Population dynamics of the common shrimp, *Crangon crangon* (L.), in Port Erin Bay, Isle of Man, Irish Sea

C.-W. Oh, R. G. Hartnoll, and R. D. M. Nash

The population structure, growth, mortality, and size at sexual maturity of the common shrimp (*Crangon crangon*) were examined in Port Erin Bay, Isle of Man, Irish Sea between April 1995 and July 1998. For estimation of parameters of growth and mortality, monthly length–frequency data were analysed by ELEFAN. The population consisted mostly of the first year class, with a similar size composition each year. Regressions of body wet weight on carapace length indicated isometric growth (exponents very close to 3.0). Parameters of growth were estimated, using the modified von Bertalanffy growth function (VBGF) model incorporating seasonal variation in growth. Females grew faster and reached a larger size at age than males ($K = 1.09 \, yr^{-1}$ and $L_\infty = 18.5$ mm CL for females, and $K = 0.90 \, yr^{-1}$ and $L_\infty = 15.1$ mm CL for males). The maximum life span is estimated as 3.3 years. The recruitment pattern shows one major recruitment event per year. Total mortality (Z) by length-converted catch curve was estimated at $3.96 \, yr^{-1}$, fishing mortality (F) $0.36 \, yr^{-1}$, and natural mortality (M) $3.60 \, yr^{-1}$. The size at 50% sexual maturity for females ranged from 12.0 to 12.6 mm CL. Fecundity per recruit was 6.2×10^5. The exploitation rate (E) corresponding to 50% of the unexploited stock was 0.28 at L_{25}, 0.32 at L_{50}, and 0.35 at L_{75}.

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Introduction

The common shrimp, *Crangon crangon*, occurs in shallow waters all around the North and Irish Seas and the English Channel (Tiews, 1970). This species has been extensively studied due to its abundance and commercial importance in these areas (see Tiews, 1970). Research has mainly been undertaken on North Sea populations, covering life history (Ehrenbaum, 1890; Lloyd and Yonge, 1947; Meredith, 1952), reproductive output (Jensen, 1958; Boddeke, 1982), population biology (Kuipers and Dapper, 1981, 1984; Henderson and Holmes, 1987; Beukema, 1992), seasonal migration (Boddeke, 1976; Boddeke *et al.*, 1976), and fisheries management (Boddeke, 1989). There is a sexual dimorphism in growth of *C. crangon* and a marked seasonality in growth rate (Tiews, 1954; Henderson and Holmes, 1987). To date there have not been any studies which examine the seasonal growth of the sexes separately. Von Bertalanffy growth parameters and mortality have been estimated indirectly, using information on maximum size, sex ratio, and M/K from the length composition of catches for 5 years in the German shrimp fishery (Schumacher and Tiews, 1979).

Growth in crustaceans is very difficult to estimate since exoskeletons are lost during moulting and thus cannot serve as an index of the age of an individual. Consequently analysis of length–frequency data (LFD) has been widely used to identify year classes. Von Bertalanffy growth functions (VBGF) (Beverton and Holt, 1957; Ricker, 1975) are generally fitted to the mean length at estimated age of a year class (Parrack, 1979; Garcia and Le-Reste, 1981; Frechette and Parsons, 1983; Roa and Ernst, 1996; Tuck *et al.*, 1997).

Because of asynchronous moulting of individuals within a year class, Pauly and Gaschütz (1979) modified the basic VBGF to incorporate seasonal variations in growth. The revised VBGF model is the most widely used model for decapod crustacean stocks (Pauly et al., 1984; Hopkins and Nilssen, 1990; Bergström, 1992; Ohtomi and Irieda, 1997; Alves and Pezzuto, 1998).

Dynamic pool models are widely used in fish population dynamics (Beverton and Holt, 1957; Ricker, 1975). They have become a major technique for shrimp management because they allow an evaluation of the response of yield to changes in fishing mortality and age (size) at capture, two control measures in managing a fishery. Allowing for the problems of applying dynamic pool models (yield-per-recruit (Y/R) and egg-per-recruit (E/R)) to crustacean populations, on the basis of the two growth components (increment in size and moult frequency), Caddy (1977, 1979) has incorporated the crustacean intrinsic growth characteristics into a new class of models. The new models use simple Ricker or Thompson and Bell models (Ricker, 1975). Campbell and Robinson (1983) have further modified Caddy's model. Although the shrimp stock in Port Erin Bay is not exploited this study provides insight into the response of a shrimp stock to exploitation when growth, fecundity, natural mortality, fishing mortality, and exploitation rates vary.

The study area (Port Erin Bay, Isle of Man, Irish Sea) is a small embayment which has been known to serve as a nursery ground for flatfish, mainly *Pleuronectes platessa* L. (Nash et al., 1992, 1994), and the common shrimp *C. crangon*. In this paper we estimate von Bertalanffy growth parameters and mortality from length–frequency data collected between 1995 and 1998 and compare growth between the sexes. We also estimate the annual population size and size at sexual maturity with regard to the population dynamics of this species. These results are compared with data from studies undertaken on much larger populations in the North Sea. This paper also shows the effects of brood loss, mortality, exploitation rate, and length at capture on egg-per-recruit and yield-per-recruit.

Materials and methods

Sampling

Samples of the common shrimp, *C. crangon*, were collected from Port Erin Bay, Isle of Man (54°05′N, 4°54′W) between April 1995 and July 1998. All individuals were collected between 0 and 6 m below chart datum. Sampling utilized a 1.5-m beam trawl with a fine meshed (3 × 3 mm) inner codend between April and June and a 2-m beam trawl with a codend liner (6 × 6 mm) during the rest of the year (July to March). Sampling was undertaken once every 2–4 weeks

depending on weather. Five transects, orthogonal to the shore, were sampled covering a combined area of 1850 m^2. Between November 1997 and April 1998, additional samples of shrimp were collected with a 2-m beam trawl with 6 mm codend liner. These samples were not included in the estimations of population size because these were not quantitatively collected samples.

Sample analysis

Samples were preserved in 4% formaldehyde for a day and then transferred to 70% ethanol for storage. Sex was determined by the size and shape of the endopodite of the first pleopod and the presence or absence of the appendix masculina. Carapace length (CL), the shortest distance between the posterior margin of the orbit and the mid-dorsal posterior edge of the carapace, was measured using an ocular micrometer. Total length (TL) was measured similarly. Shrimps were blotted dry, and wet weight (BW) determined to the nearest 0.001 g using an electronic digital balance. Weights were not corrected for preservation. The weight–length relationship was determined as $BW = aCL^b$.

Estimation of total abundance

Total abundance (P) was determined using the swept area (a) method:

$$a = W*D \tag{1}$$

where W is the effective width of the trawl, and D towing distance.

Total abundance (P) is therefore given as:

$$P = \left(\left(\sum_{i=1}^{n} (N_i/a_i) \right)/n \right) * (A/q) = C*(A/q) \tag{2}$$

where N_i is the catch in ith sample area, a_i the swept area in ith sample area, n the number of hauls, C mean catch per area, q the catchability coefficient, and A area occupied by the population. The catchability coefficient (q) for the shrimps is not known, so for the calculation of total abundance q was set equal to 1.

Growth parameters

Length–frequency distributions (LFD) were constructed using 1-mm length intervals of carapace length. Growth was described using the modified von Bertalanffy growth function (VBGF) (Pauly and Gaschütz, 1979):

$$L_t = L_\infty [\{1 - \exp[-K(t - t_0) - (CK/2\pi)\sin(2\pi(t - ts))]\}] \tag{3}$$

where L_∞ is the asymptotic length, K is the intrinsic growth rate, t_0 is the age at which the length of animals

is 0, C is the amplitude of seasonal growth oscillation, ts is the age at the beginning of growth oscillation, and WP (=ts+0.5) the time of year when growth is slowest.

Growth curves were estimated from the length–frequency distributions (LFD) using the ELEFAN program (Gayanilo et al., 1995), a non-parametric method to fit the modified VBGF through modes. The Rn value gives an estimator of the goodness of fit. ELEFAN estimates the growth parameters (L_∞, K, C, and WP) without standard errors. According to Pauly (1987), t_0 estimates cannot be obtained solely from the length–frequency data, so it was necessary to supply a carapace length at hatching of 0.62 CL [values converted from 2.0 TL in 1st zoeal stage described by Gurney (1982)] to the ELEFAN program to allow an estimation of t_0.

Estimates of the maximum age of individuals in the populations were made using the formula given by Taylor (1958, 1959). The maximum longevity was calculated for pooled data of immature, male, and female.

To compare the growth curves for the Irish Sea with the North Sea, data from Table 138 in Schumacher and Tiews (1979) were subjected to estimation of a von Bertalanffy growth curve using the same procedures as above.

Comparison of growth parameters

Comparison of growth performances of shrimps was made using a growth performance index (φ′) (Pauly and Munro, 1984):

$$\varphi' = 2\log_{10}L_\infty + \log_{10}K \tag{4}$$

The growth performance index is preferred for growth comparison rather than comparison of L_∞ and K individually, because these two parameters are correlated. The growth performance index is more robust than either L_∞ or K individually as it takes into account the negative correlation between the two parameters, and fulfils the requirement for a simple single parameter for comparison of growth.

Mortality

Total mortality was estimated in ELEFAN using two methods: a linearized, length-converted catch curve (Pauly, 1983, 1984) and a Jones and van Zalinge (1981) plot. The output is Z/K: thus Z can be estimated using the estimated K from the VBGF.

The study area does not support a fishery, therefore sampling can be considered as the only form of fishing mortality (F). Thus F_t can be obtained by estimating harvest rate (h_t), expressed as fraction of the sample size

(C_t) caught from the estimated population size of a sampling year (N'_t):

$$F_t = -\ln(1-h_t) \tag{5}$$

where $h_t = (C_t/N'_t)/\delta t$.

Natural mortality (M) is estimated from the formula:

$$M = Z - F \tag{6}$$

where Z is the total mortality rate, F fishing mortality, and M natural mortality.

Size at sexual maturity

Size at sexual maturity was determined by the following three criteria: (1) the presence of external attached eggs (Kensler, 1967); (2) ovarian vitellogenesis based on histological examination (Stewart et al., 1997); and (3) the presence of egg-carrying setae on the endopodites of 1st pleopod (Lloyd and Yonge, 1947). For each year the proportions of mature females by size were fitted to a logistic equation as described by Campbell (1985) and King (1995):

$$P = \frac{1}{1 + \exp(a + b*CL)} \tag{7}$$

where P is the predicted mature proportion, a and b the estimated coefficients of the logistic equation, and CL the carapace length. Parameters were estimated from a linearized log transformation of the above equation and the subsequent correlation analysis of P and CL using least-squares methods (Minitab Ver. 10.1). Size at sexual maturity (CL_{50}), corresponding to a proportion of 0.5 sexually mature, was estimated as the minus ratio of the two coefficients [$CL_{50} = -(a/b)$] (King, 1995). Differences in distributions of samples between years were determined by Kolmogorov–Smirnov two-sample test (Sokal and Rohlf, 1995) in SYSTAT Ver. 7.0.

Fecundity-per-recruit

Growth of crustaceans is a function of two components: the duration of intermoult period and the increase in size at each moult. Based on the increment–frequency approach at each moult group the empirical fecundity-per-recruit model was developed for the American lobster by Caddy (1977, 1979). It allows the egg-per-recruit for each moult group to be calculated using a simple Thompson and Bell model (Ricker, 1975).

Brood mortality during incubation in crustaceans is a common feature which reduces reproductive output and affects reproductive potential. The number of eggs per recruit (E), accounting for brood mortality (Campbell, 1985) is:

$$E = \sum_{m=1}^{N} [P_m \cdot D_m \cdot Q_m \cdot N_m] \qquad (8)$$

where $Q_m = E_m - E_m * B_m$ and $N_m = N_{m-1}$ exp $(-Z_m \Delta t_m)$. N_m is the number of females entering moult group m. P_m is the proportion of sexually mature females in m. D_m is the proportion of females extruding eggs in m. O_m is the fraction of the average number of eggs lost. E_m is the mean number of newly-laid eggs per female. B_m is the proportion of eggs lost in m. Z_m is the total mortality rate. Δt_m is intermoult period (year) for moult group m.

The input parameters used in the egg-per-recruit model were as follows:

Growth

The two growth components, increment at moult and intermoult period, of female *C. crangon* were obtained from Oh and Hartnoll (1999). The percentage moult increment was regressed on carapace length (CL) to calculate successive moult groups.

Moult Increment (%)
$\text{Log}_{10} \text{MI}_{m+1} = 2.340 - 0.216 \text{CL}_m$ (n=129, r^2=0.33)
Intermoult period
$\text{Log}_{10} \text{I}_m = 0.882 + 0.064 \text{CL}_m$ (n=129, r^2=0.56)

Proportion mature

The proportion of sexually mature (P) females was obtained by fitting a logistic function to the size-specific maturity data (C.-W. Oh, unpubl. data). From this the estimated size at 50% sexual maturity (CL_{50}) for females was 12.5 mm CL.

$$P = \frac{1}{1 + \exp^{10.35 - 0.83 \, CL}} \quad (n = 546)$$

The proportion of females extruding eggs in moult group m with extrusion factor (D_m) was set to 1.0 because *C. crangon* did not display multiple broods within an instar (Lloyd and Yonge, 1947).

Yield-per-recruit (Y'/R) and biomass-per-recruit (B'/R)

To estimate the levels of exploitation of *C. crangon* that would give optimum yields, based on the Beverton and Holt (1966) model and modified by Pauly and Soriano (1986), the relative yield-per-recruit (Y'/R) and biomass-per-recruit (B'/R) as a function of exploitation rate (E) were determined as:

$$Y'/R = EU^{M/K} \left[1 - \frac{3U}{(1+m)} + \frac{3U^2}{(1+2m)} - \frac{U^3}{(1+3m)} \right] \quad (9)$$

where: $U = 1 - (L_c/L_\infty)$, $m = (1 - E)/(M/K) = (K/Z)$, and $E = F/Z$. L_c is the 50% retention length. L_∞ is the asymptotic length from the von Bertalanffy growth equation. E is the exploitation rate. M is the natural mortality. K is the growth coefficient from the von Bertalanffy growth equation. Z is the total mortality.

The modified form allows for the input of probabilities of capture for a smaller sized shrimp, thus reducing the bias in yield estimates due to the effect of gear selection and/or incomplete recruitment. This version is especially suitable for assessing the mesh size regulation with different levels of fishing (Sparre *et al.*, 1989). The input requirements in this version are the length at first capture (L_c), L_∞, and M/K. L_c is obtained by the selection ogive based on the mathematical expression (Sparre *et al.*, 1989) in NONLINEAR estimatin of SYSTAT 7.0:

$$S(L) = \frac{1}{1 + \exp(S1 - S2 * CL)} \qquad (10)$$

where CL is carapace length and S1 and S2 are constants.

Length at which 25, 50, and 75% of the shrimps are vulnerable to the gear (L_{25}, L_{50}, and L_{75}) was estimated from the following expressions:

$$= \frac{L_{50}}{(\text{mesh size})}$$

and:

$$\text{Selection range} = L_{75} - L_{25}, \; \text{Selection factor} = \frac{L_{50}}{(\text{mesh size})}$$

From the analysis of relative yield-per-recruit (Y'/R) the exploitation rate (E_{max}) giving maximum relative yield-per-recruit was estimated. Also $E_{0.1}$, the level of exploitation at which the marginal increase in yield-per-recruit reaches 10% of its value at E=0, and E=0.5, the exploitation level which will result in a reduction of the unexploited biomass-per-recruit (B'/R), were estimated.

Relative biomass-per-recruit (B'/R) is estimated from the relationship:

$$B'/R = (Y'/R)/F \qquad (11)$$

while E_{max}, $E_{0.1}$, $E_{0.5}$ are estimated by using the first derivative of this function.

The two models were estimated, using the FAO-ICLARM Stock Assessment Tools (FiSAT) (Gayanilo *et al.*, 1995).

Results

Population structure

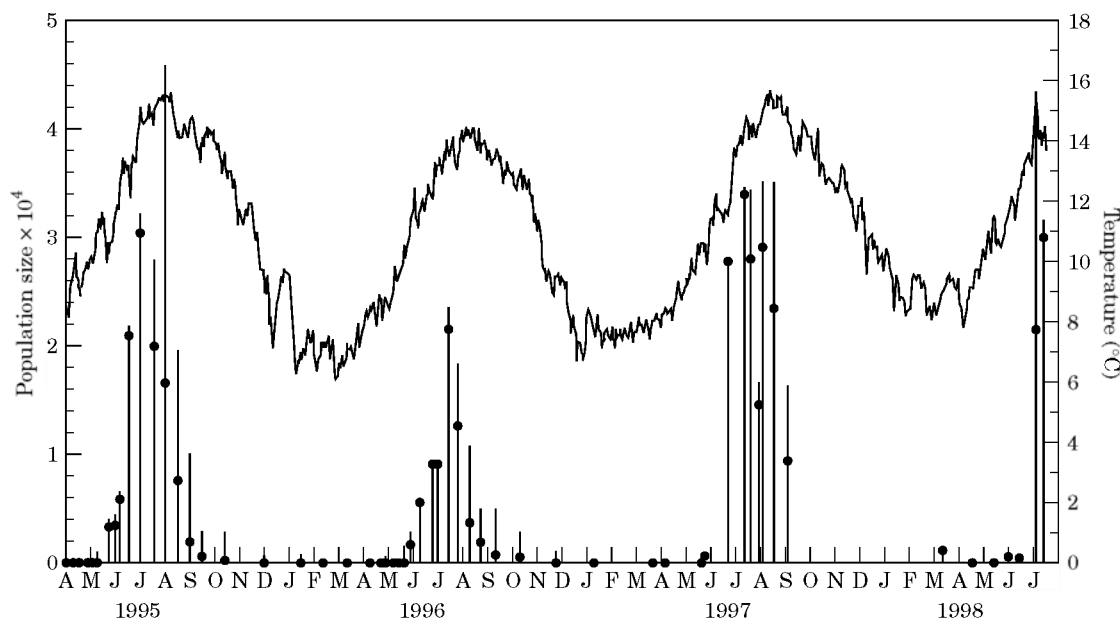Between April 1995 and July 1998, a total of 12 795 shrimps (5095 females, 3451 males, and 4249 immature)

Figure 1. Total (vertical bars) and juvenile (solid circles) population size of *Crangon crangon* and seawater temperature (continuous trace) between April 1995 and July 1998 in Port Erin Bay.

Table 1. Average annual population density and estimated population size of *Crangon crangon* in Port Erin Bay, Isle of Man between April 1995 and July 1998.

Year	1995	1996	1997	1998
Total density (1000 m^{-2})	100 (± 138)	46 (± 65)	169 (± 160)	112 (± 185)
Juvenile density (1000 m^{-2})	81 (± 123)	42 (± 74)	135 (± 134)	75 (± 123)
Population size	10 051 ($\pm 13\,711$)	4668 (± 6473)	16 920 ($\pm 16\,044$)	11 182 ($\pm 18\,463$)

were collected from the study area. The estimated population size was high in summer and low in winter during the study period, similar patterns occurring in all years (Fig. 1). Average annual density of the whole population ranged from 46 ind . 1000 m^{-2} in 1996 (lowest mean density) to 169 ind . 1000 m^{-2} in 1997 (highest mean density) (Table 1). Juvenile shrimps (<7 mm CL) constituted between 70 and 90% of the total density, ranging from 42 ind . 1000 m^{-2} in 1996 to 135 ind . 1000 m^{-2} in 1997 (Table 1). The main period of recruitment was between July and August (Fig. 1).

In all years the shrimp population consisted predominately of the 1-year class, which was similar in structure each year (Fig. 2). The estimated maximum population size was lower in 1996, and similar for the other three years, 1995, 1997, and 1998 (ANOVA; F=6.39, d.f.=3, 13, p<0.01) (Fig. 1). *A posteriori* Scheffé multiple comparison tests showed that significant differences were found between 1996 and all other years (p<0.05). The seasonal fluctuation in population size occurred simultaneously with the seasonal change in seawater tempera-

ture (Fig. 1). There was a significant relationship between ambient seawater temperature and population estimation (Fig. 3).

Length–frequency distribution and growth

The carapace length of the shrimps ranged from 0.42 to 17.28 mm. Modal progressions of 1 mm size classes over four successive years, as used in the ELEFAN program, are given in Figure 4. The best fits to the length–frequency data (LFD) identified a distinct new cohort, which becomes apparent between May and June each year.

The von Bertalanffy growth function (VBGF) parameters, estimated by ELEFAN for each sex and for both sexes combined, are summarized in Table 2. The values of L_∞ and K for combined data were 18.3 mm and 0.91 yr^{-1}, respectively. The analyses of modal progression for each sex separately showed that females ($L_\infty=18.50$ mm CL, K=1.09 yr^{-1}) are higher in L_∞ and K than males ($L_\infty=15.1$ mm CL, K=0.90 yr^{-1}). A
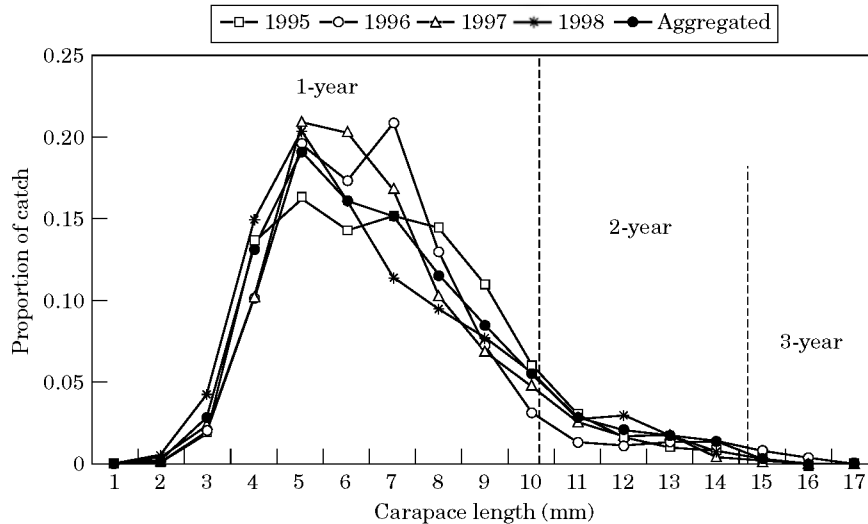
Figure 2. Size structure from annual catches of *Crangon crangon* in Port Erin Bay during 1995–1998.

von Bertalanffy plot for Schumacher and Tiews's (1979) pooling data, using the total length converted into CL, showed that the K value estimated from the slope of the regression was 1.08 (± 0.01), giving an $L_\infty = 18.87$ mm CL.

Based on the growth performance indices (φ') females of *C. crangon* showed higher growth rates than males. The φ' values ranged from 2.31 to 2.57, indicating a difference in growth pattern between the sexes. The growth curve showed a seasonal oscillation in growth (C) of 10% for females, 20% for males, and 29% for combined data. The phase of slow growth was during winter [December for combined data (WP=1.0),

Figure 3. Relationship between $\log_e$ population size and $\log_e$ ambient seawater temperature (°C) in Port Erin Bay during 1995–1998.

December for females (WP=0.92), and November (WP=0.91) for males]. Based on the growth parameters, the maximum life span (t_{max}) of the shrimps was estimated to be 3.3 years for this study and 2.7 years for Schumacher and Tiew's (1979).

The structure of the recruitment patterns obtained by the ELEFAN program indicated one normally distributed group (spring, peaking in May). However, it appears that recruitment can occur over nearly all the year (Fig. 5).

Mortality

Total mortality (Z) ($\pm 95\%$ confidence limit), calculated from the length-converted catch curves, was 3.96 (± 0.47) yr^{-1} (Fig. 6a), and Jones and van Zanlinge's (1981) Z plot gave 3.75 (± 0.34) yr^{-1} (Fig. 6B). Average fishing mortality (F), estimated from the harvest rate, was approximately 0.36 yr^{-1} (Table 3) and thus natural mortality (M) was estimated at 3.60 and 3.39 yr^{-1} from the two methods, respectively. The exploitation ratio (E=F/Z) was 0.09.

Size at sexual maturity

Between 1995 and 1998, 486 of the 5094 female *C. crangon* collected were sexually mature. The proportion of mature females by length class increased logistically with length in all of the years analysed (Tables 4 and 5). The maturity ogives indicate that 50% maturity occurred in the size range of 12.0 to 12.6 mm CL (53.7–56.5 mm TL) over the study period (Table 5). The difference in the 50% maturity size (CL_{50}) between
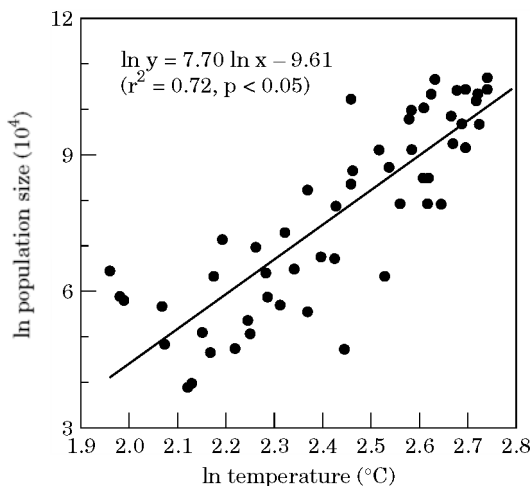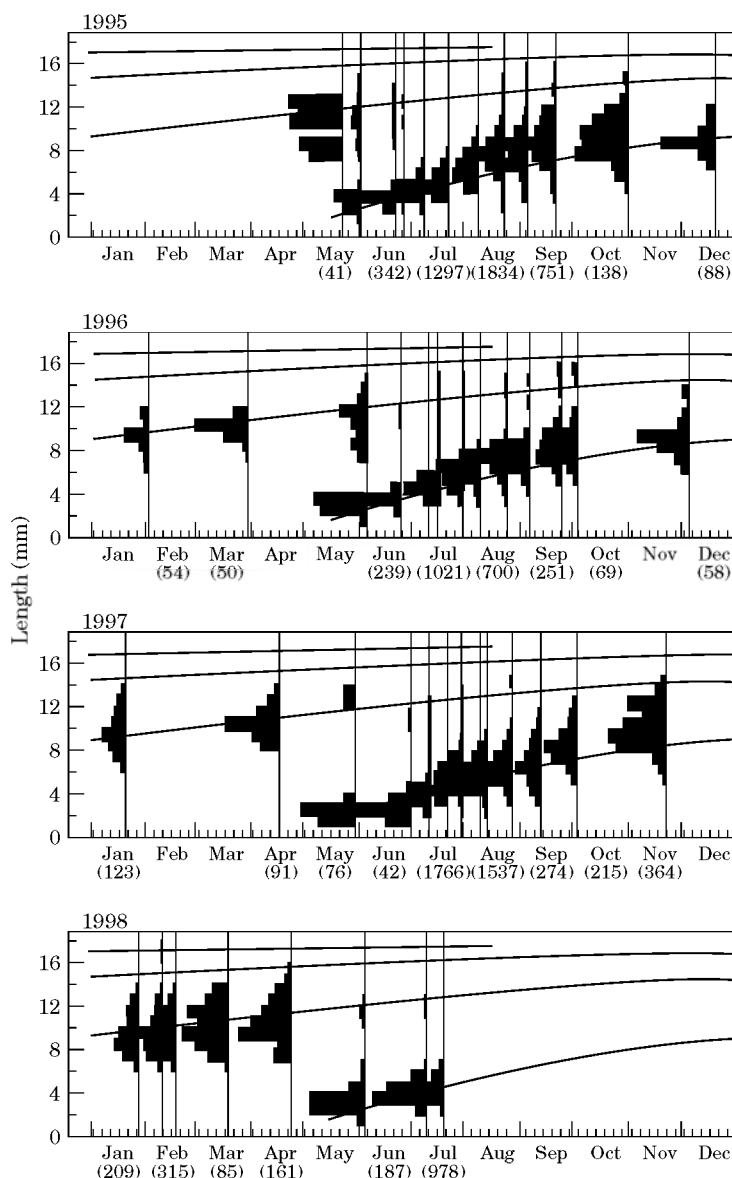
Figure 4. Length–frequency distribution, expressed as percentage, of pooled data of the common shrimp, *Crangon crangon* during four successive years in Port Erin Bay and estimated growth curves for this population. Sample size in parentheses below months.

years was not significant (Table 5). Size at onset of sexual maturity (SOM) occurred in the size range 8.5 to 9.5 mm CL (33.3–42.4 mm TL) with a little variation between years. There were no significant differences in the frequency distributions by length class between years. The estimates of the size at sexual maturity showed a successive increase in the proportion of mature shrimp with increase in length. Transition from immature to mature individuals occurs over a narrow size range (10–12 mm CL).

Carapace length (CL)–body weight (BW) and carapace length (CL)–total length (TL) relationships

For the purposes of comparisons with data from other sources regressions of body weight on carapace length were calculated. All three regressions (females, males, and combined sexes) of body weight on carapace length show that the body weight was a significantly positive allometric function of carapace length (Table 6).

Table 2. Parameter estimation of the ELEFAN analysis of length–frequency data for females, males, and combined data: L_∞, asymptotic length (mm); K, growth coefficient (yr^{-1}); C, amplitude of growth oscillation; WP, winter point; φ', growth performance index; L_{max}, the maximum size observed; Rn, score function.

	Present study			Schumacher and Tiews (1979)
	Females	Males	Pooled	Pooled
L_∞	18.50	15.10	18.30	18.87
K	1.09	0.90	0.91	1.08*
C	0.10	0.20	0.29	—
WP	0.92	0.91	0.99	—
φ'	2.57	2.31	2.48	2.59
L_{max}	—	—	17.28	17.78
95% of L_∞	—	—	17.39	17.92
Rn	319	429	305	—

*Value re-estimated fom Table 138 of Schumacher and Tiews (1979), using von-Bertalanffy plot after converting total length into carapace length.
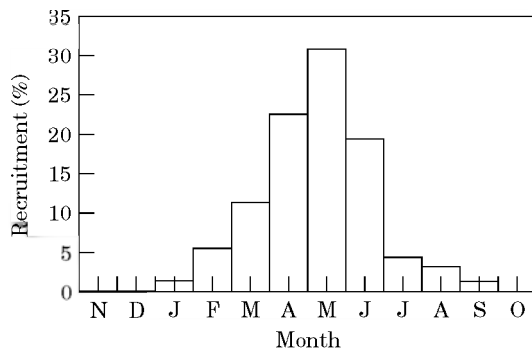

Figure 5. Recruitment pattern of *Crangon crangon* identified by ELEFAN II routine.

Differences in the regression slopes between sexes were not significant (ANCOVA: $F_{1,2852} = 0.02$: $p > 0.8$). For conversion of carapace length (CL) into total length (TL) and vice versa, the TL–CL relationship was:

$$TL = 4.546\ CL - 0.816\ (n = 245,\ r^2 = 0.99,\ p < 0.001)$$

Fecundity and brood loss

The number of eggs per female with non-eyed eggs (EN) fitted a power curve. Because there may be a seasonal variation in fecundity, the seasons were considered as winter and summer and the following relationships established:

Winter

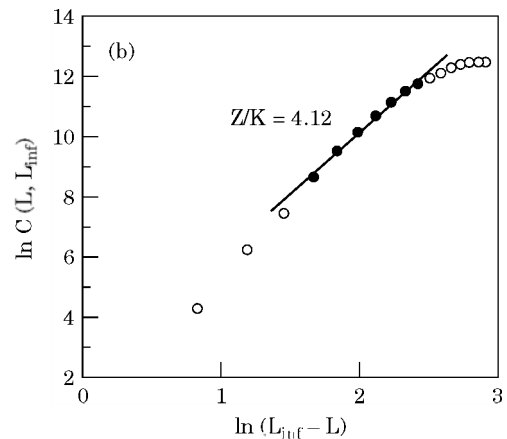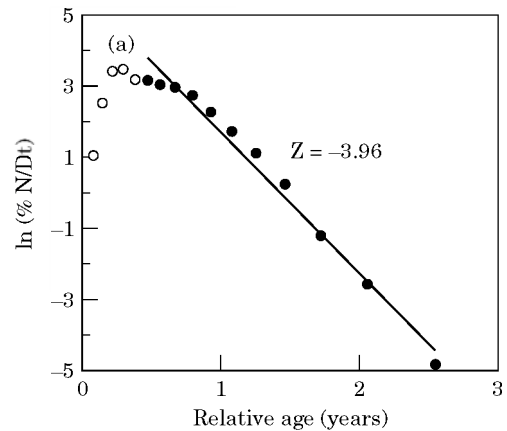$$EN = 8.305\ CL^{2.429}\ (n = 136,\ r^2 = 0.757,\ p < 0.001)$$

Figure 6. Length-converted catch curve (a) and Jones and van Zalinge plot (b) based on length-composition data for *Crangon crangon*.

Table 3. Estimation of fishing mortality by sampling. N'_t, population size of a sampling year; C_t, sampling size caught in t time; h_t, harvest rate (yr^{-1}); F_t, fishing mortality during t time.

Year	N'_t	C_t	h_t	F_t
1998	11 182	1016	0.09	0.10
1997	16 920	1801	0.11	0.11
1996	4668	2242	0.48	0.65
1995	10 051	4491	0.45	0.59
$\overline{X}$	10 705	2388	0.28	0.36

Summer

$$EN = 20.947\ CL^{2.039}\ (n = 37,\ r^2 = 0.673,\ p < 0.001)$$

Using logarithmically transformed data, an analysis of covariance (ANCOVA) showed that between the two seasons, there were no significant differences in slopes

Table 4. Number of total female (F) and mature female (MF) *Crangon crangon* by length categories (mm), and corresponding proportion of mature females, sampled from April 1995 to July 1998.

Mid-length	1995 F	1995 MF	1996 F	1996 MF	1997 F	1997 MF	1998 F	1998 MF	% mature 1995	% mature 1996	% mature 1997	% mature 1998
5.5	334	0	212	0	463	0	53	0	0	0	0	0
6.5	331	0	214	0	332	0	31	0	0	0	0	0
7.5	350	0	227	1	343	0	30	1	0	0.4	0	3.3
8.5	304	1	109	2	145	1	35	1	0.3	1.8	0.7	2.9
9.5	221	4	54	4	101	5	76	6	1.80	7.4	5.0	7.9
10.5	115	20	29	7	81	13	79	22	17.4	24.1	16.0	27.8
11.5	72	26	24	16	53	22	90	52	36.1	66.7	41.5	57.8
12.5	46	33	32	21	71	42	60	40	71.7	65.6	59.2	66.7
13.5	36	25	33	24	18	513	26	22	69.4	72.7	72.2	84.6
14.5	17	15	20	16	7	25	4	3	88.2	80.0	71.4	75.0
15.5	6	6	11	10	2	2	3	3	100	90.9	100	100
16.5	—	—	2	2	—	—	—	—	—	100	—	—
Total	1832	130	997	103	1616	103	487	150				
	1962		1100		1719		637					

Table 5. Parameters for estimation of size at sexual maturity in female *Crangon crangon*, collected from April 1995 to July 1998. CL_{50} indicates a length at 50% sexual maturity.

Equations and details	Year 1995	1996	1997	1998
Proportion mature = $1/[1+exp(a+b\ CL)]$				
a	15.65	11.41	12.39	9.73
b	−1.26	−0.92	−0.98	−0.81
CL_{50}	12.41	12.36	12.62	12.00
± CL_{50}	±0.67	±0.75	±0.83	±0.75
r^2	0.93	0.92	0.91	0.92
p	<0.001	<0.001	<0.001	<0.001

($F = 1.13$, d.f. = 1, 169, $p > 0.2$) nor intercepts, thus a common slope could be used ($F = 2.35$, d.f. = 1, 170, $p > 0.1$). The overall size-fecundity relationship is given as:

$$EN = 11.045\ CL^{2.307}\ (n = 173, r^2 = 0.745, p < 0.001)$$

Although the proportion of brood loss in *C. crangon* varied slightly with season, ranging from 0.12 in summer broods to 0.20 in winter broods, the value from the main

Table 6. Regression analysis of body weight (BW) on carapace length (CL) in *Crangon crangon*.

	n	Equations	± Slope	r^2	p
Female	1856	$BW = 0.0008\ CL^{3.09}$	±0.02	0.98	<0.001
Male	999	$BW = 0.0008\ CL^{3.09}$	±0.04	0.95	<0.001
Pooled	2855	$BW = 0.0008\ CL^{3.07}$	±0.02	0.99	<0.001

spawning was used as a current brood loss fraction for the model. To show how the brood loss (B) affects the egg-per-recruit with changes of natural mortality (M), simulations for the different fractions of brood loss were also conducted with B = 0, 0.1, 0.2, 0.3, 0.4, and 0.5.

Fecundity per recruit

The population fecundity, with a natural mortality and brood loss of $M = 3.60\ yr^{-1}$ and B = 0.2 was 6.2×10^5 (Table 7). As natural mortality increases, fewer females reach maturity and/or lay eggs and the slope of the S-shaped size-cumulative egg production curve increases more rapidly (Fig. 7). There was a gradual decrease from 13 to 14 mm CL at M = 1.0 to 10–11 mm CL at M = 5.0 in size classes with more than 50% of population fecundity. Similarly, the size class with maximum egg production gradually decreased with natural mortality, along with a marked reduction in egg production (Fig. 8; Table 8).

Table 7. Fecundity-per-recruit calculated from female *Crangon crangon* populations, assuming natural mortality (M)=3.60, and brood loss fraction (B)=0.2. %ΔS represents % moult increment.

Moult increment (%ΔS)	Size (mm) Moult group	P (L) Proportion mature	Q (L) Fecundity/ recruit	I (L) Intermoult interval	Mortality/ intermoult	Survivors	Population fecundity
12.97	6.00	0.000	0	0.045	0.163	1000	
10.40	6.78	0.009	731	0.049	0.175	837	18
8.51	7.49	0.016	920	0.052	0.188	691	9940
7.00	8.13	0.026	1111	0.055	0.200	561	16 413
6.04	8.70	0.042	1299	0.059	0.211	449	24 261
5.20	9.23	0.063	1489	0.062	0.222	354	33 295
4.55	9.70	0.091	1670	0.065	0.232	275	41 644
4.02	10.14	0.125	1850	0.067	0.243	211	49 057
3.57	10.55	0.168	2027	0.070	0.252	160	54 450
3.21	10.93	0.216	2200	0.073	0.262	120	57 001
2.91	11.28	0.270	2366	0.075	0.271	88	56 387
2.65	11.61	0.327	2528	0.078	0.280	64	53 260
2.43	11.92	0.386	2687	0.080	0.288	46	48 117
2.23	12.21	0.444	2840	0.082	0.296	33	41 680
2.07	12.48	0.500	2987	0.085	0.304	23	34 720
1.92	12.74	0.554	3133	0.087	0.312	16	28 058
1.79	12.99	0.604	3276	0.089	0.320	11	22 033
1.69	13.22	0.649	3412	0.091	0.327	8	16 764
1.58	13.44	0.689	3544	0.093	0.334	5	12 453
1.49	13.65	0.725	3673	0.095	0.341	3	9048
1.40	13.85	0.757	3798	0.096	0.347	2	6440
1.33	14.04	0.785	3920	0.098	0.354	1	4497
1.26	14.23	0.810	4043	0.100	0.360	1	3095
1.20	14.41	0.832	4162	0.102	0.367	1	2093
Total							**624 724**
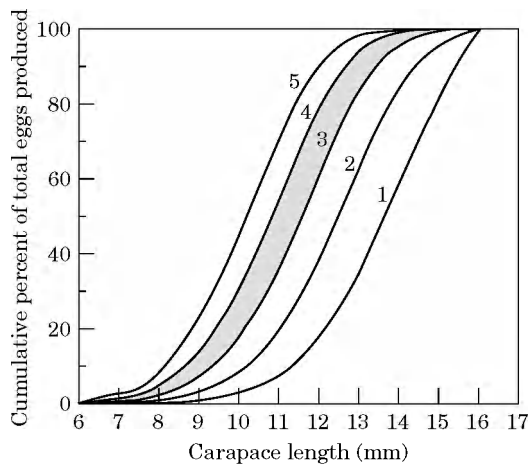
Figure 7. The relative egg production at different carapace lengths for female *Crangon crangon* from Port Erin Bay under varying natural mortality. The numbers on traces indicate natural mortality (M). Stippled areas indicate the egg production patterns for current estimated natural mortality.

Figure 8. The changes of egg production at different carapace length for female *Crangon crangon* under varying natural mortality. Stippled areas indicate the egg production patterns for current estimated natural mortality.

With decreases in natural mortality, larger number of eggs per recruit was produced irrespective of the simulated egg losses (Fig. 9). An increase in the proportion of egg loss resulted in a larger decrease in eggs per recruit.

Yield per recruit

Length at first capture (L_c)

Based on the probabilities of capture, which resulted in the selection ogive, the estimated length at capture was 4.07 mm CL at L_{25}, 5.61 mm CL at L_{50}, and 7.16 mm

Table 8. Percentage change in egg production at different instantaneous natural mortality (M) from the current egg production (6.2×10^5 at M=3.60) for the size class with maximum egg production from Port Erin Bay when B=0.2.

	Size group	Egg production ($\times 10^{-5}$)	%*
M=1.0	13.4	65.8	961
M=2.0	12.2	21.3	244
M=3.0	11.6	8.6	39
M=4.0	10.9	4.4	−29
M=5.0	10.1	2.4	−61

*Percentage change=([y/x] − 1.0) × 100 where x=current egg production and y=egg production at each mortality.
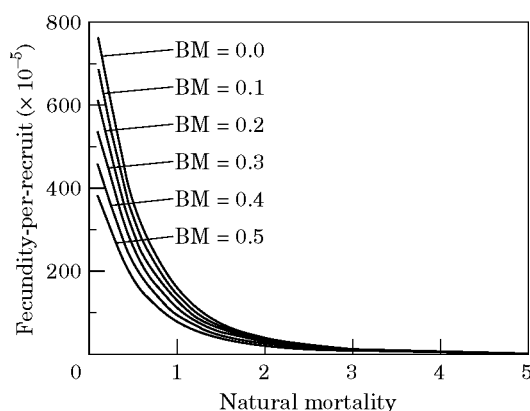
Figure 9. The effects of the combined natural mortality and brood mortality on egg production of female *Crangon crangon*.

CL at L_{75} (Table 9). The selection range was 3.1 mm CL, and the selection factor 1.87.

Relative yield-per-recruit (Y'/R)
The parameters L_∞ =18.3 and M/K=4.24 were used for the yield-per-recruit model. The yield-per-recruit and biomass-per-recruit curves, as functions of exploitation rate (E=F/Z), varied with the length at capture (Figs 10, 11). The exploitation rate (E_{max}) that gave maximum relative yield-per-recruit was 0.531 at L_{25}, 0.695 at L_{50}, and 0.920 at L_{75}. $E_{0.1}$ increased with length at capture. The exploitation rate at which the marginal increase in relative yield-per-recruit is 10% of its value at E=0, was 0.465 at L_{25}, 0.619 at L_{50}, and 0.806 at L_{75}. The exploitation rate ($E_{0.5}$) which corresponds to 50% of the relative biomass-per-recruit of unexploited stock was 0.281 at L_{25}, 0.318 at L_{50}, and 0.353 at L_{75}. This indicates that Y'/R and B'/R are sensitive to changes in length at capture (L_c) and fishing intensity.

Relative yield per recruit shows that E_{max} increased as L_c increased and the curves of yield with respect to E at higher values of L_c became flatter (Fig. 12). The change

Table 9. The number of catch and cumulative relative frequencies of *Crangon crangon* collected in Port Erin Bay during 1995–1998.

| Length interval	Mid-length (CL, mm)	Catch	Observed frequency	Cumulative frequency
0–1	0.5	0	0	0
1–2	1.5	55	0.0042	0.004
2–3	2.5	417	0.0318	0.036
3–4	3.5	1717	0.1308	0.167
4–5	4.5	2468	0.1880	0.355
5–6	5.5	2069	0.1576	0.512
6–7	6.5	1946	0.1482	0.661
7–8	7.5	1479	0.1127	0.773
8–9	8.5	1098	0.0836	0.857
9–10	9.5	751	0.0572	0.914
10–11	10.5	439	0.0334	0.948
11–12	11.5	285	0.0217	0.969
12–13	12.5	211	0.0161	0.985
13–14	13.5	124	0.0094	0.995
14–15	14.5	47	0.0036	0.998
15–16	15.5	17	0.0013	1.000
16–17	16.5	4	0.0003	1.000
17–18	17.5	1	0.0001	1.000
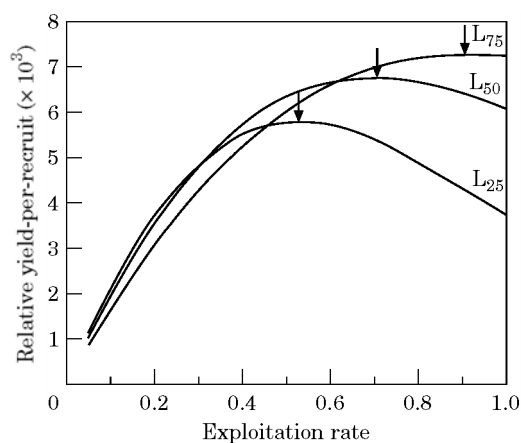
Figure 10. Changes in relative yield-per-recruit with exploitation rate of *Crangon crangon* in Port Erin Bay. Arrows indicate the maximum sustainable yield (MSY) at different size at capture (L_c).

of E_{max} with L_c is indicated by the line **MM'**. The maximum value of Y'/R was at E=0.90, corresponding to a value of L_c=7.0 mm CL. At E=0.5 the maximum Y'/R was at L_c=7.5 mm CL.

Relative biomass-per-recruit (B'/R) decreased with fishing intensity at all values of L_c, although this decrease was least when L_c was large (Fig. 13). At low values of E, B'/R increased to a maximum as L_c increased.

Discussion

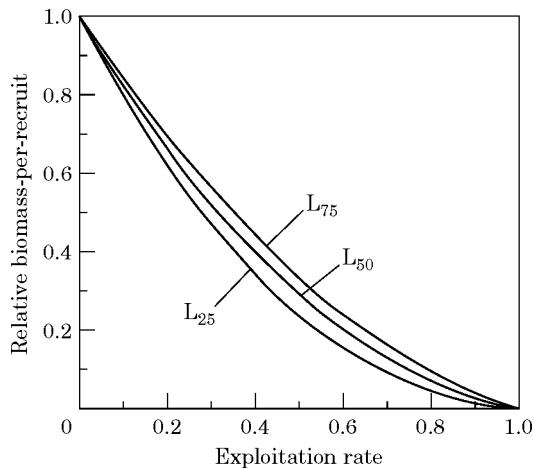There are seasonal fluctuations in abundance in the *C. crangon* population in Port Erin Bay with peak

Figure 11. Response of relative biomass per recruit on exploitation rate (E=F/Z) for *Crangon crangon* in Port Erin Bay.

abundance in summer (July to August). Maximum abundances in all years studied were coincident with the maximum water temperature, which is similar to the observations of Boddeke (1976) and Beukema (1992). The size structure of the population indicates the presence of 3 year classes, with the O-group constituting the greatest proportion of the population. This suggests that the study area plays an important role as a nursery ground of the shrimp. Overall abundance of *C. crangon* is very low during the study period.

This study indicated one major recruitment event per year. This is in contrast to previous studies which suggest breeding twice a year (Ehrenbaum, 1890; Lloyd and Yonge, 1947; Kuipers and Dapper, 1984; Henderson and Holmes, 1987). The data from this study cannot preclude the possibility of more than one major recruitment event but the clear normal distribution in recruitment abundance makes this unlikely.

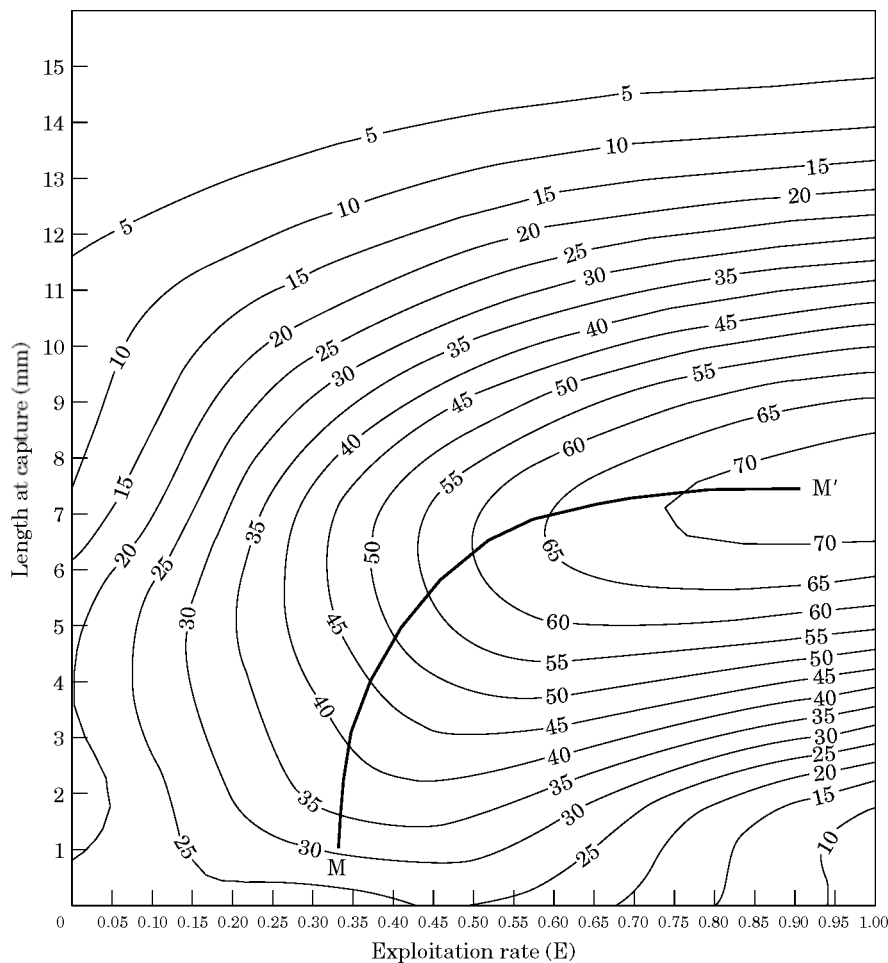The von Bertalanffy growth models fitted to the Port Erin Bay shrimp population are generally consistent

Figure 12. Isopleth diagram for relative yield-per-recruit as a function of exploitation rate (E) and size at capture (L_c). **MM′** indicates curve tracing the maximum sustainable yield (MSY).
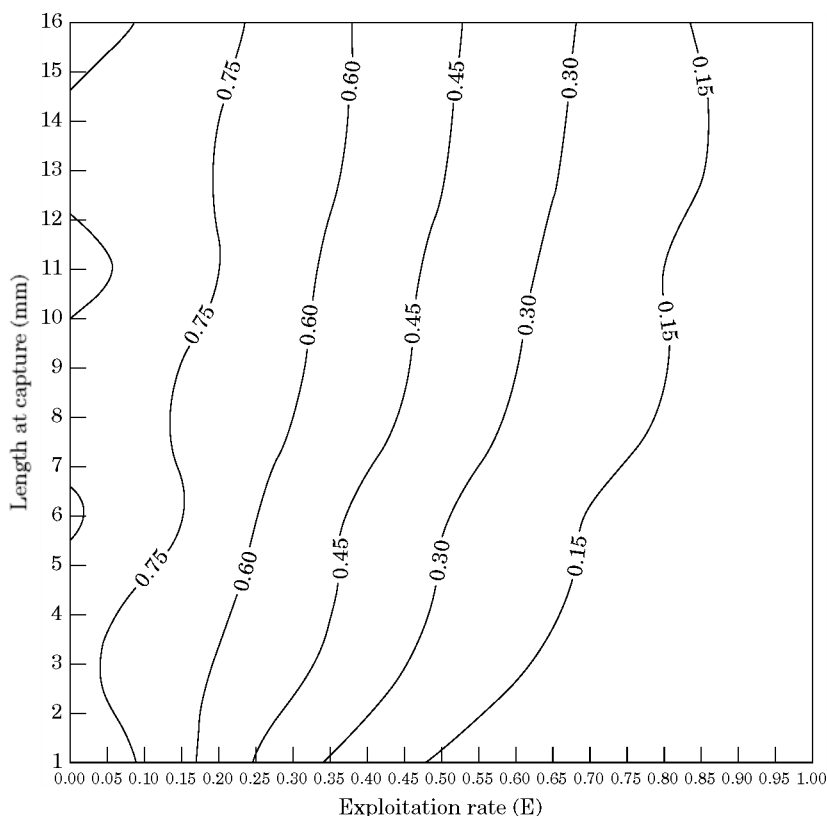
Figure 13. Isopleth diagram for relative yield-per-recruit as a function of exploitation rate (E) and size at capture (L_c).

with Schumacher and Tiews (1979) and Henderson and Holmes (1987). The use of von Bertalanffy growth models is consistent with many studies on crustacean growth (Campbell, 1983; Pauly *et al.*, 1984; Bergström, 1992; Baelde, 1994; Roa and Ernst, 1996; Ohtomi and Irieda, 1997; Alves and Pezzuto, 1998). The growth parameters (L_∞ and K) for the Port Erin Bay population are lower than those re-estimated from Schumacher and Tiews (1979) (Table 2). However, the maximum age of *C. crangon* differs between studies. This suggests that life span can differ between areas. Taylor (1958) suggests that in the cod (*Gadus callarias*) the growth parameters are significantly correlated with seawater temperature, leading to considerable variability in life span between areas. One other factor which differs between the studies in Port Erin Bay and on the German coast (Schumacher and Tiews, 1979) is the fishing pressure. The longer life span in Port Erin Bay may be partially due to a lack of fishing mortality, especially on older shrimp. There are only minor differences in the growth performance indices (φ′) between the two studies (Table 2). Sparre *et al.* (1989) points out that a species should have a similar φ′ irrespective of habitat.

In stock assessments of *C. crangon*, growth models are normally fitted to combined sex data (Schumacher and

Tiews, 1979). This method assumes that growth in carapace length is similar for both sexes. However, it has been suggested that there are differences in growth pattern between the sexes (Lloyd and Yonge, 1947; Schumacher and Tiews, 1979; Hartnoll, 1982; Henderson and Holmes, 1987). This phenomenon has been described in captive individuals (Tiews, 1954; Meixner, 1969; Oh and Hartnoll, 1999). Our results indicated that females grew faster and reached a larger size at age than males, with slow growth in both sexes during winter (Table 2). In females growth slow down coincides with the maturation and spawning periods, reflecting metabolic costs associated with reproductive activities (ovarian maturation and egg care) plus a cessation of moulting during the spawning period. These results are in agreement with Henderson and Holmes (1987). Similar patterns of growth are found in a few other species, for example, *Palaemon elegans* Rathke (Hoglund, 1943) and *Haliporoides sibogae* de Man (Baelde, 1994), but this does not appear to be the general situation for decapod crustaceans. The faster growth of females is in contrast to many other crustacean species where the males have the faster growth due to the reduction in female growth rate associated with egg production and incubation (see Hartnoll, 1982 for references).

The total mortality (Z) of *C. crangon* in Port Erin Bay was high, both methods of estimating total mortality giving similar results. ''Fishing'' mortality (F) is primarily caused by sampling as there is no fishery for *C. crangon* in Port Erin Bay. The exploitation ratio (E=F/Z), therefore, is minor (0.09), demonstrating that natural mortality (M) is the major cause of death of shrimp. High total mortality was reported by Henderson and Holmes (1987), though it was lower (2.08 yr^{-1}) than in this study (3.60 yr^{-1}).

The shrimp population size in Port Erin Bay fluctuated with seasonal variation in temperature. Maximum annual population size in summer (July to August) was not significantly different between 1995, 1997, and 1998, but was lower in 1996, coinciding with lower water temperatures. Lower population sizes in colder years is consistent with the notion presented by van der Veer and Bergman (1987) in the Dutch Wadden Sea of elevated overwintering mortality or movement offshore.

Alternative explanations for the high natural mortality include variable fish predation, and possibly an overestimation of total mortality (Z) due to emigration. In the study area most of the shrimps consist of the O-group which is vulnerable to heavy predation especially by fish (see Redant, 1984 for references). Natural mortality of postlarval shrimps has been estimated at 12.4 times the fishing mortality (Redant, 1978), and three times fishing mortality (Tiews and Schumacher, 1982) in areas of commercial exploitation. In German coastal waters Tiews (1978) noted that some 94% of the total shrimp population (mainly O-group) were taken by predatory fishes. Shrimps are a common prey item of fishes in Port Erin Bay (S. de la Rosa, pers. comm., Port Erin Marine Laboratory).

Another explanation for the elevated estimate of total mortality in Port Erin Bay is error caused by seasonal migrations, a well-known phenomenon in *C. crangon* (Ehrenbaum, 1890; Havinga, 1930; Boddeke, 1976, 1989; Janssen and Kuipers, 1980). The offshore migration of individuals in the late summer will have the effect of reducing population size and thus leads to an overestimation of total mortality.

There was no significant difference in the frequency distributions between years. The distribution in maturity at size data is consistent with the type II distribution of Trippel and Harvey (1991) and generally represents a stable population. The size at 50% maturity (CL$_{50}$) is similar to previous studies (50–55 mm TL) (Lloyd and Yonge, 1947; Tiews, 1954). However, considerable geographical variation in the size at onset of sexual maturity has been reported (see Tiews, 1970). The variation could be due to perceived differences in population abundance and structure because of variation in the characteristics of catchability of fishing gears used on different grounds, difference in growth rate between areas, or possibly

because different criteria were used to estimate the proportion mature.

Estimates of eggs-per-recruit are sensitive to the combined effects of growth, fecundity, size at sexual maturity, mortality, and brood loss. The response of eggs-per-recruit models to these varying parameters was similar to that found for other decapod crustaceans (Pollock, 1991; Campbell, 1985; Ennis, 1985). This is primarily a result of similarities in simulation models and basic life history patterns.

From the Port Erin Bay data an exploitation rate (E$_{max}$) at L$_{50}$ gives a maximum relative yield-per-recruit (Y'/R) of 0.69 which is higher than the 0.5 optimum level of exploitation reported by Gulland (1971). The Y'/R model used in this study does not give an absolute value of Y/R but the relative differences of Y/R for varying values of fishing mortality (F) and length at capture (L$_c$) or age at capture (t$_c$). The advantages of this model are that it requires fewer parameters, and is especially suitable for assessing the effect of mesh size regulations (Sparre *et al.*, 1989). There are relatively few data on the effect of environmental variability on recruitment and yield of *C. crangon* and this needs to be rectified.

Acknowledgements

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