster *Homarus americanus*. Milne Edwards. Journal of Experimental Marine Biology and Ecology, 62: 185–200.

Cole, H. A. 1965. The size distribution of *Nephrops* populations on grounds around the British Coasts. Rapports et Procès-Verbaux des Réunions, Conseil International pour l'Exploration de la Mer, 156: 164–171.

Folk, R. L. 1974. Petrology of sedimentary rocks. Austin, Tex. Hemphills.

Fournier, D. A., Sibert, J. R., Majkowski, J., and Hampton, J. 1990. MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for Southern Bluefin tuna (*Thunnus maccoyii*). Canadian Journal of Fisheries and Aquatic Sciences, 47: 301–317.

Hillis, J. P. 1988. Relation of *Nephrops* catch characteristics to sea bed sediment type. ICES CM 1988/K:37.

Nichols, J. H., Bennett, D. B., Symonds, D. J., and Grainger, R. 1987. Estimation of the stock size of adult *Nephrops norvegicus* (L.) from larvae surveys in the western Irish Sea in 1982. Journal of Natural History, 21: 1433–1450.

Nichols, J. H., and Thompson, B. M. 1988. Quantitative sampling of crustacean larvae and its use in stock size estimation of commercially exploited species. Symposium of the Zoological Society of London, 59: 157–175.

Thomas, H. J. 1965. The distribution of the Norway lobster around Scotland and the stock composition in areas of different fishing intensity. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 156: 206–208.

Tuck, I. D. 1993. *Nephrops* abundance in relation to environmental factors and fishing pressure. PhD Thesis, University of London, pp. 1–301.

Tuck, I. D., Atkinson, R. J. A., and Chapman, C. J. 1994. The structure and seasonal variability in the spatial distribution of *Nephrops norvegicus* burrows. Ophelia, 40(1): 13–25.

Tully, O., and Hillis, J. P. 1995. Causes and spatial scales of variability in population structure of *Nephrops norvegicus* (L.) in the Irish Sea. Fisheries Research, 21: 329–347.

White, R. G., Hill, A. E., and Jones, D. A. 1988. Distribution of *Nephrops norvegicus* (L.) larvae in the western Irish Sea: an example of advective control on recruitment. Journal of Plankton Research, 10: 735–747.