Abundance of the shore crab, *Carcinus maenas* (L.), estimated from mark-recapture experiments

Sten Munch-Petersen, Per Sparre & Erik Hoffmann
The Danish Institute for Fisheries and Marine Research, Charlottenlund Castle,
DK-2920 Charlottenlund, Denmark

Abstract

By multiple mark-recapture experiments, abundance and biomass of the shore crab, *Carcinus maenas* (L.), at three locations in Kattegat have been estimated. Estimates of age compositions are presented.

The estimated densities ranged from 0.001 to 5 individuals (age groups 1 to 4) per m², corresponding to 0.03 to 90 grams (live weight) per m². Estimates of population size and survival rate by two mark-recapture models are compared.

Contents

1. Introduction

The shore crab, *Carcinus maenas* (L.), is a common species in Danish waters, and it probably plays an important predatory role in the shallow water ecological system.

The distribution of *Carcinus* in Danish waters was investigated by Poulsen (1949), who also made rough estimates of relative abundance (numbers per 30 min. hauls by seine), and by Muus (1967) who observed densities of *Carcinus* of 2-5 specimens per 10 m². Rasmussen (1973) described the distribution of *Carcinus* in the Isefjord as well as the seasonal and diurnal migrations. However, none of these investigations had a quantitative aim, whereas the aim of the present work

Table 1. Survey of experiments and basic observations.

Locality	Time period	No. of traps	Shortest dist. betw. traps, m	Area covered, m²	No. of samples	Average daily catch	Average daily catch/ trap	Sex ratio in catch, %		Mean weight of the crabs, g	
								♂♂	♀♀	♂♂	♀♀
Egense	June 1978	20	25	12500	9	522	26	99	1	17.8	7.6
Egense	Aug. 1978	20	50	50000	8	372	19	81	19	18.0	8.9
Udbyhøj	June 1977	20	25	12500	6	118	6	73	27	26.5	17.2
Udbyhøj*	Sep. 1977	20	25	12500	(4)	(66)	–	82	18	29.0	16.9
Anholt	June 1977	20	50	50000	6	43	2	–	–	22.5	
Anholt*	Aug. 1977	20	50	50000	(3)	(92)	–	82	18	39.5	22.4
Anholt	June 1978	20	25	12500	6	33	2	80	20	21.4	14.4
Anholt*	Aug. 1978	20	25	12500	(4)	(47)	–	61	39	39.1	28.8
Anholt	July 1979	49	25	30625	9	87	2	97	3	33.9	17.3
Anholt	Sep. 1979	49	25	30625	4	266	5	99	1	51.2	17.9

*No adequate mark-recapture data.

has been to obtain estimates of absolute densities, and to investigate the applicability of two mark-recapture models: The Fisher and Ford model (Fisher & Ford, 1947) and the Jolly and Seber model (Seber 1973).

In the present investigation multiple mark-recapture experiments were conducted on three different locations in Kattegat. In each experiment a small 'experimental area' was selected in which either 20 or 49 traps were placed. Each experiment included 4-9 marking occasions, each of which (except in one case) were separated by approximately 24 hour intervals. Thus the traps were emptied once every day and all captured crabs were marked and released. Before being marked, the size and sex of each individual was recorded in most cases. Sub-samples for measurement of body weights were taken in order to estimate a length-weight relationship.

A total of 10 experiments were carried out. However, only 7 of these were successful as mark-recapture experiments (Table 1). Three of the experiments were disrupted due to bad weather conditions, and did only provide data on size and sex distribution.

2. Localities

The experimental areas were situated in the Kattegat (see Fig. 1), and were selected such that two types of 'Carcinus-habitats' would be considered:
1) Sheltered shallow waters.
2) The more open deeper waters.
Furthermore, practical problems of placing and handling the traps were taken into account. The Egense Strand locality is considered representative of the sheltered coastal areas (depth: 0-2 m), while the two other localities represent the deeper, more open areas (depth: 2-10 m). The Udbyhøj locality is situated a little south of
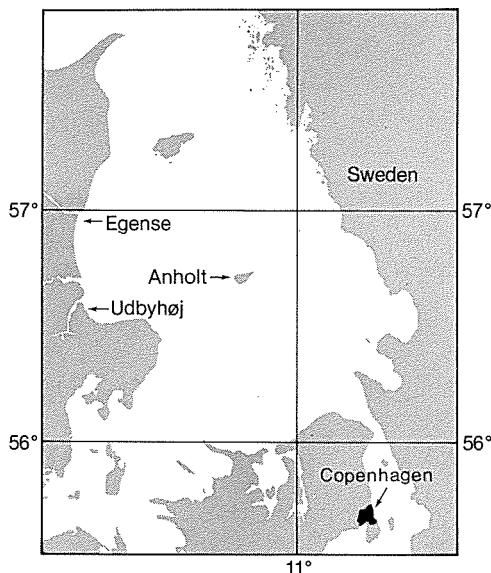
Fig. 1. Sample locations in Kattegat.

the mouth of Randers fjord, with a depth of 3-4 m and sandy bottom. At Anholt two experimental areas were used, both with hard sand bottom. In 1977 the experiments were carried out at depths of 3-4 m. In 1978 and 1979 the experiments were conducted in deeper water (6-10 m). The Egense locality is a small, sheltered bay south of the Limfjord. The depth varied from 0.5 to 1.5 m during the experiments, and the bottom consists of muddy sand covered with vegetation. Egense Strand belongs to the type of shallow water locality, which is inhabited by crabs mainly during the summer months (Muus 1967, and Rasmussen 1973). A visit to this place in late March 1978 did not reveal any crabs at all, whereas two months later the high densities given in Table 12 were found.

3. Method of capture

To ensure a high degree of uniformity of sampling in the different localities traps were considered the most appropriate sampling gear. The traps used for the experiments in 1977 and 1978 were of the creel-type (Fig. 2A) with an opening in both ends. The construction of the creels proved to be too flimsy and light in some cases. Therefore another more robust type of traps (modified Lobster pot, Fig. 2B) was introduced in 1979 in the Anholt area. In both cases the mesh size in the covering net was 11 mm from knot to knot (21 mm stretched). The traps were baited with fish. It was considered, to which degree the baiting would influence on captures during the experiment because of food saturation of those animals, which had been caught once. Other factors, such as 'learning' might work in the opposite direction. Such phenomena are difficult to assess, but in the experiments during 1979 the bait was rendered inaccessible to the crabs by enclosing it in plastic jars with small holes.
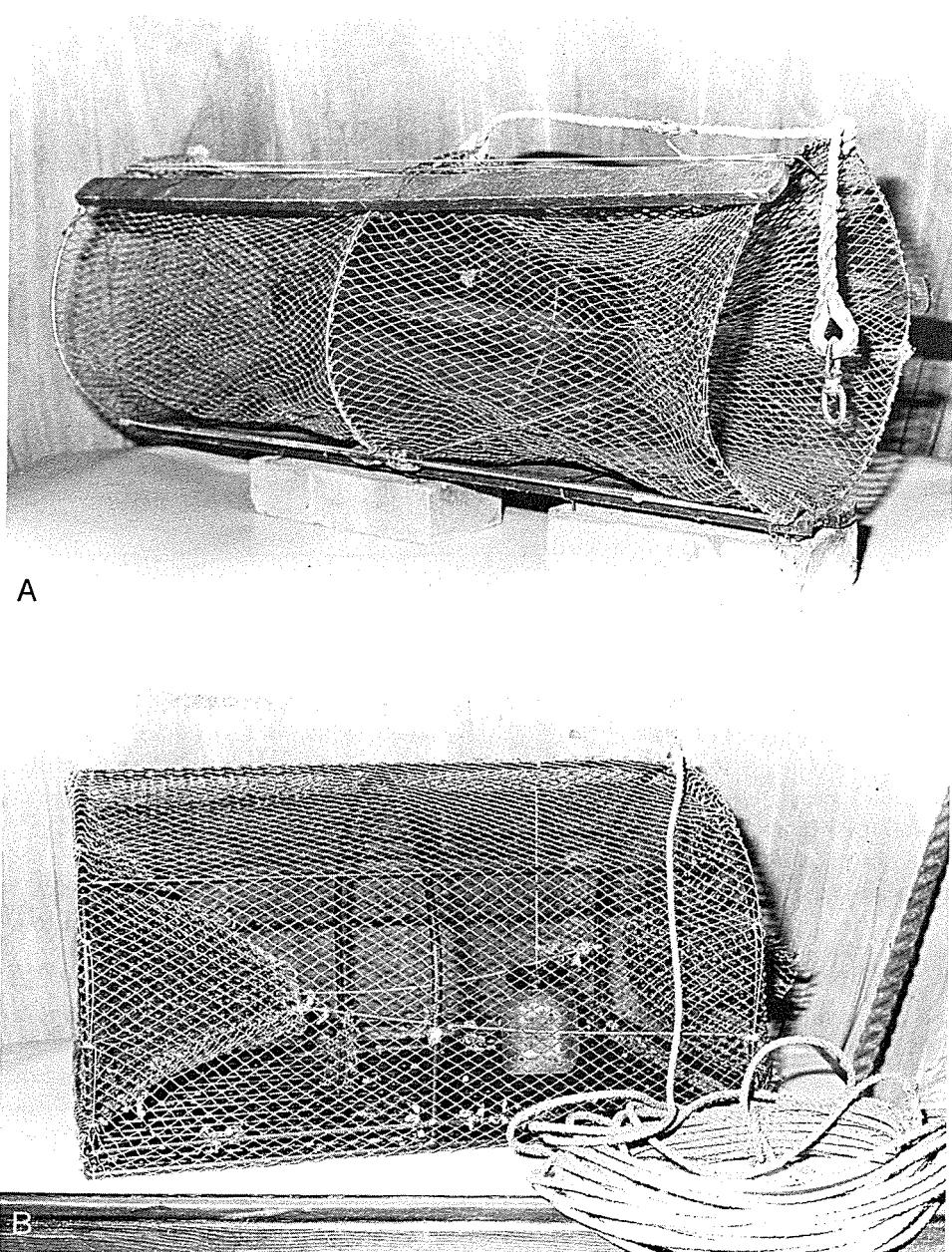
Fig. 2A & B. The traps used for catching crabs. A: the model used in 1977-78 and B: the modified lobster pot used in 1979. Note the plastic jar for keeping the bait.

The size and delimination of the experimental areas was defined by the placing of the traps. The sizes of the experimental areas varied according to the number of traps and the shortest distance between the traps (Table 1). In the experiments using 20 traps, these were placed in four rows of five traps each, forming a rectangular area of either $12\,500$ m^2 (distance between the traps: 25 m) or $50\,000$ m^2 (distance between the traps: 50 m). In the experiments using 49 traps these were placed in seven rows of seven traps each, forming a quadratic area of $30\,625$ m^2 (distance between traps: 25 m).

4. Methods of marking

In the experiments in 1977 the crabs were marked by nail varnish on the carapace, a method which was tedious, because it was necessary to dry the surface of the carapace with acetone, before putting the paint on. In the later experiments the method of Edwards (1958) was applied, which proved much faster. In this method 8 of the 10 lateral teeth of the carapace were used for marking by removing one tooth at each marking occasion, thus allowing for 8 different marks (Fig. 3).
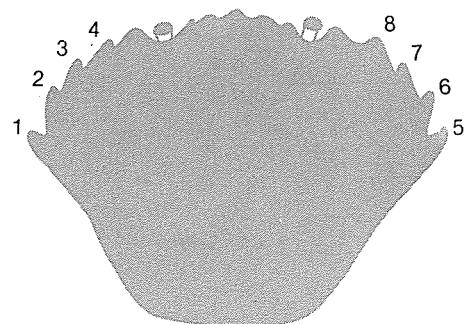
Fig. 3. The marking code. Tooth no. 1 was removed on crabs caught in sample no. 1, tooth no. 2 on crabs from sample no. 2 etc.

Because the adult crabs show the highest activity during the night, the traps were emptied in the morning. The crabs were then examined for marks, counted, measured and marked. They were released in the center of the experimental areas. In most cases it was possible to finish this procedure before noon, thus allowing time for the released crabs to get mixed in the population and to 'de-stress' before the following day's sampling. Based on observations made in laboratory the effect of the marking process on the behaviour and mortality of the crabs was believed to be negligible.

5. The models

Two models of multiple mark-recapture experiments were applied: (1) The Fisher and Ford model and (2) the Jolly and Seber model. Both models assume 'open' populations, i.e. between two sampling occasions marked animals may disappear from the population either by permanent emigration or by deaths, and new individuals may be added to the population.

In the Fisher and Ford model the survival rate, Φ, is assumed to remain constant during the experimental period, whereas the Jolly and Seber model allows for a variable survival rate and gives an estimate of Φ at each sampling occasion.

In both models the population size is estimated by the Petersen-estimate:

$$N = M \frac{n}{m}$$

where N is the estimated population number; n is the number of individuals in the sample, m the number of marked individuals in the sample and M is the number of marked individuals in the population immediately before the sample is taken ('marks at risk'). In the present work the modified Petersen-estimate:

$$N = M \frac{n+1}{m+1}$$

has been used as it can be shown that for small values of m and n, this estimate will

Table 2. Basic definitions and derivations of the two mark-recapture models.

Basic observations					Fisher & Ford (constant survival rate)			
A	B	C	D	E	F	G	H	I
Day no. i	Total no. caught on day i	No. of marks re-leased on day i	Total no. of re-captu-res on day i	m_{ji}: the no. of animals marked on day j, and recaptured on day i. ($\sum_j m_{ji} = m_i$)	No. of marked animals in the population on risk day i. Φ = survival rate	No. of days survived by marked animals on day i	Mean no. of days survived by marked animals on day i	Estim. no. of days survived by recaptures on day i
1	n_1	r_1	$m_1 = 0$	undefined	$M_1 = 0$	$D_1 = 0$	$A_1 = 0$	0
2	n_2	r_2	m_2	m_{12}	$M_2 = \Phi(M_1 + r_1 - m_1) =$ $\Phi(r_1 - m_1)$	$D_2 = 1 \cdot \Phi(r_1 - m_1)$	$A_2 = \dfrac{D_2}{M_2} = 1$	$A_2 m_2$
3	n_3	r_3	m_3	m_{13}, m_{23}	$M_3 = \Phi(M_2 + r_2 - m_2) =$ $\Phi^2(r_1 - m_1) + \Phi(r_2 - m_2)$	$D_3 = 2\Phi^2(r_1 - m_1)$ $+ 1\Phi(r_2 - m_2)$	$A_3 = \dfrac{D_3}{M_3}$	$A_3 m_3$
4	n_4	r_4	m_4	m_{14}, m_{24}, m_{34}	$M_4 = \Phi(M_3 + r_3 - m_3) = \cdot$ $\Phi^3(r_1 - m_1) + \Phi^2(r_2 - m_2)$ $+ \Phi(r_3 - m_3)$	$D_4 = 3\Phi^3(r_1 - m_1)$ $+ 2\Phi^2(r_2 - m_2)$ $+ 1\Phi(r_3 - m_3)$	$A_4 = \dfrac{D_4}{M_4}$	$A_4 m_4$
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
i	n_i	r_i	m_i	$m_{1i}, m_{2i}, ... m_{i-1,i}$	$M_i = \sum\limits_{j=1}^{i-1} \Phi^{i-j}(r_j - m_j)$	$D_i = \sum\limits_{j=1}^{i-1} (i-j)\Phi^{i-j}$ $(r_j - m_j)$	$A_i = \dfrac{D_i}{M_i}$	$A_i m_i$
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
$I-1$	n_{I-1}	r_{I-1}	m_{I-1}	$m_{1i}, m_{2i}, ... m_{I-2,i}$	$M_{I-1} = \sum\limits_{j=1}^{I-2} \Phi^{I-1-i}(r_j - m_j)$	$D_{I-1} =$ $\sum\limits_{j=1}^{I-2} (I-1-j)\Phi^{I-1-i}$ $(r_j - m_j)$	$A_{I-1} = \dfrac{D_{I-1}}{M_{I-1}}$	$A_{I-1} m_{I-1}$
I	n_I	$r_I = 0$	m_I	$m_{1i}, m_{2i} ... m_{I-1, i}$	$M_I = \sum\limits_{j=1}^{I-1} \Phi^{I-i}(r_j - m_j)$	$D_I = \sum\limits_{j=1}^{I-1} (I-j)\Phi^{I-i}$ $(r_j - m_j)$	$A_I = \dfrac{D_I}{M_I}$	$A_I m_I$

Total (cf. Eq. (1)): $\sum\limits_{i=1}^{I} A_i m_i$

be less biased (Bailey 1951). Table 2 summarizes the basic observations and calculation procedures of the two models, and describes the notation used below. Columns A-E, K show the observations and calculation of N, which apply to both models. The main difference between the two models is the derivation of M, and the estimation of survival rate, Φ.

In the Fisher and Ford model there are two steps in the calculation procedures:

1. Estimation of survival rate, Φ.
2. Estimation of M_i (marks at risk at sampling occasion i) and population number, N_i.

Φ is determined from the equation:

$$\sum_{i=1}^{I} \frac{\sum_{j=1}^{i-1} (i-j)\,\Phi^{i-j}\,(r_j - m_j)}{\sum_{j=1}^{i-1} \Phi^{i-j}\,(r_j - m_j)} \cdot m_j = \sum_{i=1}^{I} \sum_{j=1}^{i-1} (i-j)\,m_{ji} \qquad (1)$$

Fisher & Ford	Petersen	Jolly & Seber (variable survival rate)			
J	K	L	M	N	O
Observed no. of days survived by recaptures on day i	Population no. on day i	No. of marked animals not caught on day i, and subsequently caught	No. of animals marked on day i, and subsequently caught	No. of marked animals on risk day i	Survival rate of day i
0	undefined	$z_1 = 0$	$R_1 = \sum_{j=2}^{I} m_{1j}$	$M_1 = 0$	$\Phi_1 = \dfrac{M_2}{r_2}$
$1 \cdot m_{12}$	$N_2 = M_2\,\dfrac{n_2+1}{m_2+1}$	$z_2 = \sum_{j=3}^{I} m_{1j}$	$R_2 = \sum_{j=3}^{I} m_{2j}$	$M_2 = \dfrac{r_2 z_2}{R_2} + m_2$	$\Phi_2 = \dfrac{M_3}{M_2 - m_2 + r_2}$
$2 \cdot m_{13} + 1 \cdot m_{23}$	$N_3 = M_3\,\dfrac{n_3+1}{m_3+1}$	$z_3 = \sum_{j=4}^{I}\sum_{k=1}^{2} m_{kj}$	$R_3 = \sum_{j=4}^{I} m_{3j}$	$M_3 = \dfrac{r_3 z_3}{R_3} + m_3$	$\Phi_3 = \dfrac{M_4}{M_3 - m_3 + r_3}$
$3m_{14} + 2m_{24} + 1 \cdot m_{34}$	$N_4 = M_4\,\dfrac{n_4+1}{m_4+1}$	$z_4 = \sum_{j=5}^{I}\sum_{k=1}^{3} m_{kj}$	$R_4 = \sum_{j=5}^{I} m_{4j}$	$M_4 = \dfrac{r_4 z_4}{R_4} + m_4$	$\Phi_4 = \dfrac{M_5}{M_4 - m_4 + r_4}$
. . .	. . .	. . .	. . .	. . .	. . .
$\sum_{j=1}^{i-1} (i-j)m_{ji}$	$N_i = M_i\,\dfrac{n_i+1}{m_i+1}$	$z_i = \sum_{j=i+1}^{I}\sum_{k=1}^{i-1} m_{kj}$	$R_i = \sum_{j=i+1}^{I} m_{ij}$	$M_i = \dfrac{r_i z_i}{R_i} + m_i$	$\Phi_i = \dfrac{M_{i+1}}{M_i - m_i + r_i}$
. . .	. . .	. . .	. . .	. . .	. . .
$\sum_{j=1}^{I-2}(I-1-j)m_{jI-1}$	$N_{I-1} = M_{I-1}\,\dfrac{n_{I-1}+1}{m_{I-1}+1}$	$z_{I-1} = \sum_{k=1}^{I-2} m_{kI}$	$R_{I-1} = m_{I-1,I}$	$M_{I-1} = \dfrac{r_{I-1}z_{I-1}}{R_{I-1}} + m_{I-1}$	undefined
$\sum_{j=1}^{I-1}(I-j)m_{jI}$	$N_I = M_I\,\dfrac{m_I+1}{m_I+1}$	undefined	undefined	undefined	undefined
$\sum_{i=1}^{I}\sum_{j=1}^{i-1} (i-j)m_{ji}$					

The derivation of this equation is given in Table 2, columns F-J. It should be mentioned, that in the version used here, only the last previous mark is counted in case of recaptures with more than one mark (for a detailed discussion of this model, see Begon (1979)). Once Φ has been estimated, M_j is obtained from the expressions given in column F. Equation (1) may be solved by some appropriate numerical method.

The derivation of M in the Jolly and Seber model is somewhat simpler. The basic idea is to group the marked individuals in the population immediately after sampling occasion i into two groups:

1. The $M_i - m_i$ individuals, which were not caught in sample i, but of which z_i are subsequently caught.
2. r_i, the number of marks released from sample i of which R_i are subsequently caught.

The probabilities of recapture should be equal for these two groups, giving the relation:

$$\frac{z_i}{M_i - m_i} = \frac{R_i}{r_i}.$$

from which M is found (Table 2, column N). Expressions for Φ_i are given in column O. A detailed discussion of this model is given in Seber (1973).

The number of new individuals added to the population between sampling occasion i and $i + 1$, B_i, is estimated in a similar way in the two models:

Fisher and Ford: $B_i = N_{i+1} - \Phi(N_i - n_i + r_i)$.
Jolly and Seber: $B_i = N_{i+1} - \Phi_i(N_i - n_i + r_i)$.

As Φ_{I-1} and Φ_I are undefined (cf. Table 2, column O) in the Jolly and Seber model, this will also be the case for B_{I-1} and B_I.

Tables 3.1-3.7 contain estimates of the standard deviations SD_N, SD_Φ and SD_B determined as described in Seber (1973).

6. Results and discussion

6.1 Captures and recaptures

Tables 3.1A-3.7A show the daily captures (n) and recaptures (m) together with trellis diagrams, showing the number of recaptures, m_{ji}, on each sampling occasion, i, which previously were caught on sampling occasion j.

The numbers of captures per day during each experiment showed a relatively small daily variation. A relatively high catch level was found in the shallow water locality at Egense, while a low catch level was found in the deeper waters at Anholt and Udbyhøj, cf. Table 1. Also the percentages of recaptures appeared to be more or less constant in each of the 3 localities, indicating that the catchability of the crabs during the experiments was constant. The lower percentage of recaptures at Egense and Udbyhøj indicates, that in these experiments a smaller part of the total population was caught in the samples than in the Anholt area.

Table 3.1 Basic observations and estimates for the experiment at Egense, June 1978.

A: *Basic observations*

i	1	2	3	4	5	6	7	8	9	
n_i	485	977	536	826	654	296	353	277	297	
r_i	485	977	535	826	652	296	353	277	0	R_j
m_{1i}	–	5	5	4	2	2	3	1	3	25
m_{2i}	–	–	7	5	10	2	2	4	2	32
m_{3i}	–	–	–	14	10	6	1	3	2	36
m_{4i}	–	–	–	–	4	3	0	2	0	9
m_{5i}	–	–	–	–	–	3	1	0	2	6
m_{6i}	–	–	–	–	–	–	4	1	0	5
m_{7i}	–	–	–	–	–	–	–	2	1	3
m_{8i}	–	–	–	–	–	–	–	–	1	1
m_i	–	5	12	23	26	16	11	13	11	
Δt_i	–	1	1	1	1	1	1	1	1	

B: *Jolly & Seber*:

i	M_i	N_i	SD_{N_i}	Φ_i	SD_{Φ_i}	B_i	SD_{B_i}
1	–	–	–	1.230	–	97231.9	–
2	596.5	97231.9	51021.4	0.378	0.093	−12278.7	17920.8
3	591.5	24431.8	8717.0	3.954	1.490	55237.7	153590.0
4	4406.1	151826.9	62821.2	0.650	0.348	−16539.7	26218.7
5	3384.3	82100.3	39433.5	0.325	0.199	−3910.7	7553.4
6	1303.0	22764.2	12342.0	1.125	0.835	26928.0	28448.7
7	1781.0	52539.5	36345.8	0.661	0.795	−6861.5	13994.7
8	1403.0	27859.6	–	–	–	–	–

C: *Fisher & Ford*:

i	M_i	N_i	A_i	Φ	B_i
1	–	–	–		74944.1
2	459.8	74944.1	1.00		−15057.3
3	1355.4	55989.7	1.32		8283.5
4	1780.8	61361.8	1.95		1249.6
5	2449.4	59420.6	2.35	0.948	−5395.6
6	2915.5	50935.1	2.87		41078.2
7	3029.3	89364.7	3.62		−21254.2
8	3196.0	63463.5	4.25		21292.0
9	3280.1	81455.4	4.93		–

Table 3.2 Basic observations and estimates for the experiment at Egense, August 1978.

A: *Basic observations*

i	1	2	3	4	5	6	7	8	
n_i	669	368	226	695	416	152	251	201	
r_i	669	368	226	694	416	151	251	0	R_j
m_{1i}	–	7	2	6	10	1	2	2	30
m_{2i}	–	–	5	13	6	1	3	2	30
m_{3i}	–	–	–	13	3	0	0	0	16
m_{4i}	–	–	–	–	6	3	5	3	17
m_{5i}	–	–	–	–	–	3	5	8	16
m_{6i}	–	–	–	–	–	–	2	3	5
m_{7i}	–	–	–	–	–	–	–	1	1
m_i	–	7	7	32	25	8	17	19	
Δt_i	–	1	1	1	1	1	1	1	

B: *Jolly & Seber*:

i	M_i	N_i	SD_{N_i}	Φ_i	SD_{Φ_i}	B_i	SD_{B_i}
1	–	–	–	0.420	–	12950.7	–
2	280.8	12950.7	5846.2	0.968	0.292	5091.3	8572.0
3	621.2	17627.6	8146.9	1.417	0.509	132.9	10143.3
4	1190.3	25105.2	8541.4	0.305	0.112	1403.6	2177.1
5	564.7	9056.1	3301.1	0.804	0.411	5778.1	5979.0
6	768.0	13056.0	7646.6	2.508	2.805	−755.0	13601.3
7	2285.0	31990.0	–	–	–	–	–

C: *Fisher & Ford*:

i	M_i	N_i	A_i	Φ	B_i
1	–	–	–		23544.4
2	510.5	23544.4	1.00		902.6
3	664.9	18866.9	1.59		−171.2
4	674.4	14224.3	2.19	0.763	5501.2
5	1019.7	16354.3	2.11		5819.8
6	1076.4	18298.1	2.52		−936.3
7	930.4	13025.2	3.23		−965.2
8	888.4	8973.0	3.58		–

Table 3.3 Basic observations and estimates for the experiment at Udbyhøj, June 1977.

A: *Basic observations*

i	1	2	3	4	5	6	
n_i	112	145	132	82	143	91	
r_i	112	145	132	82	143	0	R_j
m_{1i}	–	4	1	0	0	0	5
m_{2i}	–	–	1	0	1	1	3
m_{3i}	–	–	–	3	3	0	6
m_{4i}	–	–	–	–	3	0	3
m_{5i}	–	–	–	–	–	2	2
m_i	–	4	2	3	7	3	
Δt_i	–	1	1	1	1	1	

B: *Jolly & Seber*:

i	M_i	N_i	SD_{N_i}	Φ_i	SD_{Φ_i}	B_i	SD_{B_i}
1	–	–	–	0.362	–	1182.6	–
2	40.5	1182.6	1446.2	0.220	0.188	1512.7	1694.6
3	40.0	1773.3	1841.4	0.628	0.479	1101.5	2599.4
4	106.8	2215.1	2034.7	0.296	0.385	334.1	542.2
5	55.0	990.0	–	–	–	–	–

C: *Fisher & Ford*:

i	M_i	N_i	A_i	Φ	B_i
1	–	–	–		1340.9
2	45.9	1340.9	1.00		2847.8
3	76.6	3397.6	1.25	0.410	364.9
4	84.7	1758.0	1.46		487.5
5	67.1	1208.3	1.76		1420.1
6	83.3	1915.5	1.58		–

Table 3.4 Basic observations and estimates for the experiment at Anholt, June 1977.

A: *Basic observations*

i	1	2	3	4	5	6	
n_i	67	46	31	39	33	42	
r_i	67	46	31	39	33	0	R_j
m_{1i}	—	1	0	0	0	0	1
m_{2i}	—	—	3	1	0	0	4
m_{3i}	—	—	—	3	0	0	3
m_{4i}	—	—	—	—	5	1	6
m_{5i}	—	—	—	—	—	8	8
m_i	—	1	3	4	5	9	
Δt_i	—	1	1	1	1	1	

B: *Jolly & Seber:*

i	M_i	N_i	SD_{N_i}	Φ_i	SD_{Φ_i}	B_i	SD_{B_i}
1	—	—	—	0.015	—	46.0	—
2	1.0	46.0	—	0.290	0.255	124.4	1412.8
3	13.3	137.8	134.8	0.097	0.053	25.7	9.6
4	4.0	39.0	3.5	0.234	0.119	51.1	51.4
5	9.1	60.2	—	—	—	—	—

C: *Fisher & Ford:*

i	M_i	N_i	A_i	Φ	B_i
1	—	—	—		110.2
2	4.7	110.2	1.00		20.1
3	3.5	27.8	1.09	0.070	15.7
4	2.2	17.6	1.12		13.5
5	2.6	14.8	1.07		8.2
6	2.1	9.2	1.09		—

Table 3.5 Basic observations and estimates for the experiment at Anholt, June 1978.

A: *Basic observations*

i	1	2	3	4	5	6	
n_i	32	26	31	37	28	45	
r_i	32	26	31	37	28	0	R_j
m_{1i}	—	2	1	0	1	1	5
m_{2i}	—	—	1	0	2	3	6
m_{3i}	—	—	—	2	1	1	4
m_{4i}	—	—	—	—	1	2	3
m_{5i}	—	—	—	—	—	1	1
m_i	—	2	2	2	5	8	
Δt_i	—	1	1	1	1	1	

B: *Jolly & Seber*:

i	M_i	N_i	SD_{N_i}	Φ_i	SD_{Φ_i}	B_i	SD_{B_i}
1	—	—	—	0.424	—	122.1	—
2	13.6	122.1	96.9	1.246	0.760	347.1	773.0
3	48.8	499.2	433.9	1.154	0.853	532.1	1049.8
4	87.5	1108.3	1027.6	0.869	1.004	−448.8	887.4
5	106.5	514.8	—	—	—	—	—

C: *Fisher & Ford*:

i	M_i	N_i	A_i	Φ	B_i
1	—	—	—		277.6
2	30.9	277.6	1.00		296.4
3	52.9	564.0	1.56	0.964	456.1
4	78.9	999.7	2.01		−432.9
5	109.8	530.8	2.39		142.7
6	128.0	654.4	2.98		—

Table 3.6 Basic observations and estimates for the experiment at Anholt, July 1979.

A: *Basic observations*

i	1	2	3	4	5	6	7	8	9	
n_i	83	121	72	74	84	135	84	91	38	
r_i	82	114	71	73	76	133	82	91	0	R_j
m_{1i}	—	8	1	2	0	1	1	0	0	13
m_{2i}	—	—	3	3	3	1	2	0	0	12
m_{3i}	—	—	—	9	1	2	0	1	0	13
m_{4i}	—	—	—	—	5	1	0	1	0	7
m_{5i}	—	—	—	—	—	15	3	2	0	20
m_{6i}	—	—	—	—	—	—	6	1	1	8
m_{7i}	—	—	—	—	—	—	—	5	0	5
m_{8i}	—	—	—	—	—	—	—	—	3	3
m_i	—	8	4	14	9	20	12	10	4	
Δt_i	—	1	1	1	1	1	1	1	1	

B: *Jolly & Seber:*

i	M_i	N_i	SD_{N_i}	Φ_i	SD_{Φ_i}	B_i	SD_{B_i}
1	—	—	—	0.637	—	708.7	—
2	52.2	708.0	376.8	0.448	0.170	720.6	593.6
3	70.9	1034.5	594.8	0.907	0.406	−312.1	511.9
4	125.0	625.0	291.7	0.248	0.102	233.3	116.7
5	45.7	388.2	149.7	1.499	0.639	523.9	847.7
6	168.9	1093.8	499.9	0.337	0.201	253.2	187.3
7	95.0	621.2	364.2	0.200	0.189	152.2	88.9
8	33.0	276.0	—	—	—	—	—

C: *Fisher & Ford:*

i	M_i	N_i	A_i	Φ	B_i
1	—	—	—		539.1
2	39.8	539.1	1.00		770.7
3	70.7	1032.2	1.27		−166.7
4	66.8	333.9	1.65		356.6
5	61.0	518.5	1.88	0.485	150.6
6	62.1	402.1	1.89		360.2
7	84.9	555.2	1.67		359.1
8	75.1	628.4	1.92		285.8
9	75.7	590.7	1.92		—

Table 3.7 Basic observations and estimates for the experiment at Anholt, September 1979.

A: *Basic observations*

i	1	3	4	11	
n_i	353	159	159	392	
r_i	353	154	152	0	R_j
m_{1i}	–	6	5	7	18
m_{2i}	–	–	8	8	16
m_{3i}	–	–	–	10	10
m_i	–	6	13	25	
Δt_i	–	2	1	7	

B: *Jolly & Seber*:

i	M_i	N_i	SD_{N_i}	Φ_i	SD_{Φ_i}	B_i	SD_{B_i}
1	–	–	–	0.572*	–	2638.0	–
3	115.4	2638.0	1370.5	0.841	0.344	317.6	1102.9
4	221.6	317.6	–	–	–	–	–

*Daily survival rate.

C: *Fisher & Ford*:

i	M_i	N_i	A_i	Φ	B_i
1	–	–	–		–
2	215.3	–	1.00		3002.3
3	131.4	3002.3	2.00		116.1
4	170.4	1947.5	1.94		–
5	188.7	–	2.07		–
6	115.1	–	3.07	0.610	–
7	70.2	–	4.07		–
8	42.8	–	5.07		–
9	26.1	–	6.07		–
10	15.9	–	7.07		147.0
11	9.7	147.0	8.07		–

6.2 *Sex distribution in the captures*

The percentages of females and males in the total captures are given in Table 1. It is seen, that the females constituted much less than half of the total (ranging from 39% to 1%). All the experiments were carried out during the summer months, and the scanty representation of female crabs in the samples, which is somewhat similar to the observations by Edwards (1958), Naylor (1962) and Rasmussen (1973) is probably due to several factors. According to Broekhuysen (1936), Ropes (1968) and Rasmussen (1973) the behaviour of adult females is different from that of males in summer. Berried (ovigerous) females (early summer months) tend to seek deeper water and show a reduced feeding activity, and in the late summer a greater part of them are moulting and mating. Such patterns in behaviour are likely to reduce the catchability by traps of females compared to that of males during the summer months.
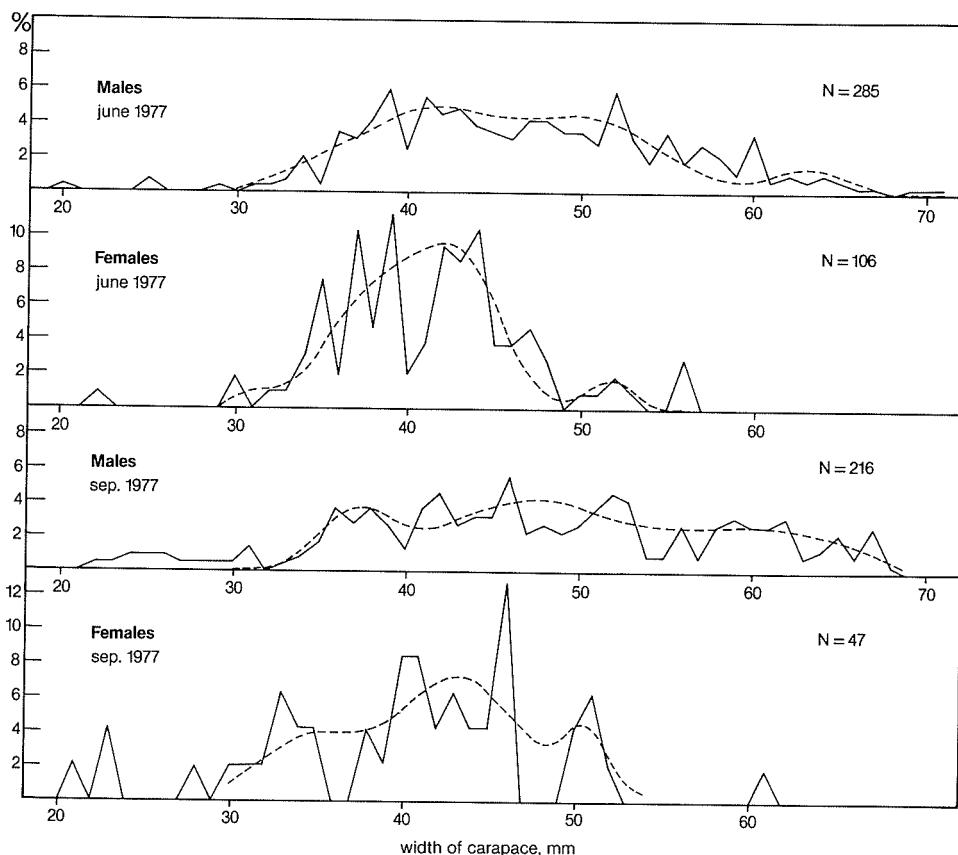
Fig. 4.1. Size distribution of crabs from Udbyhøj 1977.

6.3 *Size and age distribution*

During the experiments either all captured crabs, or subsamples were measured (the width of carapace, to the nearest mm below). Figs 4.1-4.3 show the size distributions. Due to the mesh size in the traps only crabs above 30 mm carapace width were effectively retained. It is seen, that the crabs found at the Egense locality are smaller than those found at the other two localities indicating a higher frequency of younger individuals in shallow waters. This pattern holds for both males and females.

From these observed size distributions some rough estimates of age distributions were made, based on the following data and assumptions:

a. Adult crabs moult only once a year, mainly during June to August. The mean size of an age group after the moult will on the average correspond to the mean size of the one year older age group before the moult.

b. The average size of the age groups given by Broekhuysen (1936), see Table 4.

c. The size distribution of an age group is approximately normal.

The observed size distributions found in the samples (Fig. 4.1-4.3) were split into separate normal distributions by means of logarithmic transformation of the observed size frequencies (cf. Bhattachyara (1967)). In this process the sizes at age given by Broekhuysen (1936) were used as 'guide values' to the size range in which
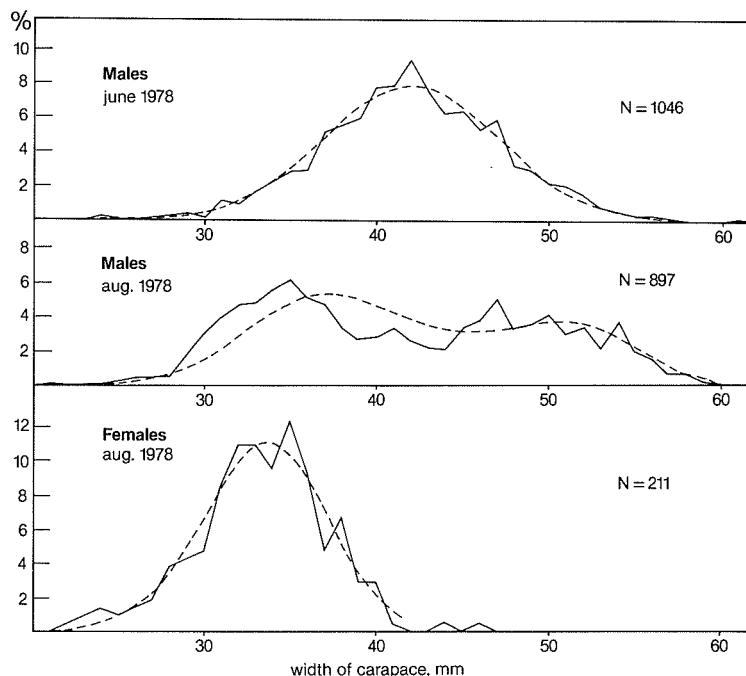

Fig. 4.2. Size distribution of crabs from Egense 1978.
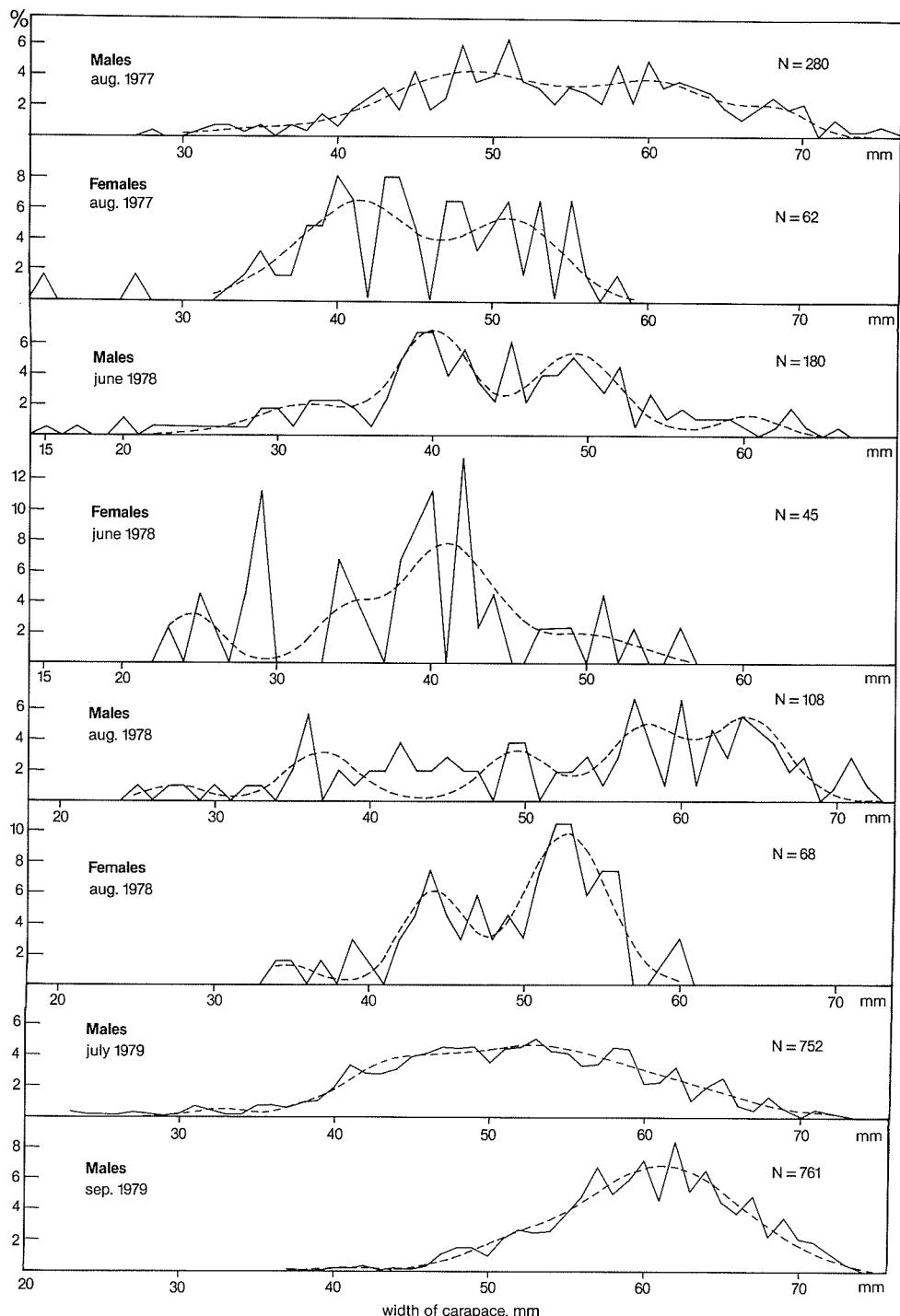
Fig. 4.3. Size distribution of crabs from Anholt 1977-79.

Table 4. Estimated mean size (width of carapace, mm) at age.

Experiment	Age group (Males)				Age group (Females)			
	1	2	3	4	1	2	3	4
Egense, June 1978	38.6	42.1	45.7	–	–	–	–	–
Egense, Aug. 1978	36.9	48.1	52.3	–	32.5	33.7	37.5	–
Udbyhøj, June 1977	34.8	41.2	50.8	63.2	31.0	38.6	43.3	51.7
Udbyhøj, Sep. 1977	37.1	47.6	59.7	65.4	34.9	43.4	50.7	61.0
Anholt, June 1977	–	–	–	–	–	–	–	–
Anholt, Aug. 1977	34.0	48.4	60.7	68.4	35.5	41.4	51.2	–
Anholt, June 1978	31.7	40.0	49.1	60.2	39.1	41.7	49.5	–
Anholt, Aug. 1978	35.1	49.5	57.8	64.4	34.8	44.2	52.7	–
Anholt, July 1979	32.5	43.5	52.4	62.1	–	–	–	–
Anholt, Sep. 1979	41.2	50.7	60.8	64.3	–	–	–	–
Data from Broekhuysen (1936)	36	42	48	56	25	36	42	50

Table 5. Mean size (mm) of *Carcinus* from the Isefjord, year class 1954 (unpubl. data, Rasmussen 1973).

	Age group (Males)				Age group (Females)			
	1	2	3	4	1	2	3	4
July 1955	26.0	–	–	–	26.0	–	–	–
May 1956	–	38.6	–	–	–	33.9	–	–
July 1956	–	42.7	–	–	–	35.3	–	–
Aug. 1956	–	47.1	–	–	–	40.3	–	–
July 1957	–	–	54.4	–	–	–	41.3	–
Aug. 1957	–	–	59.8	–	–	–	43.4	–
May 1958	–	–	–	56.2	–	–	–	45.9
July 1958	–	–	–	58.6	–	–	–	41.0
Aug. 1958	–	–	–	61.8	–	–	–	47.4

Table 6. Estimated age distribution (%).

Experiment	Age group (Males)				Age group (Females)			
	0+1	2	3	4	0+1	2	3	4
Egense, June 1978	11.8	77.5	10.8	–	–	–	–	–
Egense, Aug. 1978	56.5	32.5	11.6	–	27.6	72.3	2.0	–
Udbyhøj, June 1977	3.5	48.9	39.9	7.8	2.9	53.5	39.1	5.6
Udbyhøj, Sep. 1977	15.3	58.3	18.7	8.9	27.6	61.4	13.3	–
Anholt, June 1977	–	–	–	–	–	–	–	–
Anholt, Aug. 1977	3.0	56.6	32.9	7.7	2.8	57.2	41.3	–
Anholt, June 1978	15.5	40.0	37.9	6.6	30.5	57.5	14.4	–
Anholt, Aug. 1978	21.8	17.1	29.1	32.1	5.4	30.5	65.0	–
Anholt, July 1979	2.1	20.1	60.2	17.7	–	–	–	–
Anholt, Sep. 1979	1.0	7.5	84.3	7.4	–	–	–	–

the calculated means of the normal distributions should lie, while at the same time the calculated composite distributions should fit the observed ones reasonably well. It was assumed, that the crabs in the samples from May and June had not moulted yet, while in the samples from August and September all the crabs would have moulted. In Fig. 4.1-4.3 the calculated distributions are shown as the smooth curves.

Tables 4 & 6 give the estimated mean size at age and age distribution in the captures. In case of the adult males for which the samples are assumed to be representative, it is seen that the growth increment (one moult) between the two sampling periods roughly corresponds to the size differences of the age groups at the first sampling period. Obviously the 1-group (from the previous year's spawning) is not fully represented in the samples.

These estimates of size at age agree well with some unpublished data on the growth of *Carcinus* from the Isefjord investigation, Table 5 (Rasmussen 1973). At this locality not every year yields conditions which are favourable for a successful settlement and metamorphosis of the larvae, rendering it possible to distinguish particular successful year classes as for instance the 1954 year class, which could be followed for 4 successive years.

6.4 *Length-weight relationship*

The sub-samples for measuring individual body weight were taken to estimate parameters of a length-weight relationship. These were used for transforming the number of crabs by length group per m² from the various areas into biomass estimates (Table 11). Both the allometric ($w = A \cdot L^B$) and isometric model ($w = Q \cdot L^3$) were considered. The simpler isometric model was applied, as it fitted the data adequately for the purpose (Fig. 5).
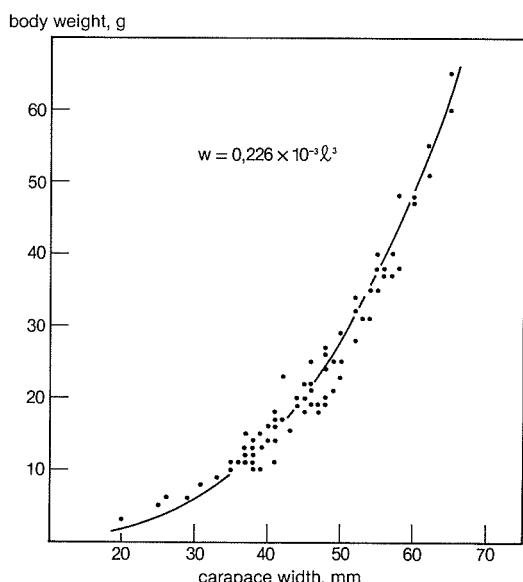

Fig. 5. Lenght/weight relationship for male and female shore crabs in Kattegat. (Wet weight against width of carapace.)

Table 7. Estimated Q-values in $w = Q \cdot L^3$.
(w = weight (grams), L = width of carapace (mm)).

	Males	Females	Males + Females
Q	0.221×10^{-3}	0.232×10^{-3}	0.226×10^{-3}

Table 7 shows the estimated parameter (Q) for both males and females separately, and the two sexes pooled. The differences between the parameter values for males and females are not significant, and in the estimates given in Table 11 the pooled estimate is used.

6.5 Estimates of abundance

When comparing the fluctuations in the estimates of population size by area from the two models the impression is somewhat discouraging (Tables 3.1-3.7). Only the data from one experiment (Anholt, June 1978 (Table 3.5)) yield patterns, which are similar in the two models, and one is inclined to believe that this similarity might be due to chance, especially because the estimated variances given by the Jolly and Seber model are large and indicate a low precision of the estimates. However, when comparing the mean values of the two sets of N there seems to be an acceptable agreement (N of the last day (I) from the Fisher and Ford model is excluded in order to render the means comparable), see Table 8. As the Fisher and Ford model in general seems to be the more robust of the two models, when the data are somewhat scanty (Begon 1979), the estimates used for the density figures given in Table 9 are those from the Fisher and Ford model.

The under-representation of females in the samples (cf. Sect. 6.2) makes the transformation of the estimated population numbers into density figures (numbers and weight per m^2) problematic. However, to maintain consistency with the explanation of the scarce female representation in the captures given in sect. 6.2, it seems reasonable to raise the figures to 50% females in case of the localities at Udbyhøj and Anholt, while in the case of Egense Fjord to accept the observed sex

Table 8. Mean values of estimated population size (N_i).

Experiment	Arithmetic mean		Geometric mean	
	J & S	F & F	J & S	F & F
Egense, June 1978	65536	65068	51696	64045
Egense, Aug. 1978	18296	17385	16698	17057
Udbyhøj, June 1977	1540	1926	1464	1764
Anholt, June 1977	71	43	62	30
Anholt, June 1978	561	593	432	537
Anholt, July 1979	678	573	615	541
Anholt, Sep. 1979	2585	2475	2585	2418

Table 9. Estimates of density and biomass.

Experiment	Average population number (F & F)	Average population number raised to 50 % females	Numbers per m²	Biomass grams*/m²
Egense, June 1978	65068	–	5.21	92.2
Egense, Aug. 1978	17385	–	0.35	5.7
Udbyhøj, June 1977	1926	2812	0.22	4.9
Anholt, June 1977	43	71	0.001	0.03
Anholt, June 1978	593	973	0.08	1.4
Anholt, July 1979	573	1112	0.04	0.9
Anholt, Sep. 1979	2475	4900	0.16	5.6

*Live weight. See Sect. 6.4

distribution of the captures as representative of the area. Table 9 summarizes the estimates of density and biomass during the various experiments. Taking into account these assumptions and also year to year fluctuations in abundance, the differences in abundances during the various experiments should be assessed cautiously. However, both the extremely high density during the first experiment at Egense and the very low density found during the first Anholt experiment are conspicuous compared to the other estimates.

The low density found at Anholt in 1977 may be explained by the type of experimental area selected that year: An exposed coastal area with a rather bare sand bottom, with sparse possibilities of hides and probably also limited amounts of available food. The high density at Egense during early summer indicates large amounts of food available to the crabs during this period, and this is likely in this type of habitat. Egense Strand is not inhabited by crabs or any other similar type of omnivorous predator during the winter months, and an accumulation of dead animals is likely to take place in such an area during the winter months, when the rate of predation and also decomposition is very low due to frequent exposure to cold and even frost.

The estimated density figures for *Carcinus* in a tidal area at the south coast of England (Edwards 1958), using the Fisher and Ford model (from about 0.7 to 4.8 individuals per m² on the average) are similar to those found at Egense Strand.

6.6 Estimates of survival rate

Table 3.1-3.7 (B & C) and Table 10 contain the estimates of Φ by the two models. As the experimental periods were very short compared to the life span of the crabs, any effect of mortality on the estimates is considered negligible. Thus any estimated survival rates < 1 would merely indicate emigration of marked individuals from the experimental areas. The daily survival rates may be conceived as parameters for, how stationary the crabs are during the experiments. For instance, a daily survival rate of about 0.5 (Anholt, July and September 1979) implies, that after the

Table 10. Comparison of estimates of survival rates.

Experiment	Jolly & Seber*	Fisher & Ford
Egense, June 1978	0.84	0.95
Egense, Aug. 1978	0.84	0.76
Udbyhøj, June 1978	0.35	0.41
Anholt, June 1977	0.10	0.07
Anholt, June 1978	0.85	0.96
Anholt, July 1979	0.49	0.49
Anholt, Sep. 1979	0.65	0.61

*Geometric means: $\sqrt[I-2]{\prod\limits^{I-2} \Phi_i}$

8 days following the first sampling occasion more than 99 % of the crabs present within the experimental area at the beginning of the experiment have left the area. The estimated values of Φ indicate a higher degree of stationarity by the crabs in the sheltered Egense locality, than by those occurring in the open areas.

As mentioned in sect. 3, the experimental areas were defined only by the placing of the traps, and it is very likely, that during the experiments not only emigration but also reimmigration took place. In this case the assumption of permanent emigration does not hold, although this will not in practice affect the abundance estimates, but it is readily seen (Table 2, column O) that the values of Φ never should exceed 1, if the emigration is permanent.

The Jolly and Seber estimates of survival rate are subject to large fluctuations and in some cases (especially during the experiments in Egense) become greater than 1. But the variances are large, and it is impossible to assess whether the values of $\Phi > 1$ are caused by re-immigration or they merely reflect insufficient recapture data to this model.

The survival rate estimated by the Fisher and Ford model can be regarded as a mean survival rate estimated from the total amount of recapture data. Any possible influence of re-immigration in the single estimate of Φ will be leveled by the emigration during the experimental period. When comparing the observed number of days survived by the marked individuals at the i'th sampling occasion:

$$\sum_{j=1}^{i-1} (i-j) m_{ij}$$

with the estimated value $(A_i \cdot m_i)$ using a χ^2-test (cf. Begon 1979)), the differences do not seem to be significant (Table 11). Apparently the data fit into the assumption of a constant survival rate (Fisher and Ford model), while when used in the Jolly and Seber model yield survival rates, which are subject to large fluctuations.

Table 10 shows the mean values (geometric means) of the Jolly and Seber estimates compared to the Fisher and Ford estimates. The agreement between the two sets is rather good, indicating that the fluctuations in the Jolly and Seber estimates probably are random. These examples also illustrate a main weakness in

Table 11. χ^2-tests of constancy of survival rates (F & F) during experimental periods (see text).

Experiment	χ^2	d.f.	P
Egense, June 1978	2.92	6	>0.8
Egense, Aug. 1978	8.69	5	>0.1
Udbyhøj, June 1977	3.69	4	>0.4
Anholt, June 1977	0.11	3	>0.9
Anholt, June 1978	1.17	3	>0.7
Anholt, July 1979	5.07	6	>0.4
Anholt, Sep. 1979	0.22	1	>0.6

the Jolly and Seber model from a practical point of view: The many different parameters usually require more data than it is practically possible to obtain. A detailed discussion of the Jolly and Seber model versus other models is given by Cormack (1979).

6.7 The standing crop of Carcinus in Kattegat

Even though the estimates of density and biomass shown in Table 9 should be assessed cautiously, they may form a basis for some considerations on the total biomass (standing crop) of Carcinus in Kattegat, cf. Fig. 1. Two estimates are presented in Table 12.

Both estimates are based on the assumption, that the total area in Kattegat inhabited by Carcinus consists of all areas with depths ranging from 0 to 10 m. Although Carcinus is found at depths beyond 10 m, it is between 0 and 10 m the typical habitat of this species is found. Within this range we have distinguished between the shallow waters along the coast (depth: 0-2 m) represented by the locality of Egense, and areas with depths of 2 to 10 m represented by the localities Udbyhøj and Anholt. This crude division is in fair accordance with the distribution presented by Poulsen (1949). The sizes of these two areas within Kattegat were estimated planimetrically on a chart.

Both options presented in Table 12 assume an average biomass at depths of 2 to 10 m calculated as the simple mean of the figures for Udbyhøj and Anholt. The

Table 12. Estimates of standing crop of Carcinus in Kattegat. Option 1: Depth 0-2 m, data from Egense Aug. 1978. Depth 2-10 m, data from Anholt and Udbyhøj. Option 2: Depth 0-2 m, data from Egense June 1978. Depth 2-10 m same as option 1. (c.f. Table 9).

Depth	Size of area, km²		Biomass, g/m²		Standing crop, tons
	0-2 m	2-10 m	0-2 m	2-10 m	
Option 1	469	4777	5.7	2.6	15000
Option 2	469	4777	92.2	2.6	56000

options differ only in the two very different biomass figures from the Egense experiments, cf. Sect. 6.5. However, as it is especially in the shallow waters the large seasonal and yearly fluctuations in abundance are recorded (Rasmussen 1973), these two options may indicate likely magnitudes of the biomass of this species in Kattegat. These are of similar orders of magnitude as those of two other important species, namely plaice and cod (20 000-30 000 tonnes) (Anon. 1981).

As stated above these estimates should be assessed cautiously, but it should be pointed out, that they coincide well with the figure of 50 000 tonnes for 'large Crustaceans and snails' in Kattegat presented (as an educated 'guesstimate') by Petersen (1915).

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