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The application of fecundity estimates to determine the spawning stock biomass of Irish Sea *Nephrops norvegicus* (L.) using the annual larval production method

R. P. Briggs, M. J. Armstrong, M. Dickey-Collas, M. Allen, N. McQuaid, and J. Whitmore

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Ovigerous female *Nephrops* were collected by trawl and creel and maintained in individual containers over the nine-month incubation period to investigate aspects of fecundity. Females which extruded eggs in captivity shortly after capture provided an estimate of mean realised fecundity of 104.3 eggs g^{-1} live weight (s.e.=2.7). Egg loss during incubation, estimated by sampling ovigerous females from research trawl hauls at different times of year, was 36.7 eggs g^{-1} (s.e.=3.3). A similar value was obtained by monitoring individuals kept in the hatchery. Mean effective fecundity at the time of hatching was estimated as 67.6 eggs g^{-1} (s.e.=4.3) and is the difference between the number of eggs extruded (realised fecundity) and egg losses during incubation. The abundance of larvae at development stages I, II, and III was estimated over a series of surveys using high-speed plankton samplers. Abundance values were converted to daily production values using relationships between temperature and stage-duration. Annual larval production by stage was estimated by fitting Gaussian curves to the survey estimates. The mortality rate of larvae ($Z=0.033$ d^{-1}; s.e.=0.006) was estimated from the values of annual production by stage, using a maximum likelihood method. Annual production at hatching, estimated as the intercept of the mortality curve, was 440×10^9 larvae (s.e.=62×10^9). The biomass of mature female *Nephrops* in the western Irish Sea in 1995 was estimated from annual larval production and mean fecundity to be 6290 t (CV=0.17). The current ICES estimate of female SSB in 1995 of 7750 t, obtained from analysis of commercial catch data, lies within the 95% confidence limits for the ALP estimate. This indicates that current estimates of fishing mortality for female *Nephrops* in the Irish Sea may be robust.

Keywords: annual larval production, larval development, larval mortality, *Nephrops norvegicus*, stock assessment, survey.

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R. P. Briggs, M. J. Armstrong, M. Dickey-Collas, and M. Allen: Agricultural and Environmental Sciences Division, Department of Agriculture and Rural Development, Newforge Lane, Belfast, BT9 5PX, Northern Ireland. N. McQuaid: Centre of Marine Resources and Mariculture, Portaferry, County Down, Northern Ireland. J. Whitmore: formerly Fisheries Research Services Division, The Marine Institute, Abbotstown, Dublin. Correspondence to: R. P. Briggs: tel: +44 28 90 255503; fax: +44 28 90 382244; e-mail: richard.briggs@dardni.gov.uk

Introduction

The Norway lobster, *Nephrops norvegicus*, is the target of the most valuable fishery in the Irish Sea, with annual landings of over 8000 t (Briggs, 1997). The fishery is prosecuted mainly by otter-trawl vessels from Northern Ireland and the Republic of Ireland. Two separate populations of *Nephrops* exist in areas of muddy sediments in the eastern and western Irish Sea (Figure 1). The western population occupies a much larger area of mud than in the east, and provides the bulk of the commercial landings. Scientific advice for management of the fisheries is provided to the European Commission by the International Council for the Exploration of the Sea (ICES). The ICES assessment of the western Irish Sea stock is currently carried out using the age-based method Extended Survivors Analysis (XSA) applied to annual catches-at-age from the

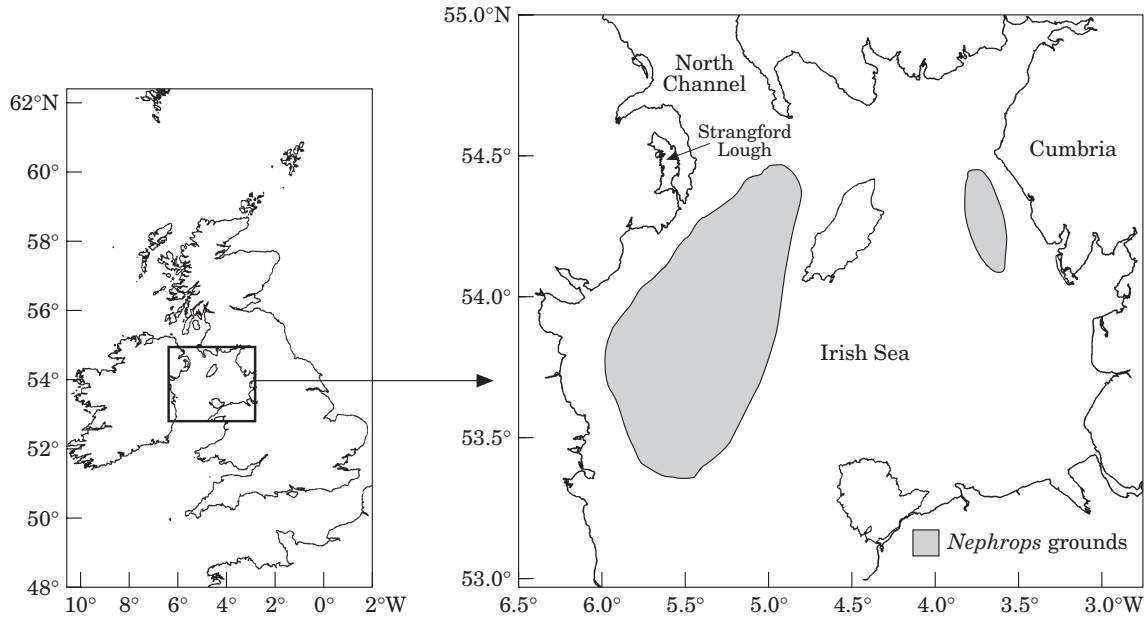

Figure 1. Location of western and eastern *Nephrops* grounds in Irish sea (shaded area). The position of Strangford Lough is also shown.

western Irish Sea. As individual *Nephrops* cannot be aged because they shed their exoskeleton at ecdysis, leaving no hard tissue with annual growth markings, annual length compositions have been decomposed to age using experimental and/or field estimates of growth parameters (Hillis, 1979). The XSA estimate of biomass of mature female *Nephrops* in the western Irish Sea stock in 1995 was 7750 t (XSA) with an implied annual removal by fishing fleets of some 43% of the stock of females (fishing mortality, F=0.63; ICES, 2001).

To date, the ICES assessments of Irish Sea *Nephrops* stocks have been totally dependent on data from commercial fisheries. Although trawl surveys are routinely carried out, catch rates are strongly influenced by environmental variables influencing the pattern of emergence from burrows (Chapman and Rice, 1971). Other survey methods for estimating the biomass of *Nephrops* have been developed to circumvent such problems. These include the counting of burrow clusters recorded using underwater television (UTV) (Bailey *et al*., 1993; Tuck *et al*., 1997a), and the annual larval production (ALP) method (Thompson *et al*., 1986; Nichols *et al*., 1987; Tuck *et al*., 1997b). The ALP method provides direct estimates of biomass of mature females based on plankton surveys and sampling of adults, and is an extension of the annual egg production method applied to finfish stocks (Armstrong *et al*., 2001). Tuck *et al*. (1997b) found good agreement between estimates of biomass of Firth of Clyde *Nephrops* from UTV surveys, ALP surveys, and analytical assessments using commercial fisheries data. An application of the ALP method to western Irish Sea *Nephrops* in 1982 and 1985 gave biomass estimates for mature females of 8000–12 000 t (Thompson *et al*., 1986; Nichols *et al*., 1987). ICES did not assess *Nephrops* in the early 1980s so it was not possible for these authors to draw comparisons with results from other methods and they did not determine fecundity specific to the Irish Sea stocks.

One of the weaknesses of the ALP method as applied to *Nephrops* has been the poor assessment of fecundity (Smith, 1987) and the stock-specific nature of the reproductive strategies of *Nephrops* (Froglia and Gramitto, 1979; Figueiredo *et al*, 1982; Tuck *et al*., 1997b). The present study was established to obtain the first estimates of fecundity for *Nephrops* in the Irish Sea and improve the methods. Fecundity and losses of eggs during incubation were investigated from field and laboratory work carried out in 1997 and 1998. The estimates of fecundity were then used in conjunction with values of larval production obtained in 1995 (Dickey-Collas *et al*., 2000a,b) to give an estimate of spawning stock biomass of western Irish Sea female *Nephrops*. This paper summarizes these investigations, presents estimates of biomass of mature female *Nephrops* in the western Irish Sea, and compares these with the equivalent estimates from ICES assessments.

Methods

Realised fecundity

In the present paper, the term "realised fecundity" (E, eggs female^{-1}; E_g, eggs g^{-1}) is applied to counts of the

number of eggs extruded onto the pleopods of *Nephrops* at the time of fertilisation, as described by Farmer (1974). Enumeration of eggs in the ovary or potential fecundity, as described by Thomas (1964) and Tuck *et al.* (2000), was not attempted.

An outdoor, roofed hatchery was established at the Centre of Marine Resources and Mariculture (C-Mar) in Portaferry, Northern Ireland to investigate aspects of *Nephrops* fecundity and larval development. Seawater from Strangford Lough (Figure 1) was pumped into a reservoir tank and passed through a filtration system before flowing into the top of 245 l holding tanks from which water upwelled into chambers holding individual *Nephrops*. Each chamber contained a section of plastic tubing to provide shelter. Animals were fed once a week on cooked mussel (*Mytilus edulis*). Temperature and salinity were recorded twice weekly using a WTW microprocessor conductivity meter. Debris, uneaten food, and shed eggs were removed at regular intervals from each chamber by siphoning water through a small sieve.

Adult female *Nephrops* were collected by trawling in the western Irish Sea and by creeling in Strangford Lough during autumn 1997 and 1998, and transferred first into holding tanks for a settling period before transfer to individual chambers. A number of females extruded eggs onto the pleopods after transfer to the hatchery, providing an opportunity to measure realised fecundity. A sample of 50 individuals of mean carapace length 27.3 mm bearing extruded eggs were sacrificed and preserved individually in 4% formaldehyde. The eggs were removed from the pleopods and counted under a binocular microscope. Realised fecundity was recorded in absolute numbers of eggs per individual, and converted to eggs g^{-1} using the following relationship between weight (W) and carapace length (CL) for non-ovigerous females (Pope and Thomas, 1955):

$$W = 0.00068\ CL^{2.96}\ (W \text{ in g; CL in mm}) \quad (1)$$

Mean weights at length investigated during the present study did not differ significantly from those predicted from the Pope and Thomas equation, which is also incorporated in the ICES assessments to estimate weight from length. The parameters of the power-curve relationship $E = aCL^b$ between realised fecundity and carapace length were estimated by non-linear least squares predictive regression. A linear least-squares regression was fitted to the data on realised fecundity and predicted female weight. The significance of the relationship between carapace length and E_g was investigated.

Effective fecundity

Ovigerous females collected by trawling and creeling were successfully maintained in individual containers in the hatchery over the nine-month incubation period. Loss of eggs during incubation (cumulative number, in eggs g^{-1}) was investigated by collecting shed eggs from the individual containers. Egg loss was also evaluated as the difference between realised fecundity, estimated from the 50 females sacrificed at the start of the experiment, and numbers of larvae hatching.

The pattern of egg loss during incubation was investigated in the wild population by collecting samples of ovigerous females from research trawl surveys of the western Irish Sea at different times during incubation. Surveys with the same trawling procedures were carried out at the time of extrusion and fertilisation (August 1997, 50 females), part way through incubation (October 1997, 28 females), and immediately prior to hatching (April 1998, 29 females). The size range of animals collected was 20–35 mm and was representative of the size range in the population. The loss of eggs g^{-1} (E_L) over the incubation period was estimated from a regression of mean fecundity against time. As the same trawling and sampling procedures were adopted at each trawl station, it was assumed that the same number of eggs g^{-1} was lost during each trawling operation. Estimates of egg loss during trawling was inferred by comparing the number of eggs extruded in captivity by females caught by trawl in August, with the expected eggs g^{-1} in ovigerous females from the same trawls. The expected fecundity was obtained from the regression of fecundity against month of capture in trawl-caught ovigerous females. Egg loss during capture was expressed as an absolute number of eggs and as a percentage of fecundity.

Effective fecundity, E_r, and its variance, Var (E_r), were estimated as:

$$E_r = E_g - E_L \quad (2)$$

$$\text{Var}\ (E_r) = \text{Var}\ (E_g) + \text{Var}\ (E_L) \quad (3)$$

where E_L is the number of eggs g^{-1} lost during the incubation period and E_g is the realised fecundity, i.e. the number of eggs extruded per g of female.

Annual larval production at time of hatching

Dickey-Collas *et al.* (2000a) give annual larval production estimates at the median age of each stage i (ALP_i) in 1995. To use the ALP method fully for the determination of SSB, the annual larval production at the time of hatching (time zero) must be estimated (ALP_0). The full methods of larval collection and survey design are given in Dickey-Collas *et al.* (2000a) and Armstrong *et al.* (2001). The relationships between sea temperature and larval development rate, required for converting estimates of abundance to daily production, are given in Dickey-Collas *et al.* (2000b). Noting that the survey estimates of mean daily larval production at stages I and

II given in Dickey-Collas *et al.* (2000a) follow a bell-shaped pattern over time, a method was developed to integrate the production estimates over time by fitting Gaussian curves of the form:

$$y_d = \alpha + \frac{\beta}{\sqrt{2\pi\sigma^2}} \exp\left[\frac{-1}{2\sigma^2}(d-\mu)^2\right] \quad (4)$$

Where α, β, σ, and μ are fitted parameters, and y_d is the daily production of larvae at time d. The parameters were estimated from the survey estimates of daily larval production using a maximum likelihood estimator in Genstat® (Payne *et al.*, 1993). Annual larval production was calculated as the area under the curve, estimated by the Composite Simpson's rule:

$$\int_a^b f(x)dx = \frac{h}{3}(f_1 + 4\times f_2 + 2\times f_3 + 4\times f_4 + 2\times f_5 + \ldots + 2\times f_{n-2} + 4\times f_{n-1} + f_n) \quad (5)$$

where n is the number of evenly spaced points along the interval [a,b] and $h=(b-a)/(n-1)$. The number of points used was increased until convergence took place.

On the assumption that the samples that have been collected provide the best information about the density distribution of the population, the station estimates of daily production were randomly re-sampled to generate 1000 bootstrap data sets (Manly, 1997). The original station weightings were retained. Estimates of Gaussian parameters and annual larval production were obtained from each data set, and means and standard deviations were calculated.

Annual larval production appeared to decline exponentially through stages I to III according to the function:

$$ALP_i = ALP_0 \exp(-Z.\ age_i) \quad (6)$$

where Z is the instantaneous daily mortality rate and age_i is the mean age of stage i larvae. However, with only three data points to estimate two parameters, variance estimates from a simple regression were considered inappropriate and likely to underestimate the true uncertainty in the parameters. Further, the variance of the ALP_i estimates is not considered. Estimates of daily larval mortality rate Z and annual larval production at hatching, ALP_0, were therefore obtained by maximising the likelihood function:

$$L[ALP_0, Z] = \prod_i \exp\{-0.5[(ALP_i - X_i|ALP_0, Z)/SE(ALP_i)]^2\} \quad (7)$$

where X_i is the expected annual production of larvae of stage i conditional on a given combination of ALP_0 and Z. The variables ALP_i and $SE(ALP_i)$ are the survey estimate of annual production of stage i larvae and its standard error respectively. Likelihood values were calculated for 5000 pairs of ALP_0 and Z values generated randomly from uniform prior probability distributions specified to give full descriptions of the posterior probability distributions. The expected mean age of larvae at each stage was calculated for each random value of *Z*, as the median overestimates the average age of larvae in the sea. The 95% confidence intervals were calculated from the 2.5th and 97.5th percentiles of the posterior probability distributions of each parameter, and an approximate standard error for each parameter was estimated assuming this range represented four standard deviations. The maximum likelihood estimates for the parameters were estimated using a constrained search.

Estimating spawning stock biomass using the annual larval production method

The ALP method estimates the spawning biomass (SSB) of mature females required to produce the observed annual production of planktonic larvae at hatching (ALP_0):

$$SSB = \frac{ALP_0 \times 10^{-6}}{Er} \quad (8)$$

where SSB is the spawning biomass of female *Nephrops* in tonnes; ALP_0 is the total number of larvae at hatching produced during the season, estimated from plankton survey estimates of annual production by development stage and an estimate of larval mortality, and E_r is the effective fecundity (Figueiredo *et al.*, 1982) expressed as numbers of eggs g^{-1} of mature females at time of hatching.

Results

Realised fecundity

Fifty female *Nephrops*, with an average carapace length CL of 27.3 mm, extruded eggs in captivity. The bulk of these females were in the size range 23–31 mm CL, which was considered representative of the *Nephrops* population in the Irish Sea. The relationship between realised fecundity, E, and weight of individual females was linear (Figure 2a) with a positive intercept that was not significantly different from zero at the 5% error level. The relationship with carapace length CL was best described by a power curve $E=a\ CL^b$ with exponent b of 2.566, s.e.=0.206 (Figure 2b). As the intercept of the fecundity vs. weight regression was positive (a=0.259, s.e.=0.18), the relative fecundity (eggs g^{-1}) declined slightly with increasing carapace length (Figure 2c), although the slope was not significantly different from zero at the 5% error level and the correlation was low ($r=-0.24$). In the absence of a significant relationship between size and relative fecundity, the mean value of E_g

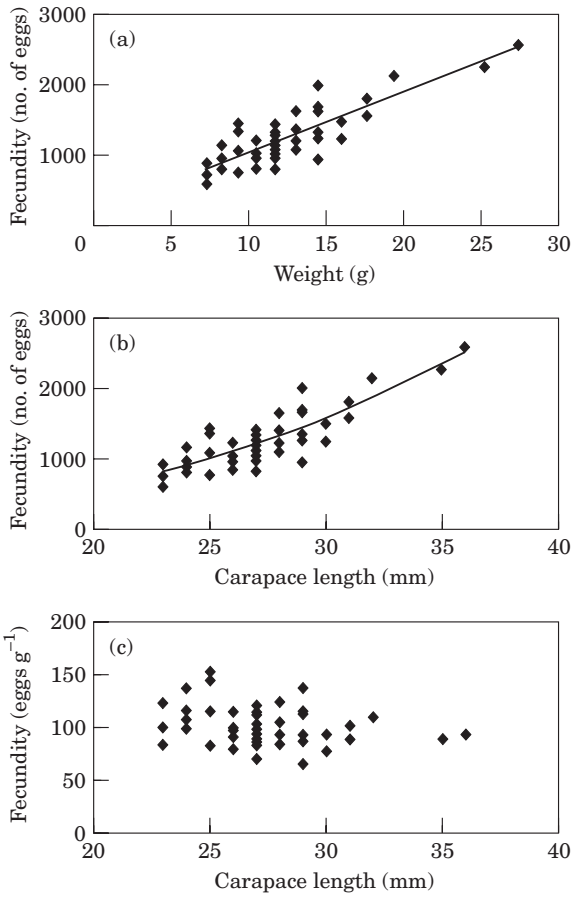

Figure 2. Realised fecundity (E): relation between the number of eggs extruded in captivity and (a) female weight and (b) female carapace length (mm). The poor relationship between number of eggs extruded per unit weight (E_g) of female *Nephrops* is also shown (c).

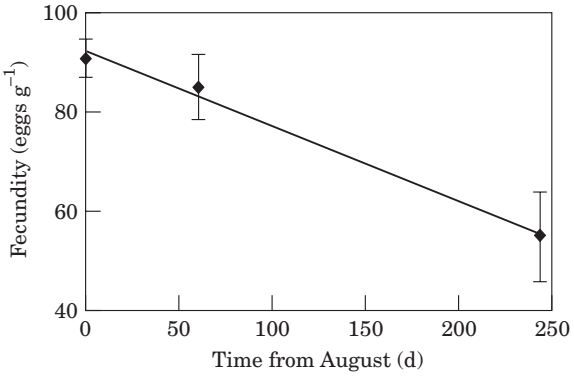

Figure 3. Decline in fecundity of *Nephrops* in trawl samples collected in August 1997, October 1997, and April 1998. Error bars are confidence limits for means.

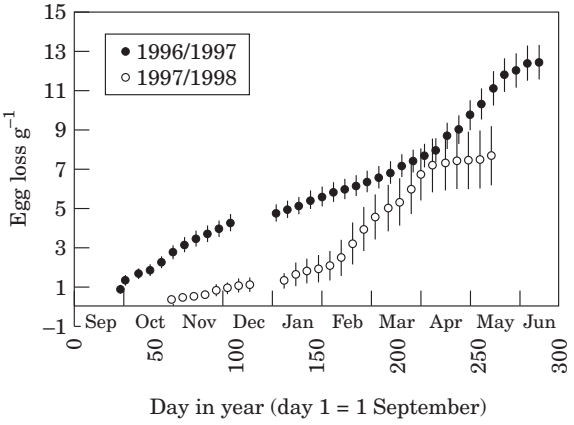

Figure 4. Cumulative mean egg loss per gram for 1996/1997 and 1997/1998 against time for captive *Nephrops*. Vertical bars indicate standard errors.

for the population was taken as the mean of the 50 individual values (104.3 eggs g^{-1}; s.e.=2.7).

Effective fecundity

The number of eggs g^{-1} in female *Nephrops* collected by trawl in the same area of the western Irish Sea declined from August to April over the incubation period (Figure 3). This decline was assumed to reflect losses of eggs during incubation. A linear regression fitted to the three observations fell within the 95% confidence limits for the means. The predicted fecundity was 92.3 eggs g^{-1} (s.e.=2.07) in August and 55.6 eggs g^{-1} (s.e.=2.51) in April. Total loss of eggs during incubation, assuming the same rate of loss during trawling at each time of year, was 36.7 eggs g^{-1} (s.e.=3.3).

Counts of detached eggs in the laboratory incubation chambers showed a continual loss throughout the incubation period (Figure 4). The rate of loss was much lower than inferred from the sequential trawl samples. The cumulative loss curve showed variations over time with an increased loss rate at the commencement of hatching from mid-April in 1996/1997 and from mid-February in 1997/1998. Lower ambient water temperatures during the winter months in 1996/1997 may have accounted for the observed delay in hatching in that year. Increased loss of eggs during the hatching period may be attributed to the stress caused during removal of larvae for stage duration studies and to the females removing eggs that were not sufficiently developed to hatch.

As the fecundity of the laboratory animals could not be estimated directly, a sample of trawled ovigerous females was sacrificed at the commencement of the 1997/1998 study and had a mean fecundity of 62.3 eggs g^{-1} (s.e.=4.9; n=24). This was 40% lower than the realised fecundity estimates of 104 eggs g^{-1} based on counts of newly extruded eggs. The difference is most

likely to represent loss of eggs in the trawl and during transportation of the live animals to the laboratory. The average number of larvae hatching in 1998 was 19.8 larvae g^{-1}, indicating a potential loss during incubation of 42.5 eggs g^{-1}, of which only 6.8 eggs g^{-1} comprised detached eggs collected from the incubation chambers. An unaccounted average loss of 35.7 eggs g^{-1} had therefore occurred. It is likely that this loss represented detached eggs ingested by the females during incubation.

The total loss of eggs in the laboratory animals was, in absolute terms, very close to the figure obtained for *Nephrops* in sequential trawl samples (36.7 eggs g^{-1}). However, the losses in the aquarium represented 61% of initial fecundity compared with 40% in the trawl samples. This reflected the smaller initial fecundity in the aquarium specimens.

The difference between realised fecundity (104.3 eggs g^{-1}) and the number of eggs lost during the incubation period (36.7 eggs g^{-1}) was taken as an estimate of effective fecundity, E_r, of 67.6 eggs g^{-1} (s.e.=4.3). This value was used to estimate female SSB of western Irish Sea *Nephrops*. The loss of eggs in the trawl was the difference between the realised fecundity and the intercept of the fecundity-time regression (Figure 3) and was 12 eggs g^{-1}, or 11.5%.

Larval production at hatching

The production of stage I larvae peaked during the first week in May (Figure 5) and the majority of hatching occurred over a 5.5-week period. The Gaussian model fitted well to the survey estimates of production at stages I and II, and the bootstrap estimate of annual production at stage I had a low CV of 0.12 (Tables 1 and 2). Precision of the production estimates declined rapidly with increasing larval stage (Table 1). The ALP_i estimates declined exponentially over time (Figure 6). The estimate of larval mortality rate was 0.027 d^{-1}, and the intercept of 425.1×10^9 larvae (CV=0.16) was taken as the best estimate of annual production at hatching (ALP_0).

Biomass estimates

The ALP estimate of SSB for western Irish Sea mature female *Nephrops* was 6288 t (CV=0.17). Estimates of variables contributing to this result are summarised in Table 3.

Discussion

Fecundity

This study is the first documented case of large numbers of *Nephrops* being trawled prior to becoming ovigerous and subsequently extruding eggs in captivity. Whilst it is unknown if the stress of capture and maintenance of adult females in aquaria could have affected the number of eggs extruded, the extrusion took place soon after capture and provided an estimate of realised fecundity.

Farmer (1974) estimated fecundity of 60 ovigerous *Nephrops* caught in the western Irish Sea based on the assumption that the eggs had been recently extruded. He

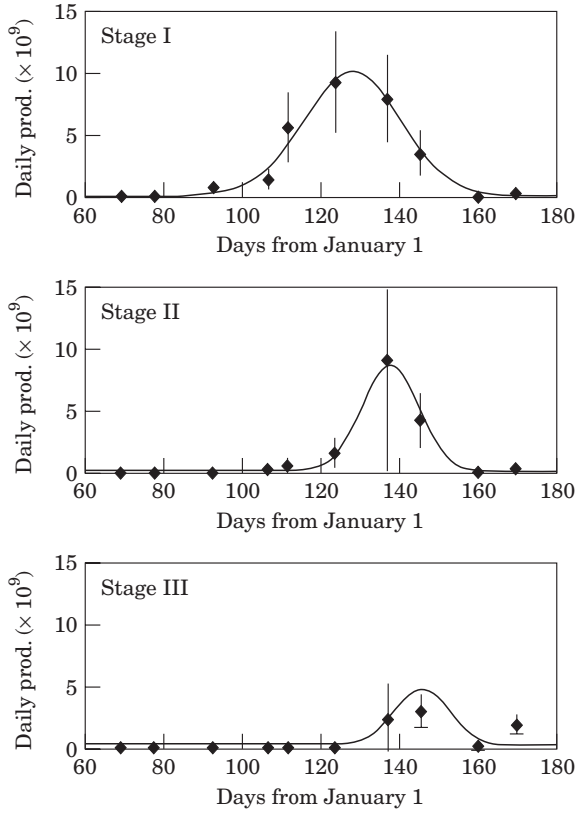

Figure 5. Gaussian production curve fitted to survey estimate of daily production of *Nephrops* larvae by stage in 1995. Vertical bars indicate 95% confidence limits.

Table 1. Annual larval production ($\times 10^9$) of *Nephrops* larvae at stages I, II, and III ($ALP_{I–III}$) and at hatching (ALP_0) in the western Irish Sea in 1995, from bootstrap estimates of annual Gaussian production curves. CV=coefficient of variation of the estimates; Z=instantaneous rate of mortality. Estimated mean age at stage is given (days).

Variable	Estimate	CV	Mean age
ALP_I	335.11	0.115	8.59
ALP_{II}	198.69	0.250	28.55
ALP_{III}	102.40	0.387	52.67
ALP_0	425.1	0.158	
Z (d^{-1})	0.027	0.369	

Table 2. Estimated parameters for Gaussian curves of daily larval production ($\times 10^9$) of each stage of *Nephrops* larvae over time in 1995. s.d.=standard deviation of 1000 bootstrap estimates of the parameters.

	Stage I		Stage II		Stage III	
Parameter	Estimate	s.d.	Estimate	s.d.	Estimate	s.d.
σ	12.37	1.56	7.31	1.78	7.09	9.19
μ	128.00	1.71	137.77	1.94	145.86	16.21
β	318.11	38.58	160.92	48.21	81.58	270.52
α	0.08	0.13	0.21	0.07	0.22	0.14
r^2 (%)	93.9	5.0	98.4	2.5	73.0	13.4

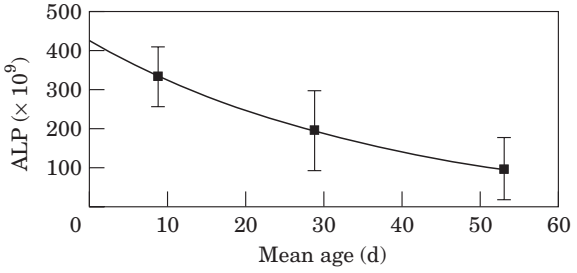

Figure 6. Mortality curves fitted to annual larval production estimates at each stage. Production estimates based on bootstap estimates of Gaussian production curves. Error bars represent two standatd errors.

Table 3. Estimates of annual larval production at hatching (ALP_0), realised and effective fecundity (E_g, E_r), and spawning biomass (SSB) for female *Nephrops* in the western Irish Sea.

Parameter	Mean	CV
ALP_0 ($\times 10^9$)	425.1	0.158
E_g (eggs g^{-1})	104.3	0.026
E_r (eggs g^{-1})	67.6	0.064
SSB (t)	6 288	0.170

obtained the following linear relationship with carapace length CL (in cm):

$$E = 782.041CL - 1376.421$$

For a mean CL of about 27 mm, roughly the mean size of females caught by trawl in the present study, this relationship predicts a mean fecundity of 735 eggs per female or 62.7 eggs g^{-1}. This lies between the values obtained from *Nephrops* trawled in October 1997 and April 1998, and 40% below the realised fecundity estimate for 1997, suggesting substantial loss of eggs in the trawl in Farmer's samples. A more recent study of potential fecundity of *Nephrops* was carried out by Tuck *et al.* (2000) using counts of oocytes in ovaries of specimens collected in the Firth of Clyde, approximately 150 km north of the western Irish Sea stock. The Irish Sea realised fecundity estimate of 104.3 eggs g^{-1} are encompassed by the range estimated from different stations in the Clyde of 85.9–114.6 eggs $^{-1}$.

Table 4. Reported levels of egg loss from spawning to hatching in *Nephrops*.

Study	Area	% egg loss
Froglia and Gramitto (1979)	Adriatic	66
Chapman and Ballantyne (1980)	Moray Firth	31–51
Morizur (1981)	Bay of Biscay	45–50
Figueiredo *et al.* (1982)	Portuguese Coast	68
Smith (1987)	Clyde	18
Farina *et al.* (1999)	Galicia	44
Mori *et al.* (1998)	North Tyrrhenian Sea	49.5

Egg counts from animals trawled between spawning and hatching gave egg loss estimates equivalent to 35% of realised fecundity. A variety of factors could cause egg loss, such as the failure of eggs to be fertilised, the removal of dead eggs by the female and mechanical loss due to abrasion (Figueiredo and Nunes, 1965; Figueiredo, 1979; Smith, 1987). The level of egg loss varies between studies (Table 4), and will be affected by the incubation period which is 7.5 months in the Bay of Biscay and approximately nine months in the Clyde and Irish Sea. The aquarium studies indicated the difficulty in monitoring egg loss in captive animals. Although regular attempts were made to remove detached eggs from the incubation chambers, a balance had to be maintained between removal of detached eggs and causing stress to the animals. It is not known how this stress compares to that caused in the wild by predators or interaction with other *Nephrops* or co-occurring benthic species. An unaccounted egg loss of 35.7 eggs g^{-1} was noted during the study and was attributed to ingestion of detached eggs by the adults; this was supported by an absence of unhatched eggs remaining on females after the hatching season.

The apparent number of eggs lost over the incubation period in the samples was considered to reflect the average loss in the population over the incubation

period. Egg loss during trawling was observed and is a well-known phenomenon in *Nephrops* fisheries (Chapman and Ballantyne, 1980). This could not be estimated directly, as there was no means of capturing ovigerous females at the same time using a method not causing abrasion of the eggs or excessive activity of the females. Ideally, methods of capturing *Nephrops* with little or no mechanical abrasion of the egg clusters or excessive activity of the females are required. However, as the surface area of the egg cluster is not fully exposed, it is possible that abrasion or other processes could remove a higher proportion of eggs from individuals with a lower than average fecundity than from those with a high fecundity.

The use of pots or creels is a possible method for estimating fecundity with minimal egg loss, but this method could only be carried out in areas not trawled commercially. In the present study, short-duration trawling was adopted to capture ovigerous female *Nephrops* at several times during the incubation period. Trawling was also used by Tuck *et al.* (2000) to study fecundity in Scottish stocks. Egg losses during trawling appear small compared with subsequent losses during incubation. The figure of 11.5% loss during trawling, calculated in the present study, is at the lower end of the 11–22% range suggested by Chapman and Ballantyne (1980) from comparisons between trawl-caught and creel-caught individuals. Tuck *et al.* (2000) considered the latter study might not give correct results because of small-scale spatial variations in fecundity.

Previous attempts to hold ovigerous females throughout the incubation period have not always been successful. Salhauge and Ulmestrand (pers. comm.) found that trawl caught *Nephrops* did not survive more than a few days, while early attempts by Figueiredo (1979) to hold ovigerous *Nephrops* in aquaria were unsuccessful because females removed all their eggs before eggs were fully mature. Improved husbandry techniques, reduced stress to the individuals, and a high standard of water quality have contributed to the success of the present study in maintaining trawl-caught female *Nephrops* in captivity for over two years.

Larval production

The pattern of larval production in 1995 was consistent with observations in 1982 and 1985 (Nichols *et al.*, 1987; Dickey-Collas *et al.*, 2000a) and the annual larval production was also similar. Throughout the surveys in 1995, efforts were made to minimise the errors associated with poor sampler performance. High-speed plankton samplers are thought to be efficient at catching *Nephrops* larvae (Nichols and Thompson, 1988) and the larvae are easily distinguishable from other zooplankton (Williamson, 1983). The surveys covered the spatial and temporal extent of the hatching, and there was very little loss due to migration out of the study area (Angelico, 1999).

The estimates of larval production could be biased by variations in the catchability of the larvae with time of day or an unsuitable measure of temperature being used in the determination of stage duration. In the laboratory experiments described here hatching occurred throughout the 24-h period, with peaks at night. This was also observed by Moller and Branford (1979). In contrast, Farmer (1974) noted that hatching only occurred at night. The pre-zoeae hatched in the present study were non-motile and took a few minutes to moult to the first stage zoeae, after which they were observed swimming directly to the water surface. Hence, stage I production is unlikely to be constant throughout the day. Dickey-Collas *et al.* (2000a) could not detect a significant diel signal in abundance of stage I larvae at the plankton stations in 1995. They argued that any signal would probably be masked by the long duration of the stage (>15 days).

As most of the larvae are found in the upper water column (Hillis, 1974; Lindley *et al.*, 1994; Angelico, 1999), the integrated water column temperature may not be suitable for the determination of stage durations. Nichols *et al.* (1987) also questioned the use of the integrated temperature. Dickey-Collas *et al.* (2000a) compared the estimates using integrated and surface water column temperatures and found that the estimates of ALP only changed by 2.5%. A change of this size is much lower than the variance associated with sampling or the errors associated with stage duration to temperature relationship, hence has very little impact on the overall estimate of total ALP.

The bootstrap method of determining annual larval production based on fitting of Gaussian curves gave similar estimates for stage I and II compared to the non-parametric trapezium method used by Dickey-Collas *et al.* (2000a) on the same survey data. Whilst the precision of the bootsrap method appeared poorer at stages II and III than obtained using the trapezium method, the annual production estimates conformed more closely to the exponential mortality model. Ultimately, the choice of method of integrating survey estimates over time rests on the extent to which the annual production cycle is believed to follow a definable distribution. In the present study, the Gaussian model explained 94–98% of the variation in survey estimates of production at stages I and II, and 73% at stage III (Table 2). However, methods for integrating survey estimates of larval production over time may not cope well with the pseudo-synoptic nature of plankton cruises. General Additive Models (GAMs) have been used for estimating fish egg productions in the Irish Sea (Fox *et al.*, 2000) and appear to cope well with the temporal and spatial distribution of plankton in the Irish Sea. The development of such models for

the assessment of the population dynamics of other planktonic organisms should be encouraged.

Mortality of *Nephrops* larvae appeared to follow the exponential model, although this conclusion is based on only three observations. Variations in mortality probably occur throughout the hatching season, which covers a significant part of the spring and summer production in the Irish Sea. The probability of a larva dying may be affected by several factors, including temperature, food supply, vulnerability during ecdysis, and changes in the size of the larva following ecdysis. The decline in larval production between stage I and II in 1995 was very similar to values obtained by Dickey-Collas *et al.* (2000a) using survey data collected in the western Irish Sea in 1982 and 1985.

Estimate of SSB

The estimate of female SSB in 1995 has been made assuming the same effective fecundity as estimated from laboratory and field observations in 1997 and 1998. Hence, the results may contain some bias. The magnitude of inter-annual variations in potential fecundity is not known. Observations by Tuck *et al.* (2000) show relatively small-scale spatial variations in potential fecundity at a given carapace length, indicating the need for random sampling of the whole population for fecundity.

The areas of potential *Nephrops* habitat in the western Irish Sea, inferred from British Geological Society charts, are approximately 1880 km^2 of muddy sediments and 1540 km^2 of muddy sand. Assuming the population to be confined to these sediments, the mean density of mature female *Nephrops* in 1995 was 1.8 g m^{-2}, based on the ALP estimate of 6288 t SSB. For a mean mature female size and weight of 27.4 mm CL and 12.25 g, this implies a density of some 0.15 mature females m^{-2}. The overall density of mature males and females is therefore expected to be more than 0.3 individuals m^{-2}, assuming a sex ratio of around 50%. This falls within the mean density range reported from underwater television (UTV) surveys of the firth of Clyde (Tuck *et al.*, 1997a,b) and elsewhere in Scottish waters (Bailey *et al.*, 1993, 1995). Irish Sea UTV studies, (R.P.B. and M. Service, unpublished results) have indicated that *Nephrops* densities vary in different parts of the Irish Sea and support the *Nephrops* variability reported from trawl surveys by Briggs (1995) where catch rates varied from 500 to 5000 animals per nautical mile trawled. Analysis of bottom sediments in conjunction with hydroacoustic ground discrimination research, using RoxAnn (M. Charlesworth, pers. comm.), have described spatial variability in sediment structure and chemical composition of the western Irish sea mud patch. This could account for the observed variations in *Nephrops* populations originally proposed by Hillis (1988) for the Irish Sea and by Bailey and Chapman (1983) for Scottish *Nephrops* stocks (reviewed by Alfonso-Dias, 1997). It is therefore possible that the *Nephrops* density estimated from this study represents the mean of a range of values, as seen for the Firth of Clyde, where densities of 0.074 m^{-2} in the north to 1.48 m^{-2} at a more southern station have been reported (Tuck *et al.*, 1997a,b).

Comparison with ICES estimates of *Nephrops* biomass

The XSA estimate of female SSB in 1995 (7750 t; ICES, 2001) was within the 95% confidence limits of the ALP estimate (4150 t–8430 t) for that year. The SSB value given by XSA is calculated assuming knife-edge maturity of female *Nephrops* at three years of age. This will differ to some extent from the actual pattern in the population in 1995. To investigate the magnitude of possible bias, a length cohort analysis (LCA) was carried out using a length-based maturity ogive based on sampling in the present study, and compared with an equivalent run using the knife-edge maturity of 24 mm adopted by ICES for LCA (Briggs, 1988). The estimate of SSB of females using the new ogive was 12% higher than obtained with the knife-edge maturity. Hence, the XSA may slightly under-estimate the SSB in 1995 due to the maturity ogive adopted, although the estimate is likely to remain close to the upper 95% confidence limit of the ALP estimate.

The similarity between ALP and XSA estimates of biomass supports the ICES assessment of fishing mortality on mature female *Nephrops* in the western Irish Sea ($F=0.63$; ICES, 2001), which indicates that fishing is the main source of mortality on this component of the stock. This conclusion rests on the assumption that the values of natural mortality (M) used in the assessment are within reasonable bounds of the true values. The values used by ICES for female *Nephrops* are $M=0.3\ yr^{-1}$ for immature individuals and $0.2\ yr^{-1}$ for mature ones, the difference representing a belief that the extended time spent in burrows by mature females reduces their vulnerability to predators. To test for sensitivity of the ICES estimates to these assumptions, further XSA runs were carried out using the data given in ICES (2001), varying the vector of M values whilst keeping all other model inputs constant. Reductions in M brought the XSA estimate closer to the point estimate from the ALP method (Figure 7). Such low values for natural mortality seem unlikely for *Nephrops* despite the length of time spent by females in their burrows. Increasing M beyond $0.2\ yr^{-1}$ caused a rapid increase in SSB estimates and associated reduction in fishing mortality. At $M=0.4\ yr^{-1}$ on mature females, the SSB estimate exceeded 11 000 t and was well above the confidence range of the ALP estimate. However, the XSA failed to

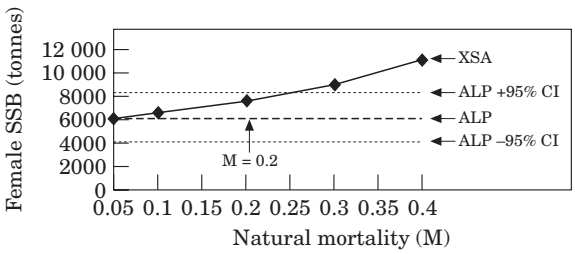

Figure 7. Estimates of female SSB in 1995 from extended survivors analysis (continuous line) at different input values of natural mortality (M) on mature females, compared with ALP estimates and 95% confident limits. The value of M = 0.2 used in the ICES XSA assessment is indicated.

converge to a solution indicating a difficulty in reconciling model estimates of population trends with the indices of abundance used to tune the analysis. Whilst this is not an exhaustive analysis, the results of the ALP surveys support the lower values of M adopted by ICES and the conclusion that fishing is the main source of mortality on female *Nephrops* in the Irish Sea.

As only limited comparisons can be made between the absolute estimates of biomass given by the different methods, due to the unknowns regarding natural mortality and other processes affecting interpretation of commercial catch data, the value of ALP estimates may lie in repeat surveys over time. The comparatively high precision of the ALP estimate of SSB for females (CV = 0.17) suggests that such surveys may be very valuable for confirming long-term trends in abundance. However, the cost of repeated within-season surveys is high and such surveys could only be repeated at intervals of several years.

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