OCCURRENCE AND POPULATION COMPOSITION OF THE EDIBLE CRAB (*CANCER PAGURUS*) ON ROCKY SHORES OF AN ISLET ON THE SOUTH COAST OF NORWAY

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Diurnal vertical movements of *Cancer pagurus* L. have been studied by skin-diving surveys on an exposed rocky islet on the Norwegian Skagerrak coast. The site studied was bounded in depth by the upper limit of *Laminaria digitata* (HUDSON) LAMOUROUX (3-5 m) and the surface. The investigation was carried out between March and December 1980. Observations clearly showed that *C. pagurus* prefers to forage in shallow water at night, and crabs were observed on all nights of the survey from late May to December. Temperatures below 5° C in the upper water layers seem to prevent crabs moving to the shore. There were statistically significant differences in the number, sex and size distribution of the crabs throughout the investigation period. This was probably due to moulting and mating. Soft-shelled crabs were observed from early August until the end of the year. Tagging of crabs showed that males were stationary, whereas females migrated over longer distances.

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KEYWORDS: *Cancer pagurus*; rocky shores; diurnal movements; population composition; tagging.

INTRODUCTION

Cancer pagurus L., the only commercial brachyuran crab in Norway, makes diurnal vertical movements on rocky shores along the southern coasts of Norway during the summer and early autumn (NORDGAARD 1912; BJERKAN 1927; DANNEVIG & GUNDERSEN 1982). According to DANNEVIG & GUNDERSEN, the crabs move towards the shore at night to forage. They are relatively young and many have recently moulted. The soft-shelled crabs need calcium for hardening of their shell and obtain this by eating young specimens of the common mussel, *Mytilus edulis* L. (BJERKAN 1927; DANNEVIG & GUNDERSEN 1982).

This type of cyclical movement of *C. pagurus* has, as far as we know, not been reported from other parts of the crab's range, which extends from the Mediterranean to northern Norway (CHRISTIANSEN 1969).

The objective of this investigation was to study the occurrence, abundance, and population composition of *C. pagurus* during the crabs' diurnal vertical movements on rocky shores. The study was undertaken between March and December 1980 at a locality on the Norwegian Skagerrak coast. The number of crabs, sex and size distribution, and presence of soft-shelled crabs were recorded. Tagging was carried out to examine whether the crabs were stationary or migrated over longer distances. The results form part of a cand. real. thesis from 1984 by one of the authors (K.K.), and have earlier been published as an abstract (KARLSSON & CHRISTIANSEN 1991).

MATERIAL AND METHODS

Study site

The study site was an exposed rocky islet, Prestholmen, on the Norwegian Skagerrak coast between Grimstad and Lillesand in Aust-Agder county (58°16.23' N, 08°32.12' E, Fig. 1). The islet, which is situated about 200 m from the mainland, is approximately 290 m in perimeter and no more than 100 m across. There is a shallow basin, 7-14 m deep, between the western part of Prestholmen and the mainland. The area north of the islet is about 10 to 30 m deep. Off the southern and eastern part there are depths down to 90 m, 200-300 m from the islet. The study area was approximately 3700 m^2, and covered a zone around the islet bounded in depth by the upper limit of the oarweed, *Laminaria digitata* (HUDSON) LAMOUROUX, at 3-5 m, and the water line. The common mussel, *Mytilus edulis*, occupied a broad zone at most of the study site during the whole investigation period.

Survey methods

The study was carried out between March and December 1980. In January and February ice prevented fieldwork. Crabs were surveyed by skin-diving between approximately 2200 h and mid-

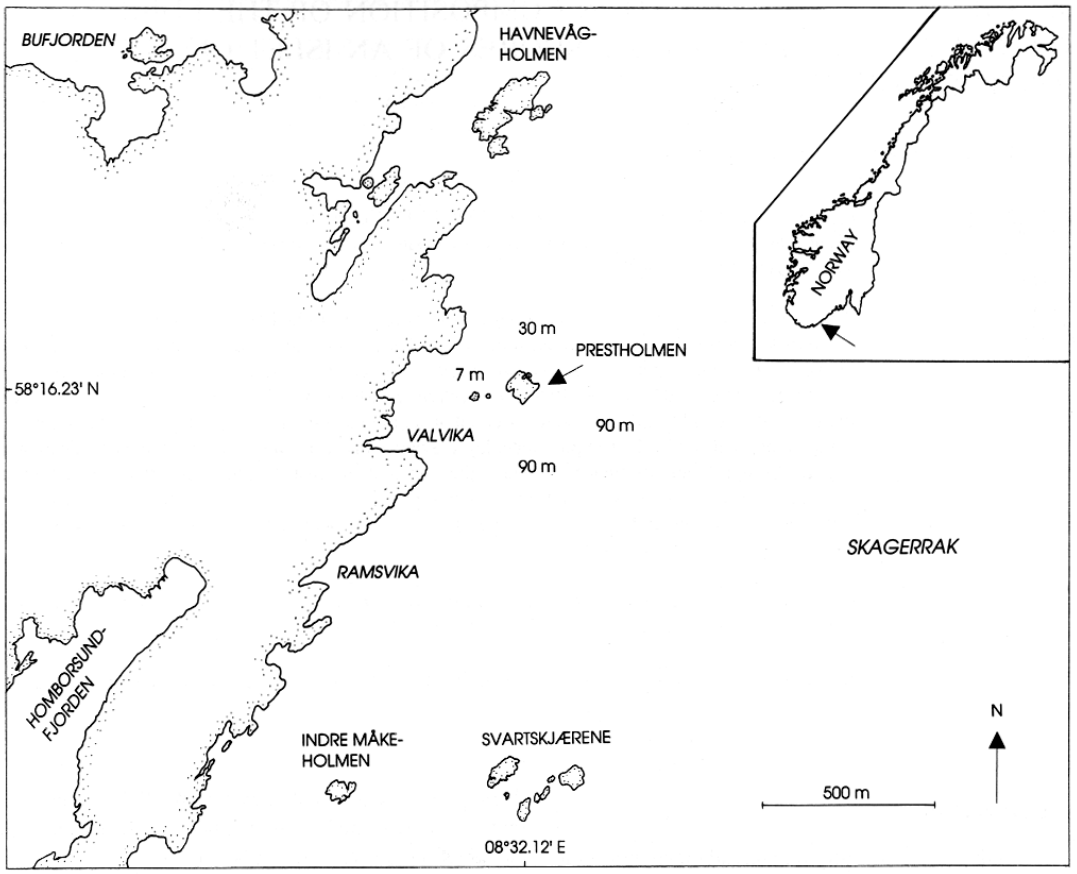

Fig. 1. Map showing the position of the islet Prestholmen on the Norwegian Skagerrak coast.

night (GMT+1), with one to six surveys every month, but nine in August and none in November. The number of crabs was counted on 26 of 33 nights, but on two nights only 1/3 of the study site was examined.

Surveys during daytime were carried out nine times between 29 June and 28 August. On 27-28 August, crabs were counted about every fourth hour during a 24-hour period.

The sex and the carapace width to the nearest cm of a random sample of individuals were determined. In order to display variation in the observed data, the data sampling has been divided into three ten-day periods for each month (i.e. 1. to 10., 11. to 20., and 21. to 30. (31.)).

The number of newly moulted (soft-shelled) crabs was registered. In this study a crab was considered as soft-shelled if the pterygostomian region yielded to thumb pressure.

Temperature and salinity were recorded SE of the islet by a T/S probe (Kent Electronic Instr. Ltd.) at 0, 1, 2, 3, and 5 m, and then every 5 m down to 30 m depth (Fig. 2). The monthly mean surface temperature for the years 1961-1990 at Torungen lighthouse about 20 km NE of Prestholmen together with measurements of the surface temperature at Prestholmen in 1980 are shown in Fig. 3.

The periodical tidal range in the area is 17 cm, whereas the maximum difference between high and low water during all surveys at Prestholmen was approximately 70 cm. The general light conditions at Prestholmen based on data from Mohn (1911) and Brahde (1970) are shown in Fig. 4.

Tagging technique

A random sample of crabs was tagged during the study period. The tag used was the 'FD-67c anchor tag' produced by Floy tag, Seattle, USA. A tagging pistol, 'Floy tag Mark II gun', equipped with a hollow needle, was used to make a hole in the pleural suture (line of separation of carapace in moulting) just above the base of the right walking legs. Then, one end of the tag consisting of a plastic pin attached to a plastic string was shot into the gill cavity. The tags contained a registration number and return address, together with a promise of reward. The advantage of a

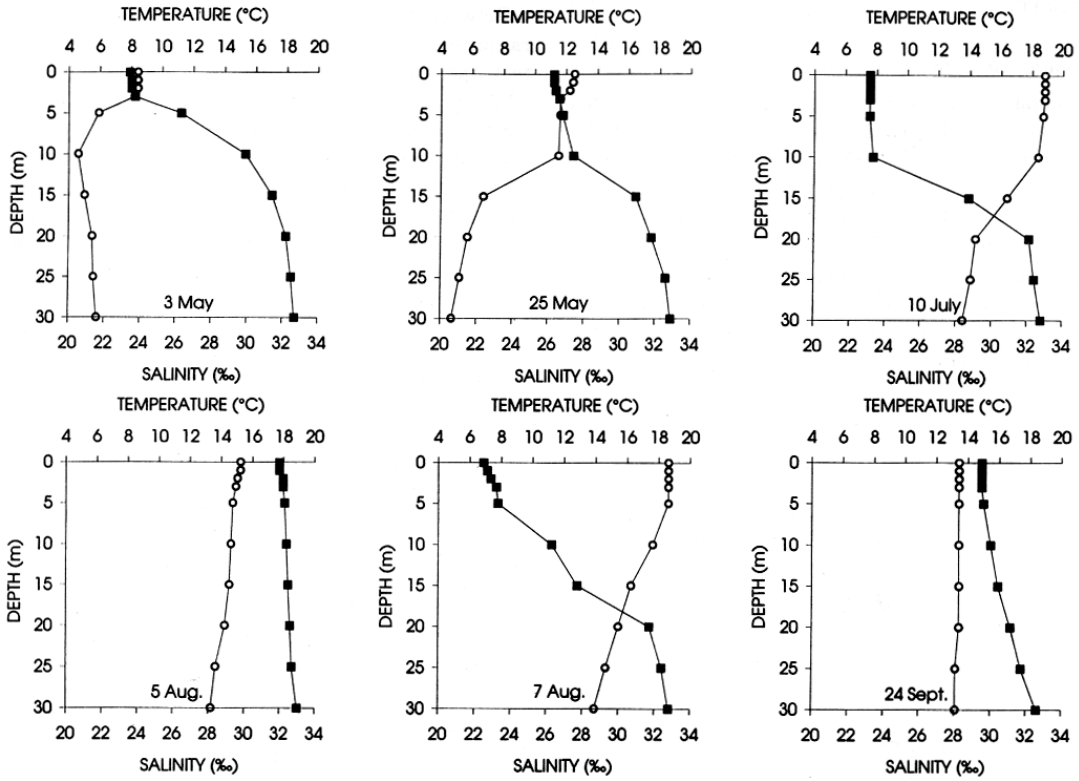

Fig. 2. Temperature and salinity at Prestholmen on six selected days between May and September 1980. Circles = temperature; squares = salinity.

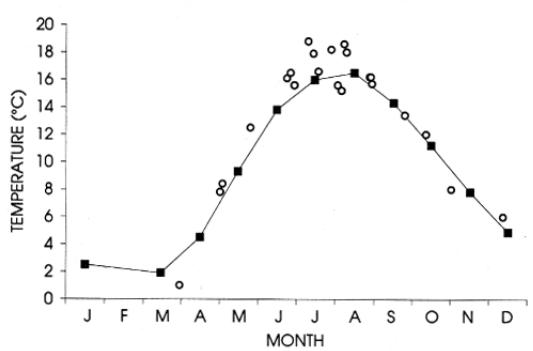

Fig. 3. Monthly mean surface temperature (except for February) at Torungen lighthouse (approx. 20 km NE of Prestholmen), 1961-1990 (data from The Norwegian Meteorological Institute). circles = surface temperatures measured at Prestholmen during fieldwork.

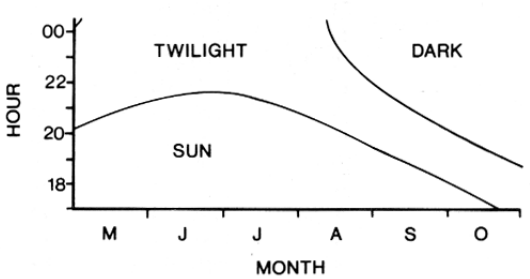

Fig 4. Light conditions at Prestholmen between 1700 h and midnight (GMT+1) from May to October. Twilight is the time from sunset until the sun is 16.5° below the horizon. Dark is the time when the sun is more than 16.5° below the horizon. (Data from Mohn 1911; Brahde 1970.)

suture tag is that it is not lost when the crabs moult (see e.g. Edwards 1979). For tagging, crabs of 15 cm width or more were preferred, because they were expected to tolerate tagging better. Measurements and tagging of crabs were carried out under water. After tagging, the crabs were released in the same place as they were captured.

RESULTS

Number of crabs at the study site

No crabs were observed during the first three nights, 30 March, 1 and 3 May. From the fourth survey on 24 May until the final survey 11 December, crabs were observed on all night surveys. The highest number counted was 237 on 22 June. In contrast, only one crab was observed during the night survey on 7 August (Table 1). No statistically significant relationship was documented between the number of crabs observed at night throughout the investigation period with respect to temperature and salinity at 0, 5, and 10 m depth (multivariate correlation analysis, SAS).

Between 29 June and 28 August, nine surveys were carried out during daytime. During these surveys, up to four crabs were observed at the study site (Table 2). On 27-28 August, surveys were made every fourth hour during a 24-hour period. The number of crabs was very low during daytime. In four surveys between sunrise and sunset only 2-3 crabs were observed, whereas 91 crabs were counted between two and three hours after sunset. Between 0200 h and 0300 h., the number had decreased to 30 crabs (Fig. 5).

On all night surveys, many crabs were occupied by eating the mussel, *Mytilus edulis*. Those crabs which did not forage were moving around.

Table 1. Number of *Cancer pagurus* and number of females and males observed at the study site at night between March and December 1980. Number of tagged and recaptured crabs are also shown. The numbers in parentheses indicate that crabs were only counted in 1/3 of the study site. - = crabs not counted.

Date	Observation time (GMT+1) Start	End	Number of crabs Observed* Total	♀♀	♂♂	Tagged	Recaptured
30 March	2140	2210	0	0	0	0	0
1 May	2210	2235	0	0	0	0	0
3	2245	2315	0	0	0	0	0
24	2220	2345	(90)	30	15	0	0
25	2230	0015	-	20	13	14	1
9 June	2225	0150	-	37	36	57	1
10	2200	2330	76	41	32	0	5
20	2215	0040	(88)	22	30	46	6
22	2200	0005	237	62	54	0	19
24	2305	0050	-	19	19	38	10
26	2200	2320	89	40	47	15	6
10 July	2200	2345	108	55	53	0	13
13	2230	0045	-	27	31	39	16
17	2200	2315	76	37	38	2	8
19	2200	0010	88	36	25	37	6
27	2200	2350	55	25	29	26	11
28	2200	2340	28	13	15	19	9
1 Aug**	2155	2350	47	26	33	38	16
4	2155	2325	53	30	16	21	9
5	2200	2335	52	28	22	14	13
6	2205	2350	32	23	7	8	7
7	2200	2240	1	0	1	2	0
9	2200	2300	12	4	7	8	2
27	2200	2230	91	-	-	0	2
28	2200	0015	114	91	23	36	1
29	2200	2335	55	40	14	15	7
24 Sept	2200	2340	149	74	27	19	3
25	2200	2320	137	76	32	28	2
26	2200	2325	99	51	19	0	0
11 Oct	2205	2335	152	88	50	0	7
30	2230	2250	22	-	-	0	0
31	2205	2255	24	11	13	0	2
11 Dec	2155	2250	28	7	21	0	0

*Where the total number is larger than the sum of females and males, the difference is due to individuals not sexed.
**In addition to the 47 crabs observed 1 August between 2155 - 2350 h, 6 ♀♀ and 6 ♂♂ found later the same night are included in the table.

Sex and size distribution

From the number of crabs observed, the sex of 1735 crabs was determined, selected from random samples taken at the study site between May and December (except November) (Tables 1, 3). The percentage of females and males observed in each of the three ten-day periods of each month was calculated based on the total number of crabs sexed during the study (i. e. 1735). The percentage of each sex was nearly similar in June and July and at one survey in late October. In May, August, September, and early October the number of females was significantly higher than the number of males (χ^2distribution, $p < 0.05$). In December 75 % of the 28 crabs examined were males.

Carapace width of random samples of crabs (608 ♀♀ and 454 ♂♂) was measured between 9 June and 31 October. The width varied from 5 to 18 cm for females, and from 5 to 19 cm for males (Fig. 6). The mean size of females (12.9 ± 0.2 cm) was significantly larger than the mean size of males (12.1 ± 0.2 cm) (t-test, $p < 0.05$).

Fig. 7 shows mean size of the crabs measured within ten-day periods each month between June and October. The size of both females and males decreased to a minimum in late July and early August respectively, increasing again during the next ten day period. The mean size of females in late July (11.5 cm) was significantly smaller than in the two first ten-days periods of June and the period from last part of August onwards (t-test, $p < 0.05$). For males, the mean size in late July (11.2 cm) and early August (11.3 cm) was significantly smaller than in early June and September, and part of October (t-test, $p < 0.05$). This indicates a reduction of the larger, sexually mature individuals in July and early August followed by an increase in the autumn.

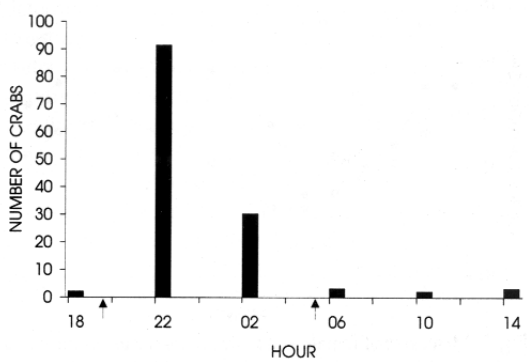

Fig. 5. Number of *Cancer pagurus* counted every fourth hour over a 24 hour period, 27-28 August 1980. The arrows indicate sunset and sunrise.

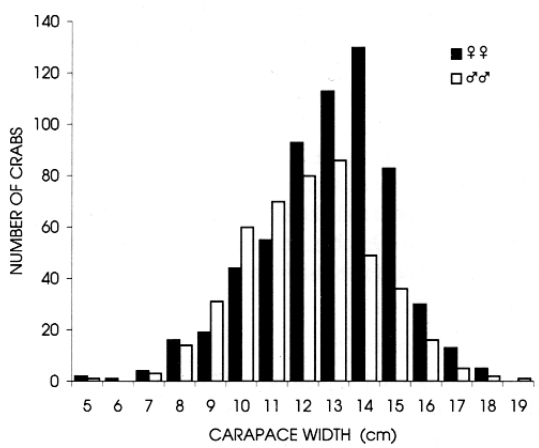

Fig. 6. Size distribution of female and male *Cancer pagurus* in random samples of crabs between 9 June and 31 October 1980.

Table 2. Number of *Cancer pagurus* observed in nine different surveys at the study site between sunrise and sunset from June to August 1980. - = sex not determined.

Date	Observation time (GMT+1) Start	End	Number of crabs observed Total	♀♀	♂♂
29 June	1020	1110	0	0	0
	1415	1510	0	0	0
13 July	1310	1435	3	0	3
18 July	1755	1850	4	2	2
6 August	1355	1415	1	1	0
27 August	1805	1850	2	0	2
28 August	0615	0650	3	-	-
	1000	1030	2	-	-
	1400	1445	3	-	-

Table 3. Sex distribution (number and percent) of *Cancer pagurus* observed at the study site at night between May and December 1980. Numbers in parentheses indicate number of surveys each month. (See also Table 1).

Month		♀♀ No.	♀♀ %	♂♂ No.	♂♂ %	Total No.
May	(4)	50	64.1	28	35.9	78
June	(6)	221	50.3	218	49.7	439
July	(6)	193	50.3	191	49.7	384
Aug	(8)	242	66.3	123	33.7	365
Sept	(3)	201	72.0	78	28.0	279
Oct	(2)	99	61.1	63	38.9	162
Dec	(1)	7	25.0	21	75.0	28
Total		1013		722		1735

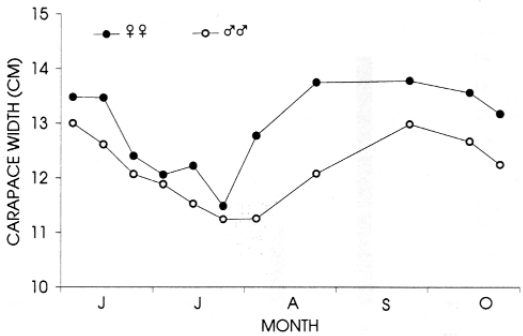

Fig. 7. Mean size of female and male *Cancer pagurus* measured within ten day periods between 9 June and 31 October 1980.

Soft-shelled crabs

Soft-shelled crabs were found from the first part of August onwards. Of the 138 crabs observed between 4 and 7 August, one soft-shelled female (13 cm) was found on 4 August, none were seen on 5, 6, and 7 August. One female (12 cm) and one male (10 cm) were found on 9 August. In late August the percentage of soft-shelled females (17.6 %) was higher than for males (5.4 %). The percentage of both soft-shelled females and males increased from August to October. In December the percentage of soft-shelled crabs was still high (Table 4).

Recapture of crabs

Between May and September 482 crabs were tagged at the study site at night (Table 1). In addition, 60 crabs were tagged slightly below the study site during the day. Of the 542 tagged crabs (304 ♀♀ and 238 ♂♂), 184 individuals (33.9 %) were recaptured. The percentage of recaptured individuals around the islet was much higher for males than for females, whereas the opposite was true for crabs found more than 0.5 km from the islet.

Of the 184 recaptured crabs, 136 (73.9 %, 56 ♀♀ and 80 ♂♂) were observed from one to seven times at the islet or less than 0.5 km from the study site (Table 5).

Forty-eight crabs (26.1 %, 39 ♀♀ and 9 ♂♂) were found between 0.5-28 km from the islet. However, none of the males were recaptured further away than 3.5 km from the islet (Table 6). The longest time between release and recapture at Prestholmen was about two years. The last recapture of a long-distance (20 km) migrant crab was about 14 months after it was tagged.

The crabs which migrated along the coast were found both NE and SW of Prestholmen (Table 6). One female was found 28 km in direct line NE of the islet about 11 months after it was tagged. Three other females which had migrated 19.3 km, 20.0 km and 21.4 km NE, were recaptured after 45 d, 50 d, and 51 d, respectively. One female was recaptured 17 km NE of the islet 35 d after tagging, and must have moved at least 500 m per day.

The size of the 16 females which had moved between 10-28 km NE varied from 12 to 17 cm (mean 14.3 cm), and the size of the seven females which had moved the same distance SW was between 11 and 15 cm (mean 12.4 cm). One of the recaptured females which was found a year after tagging 26.2 km SW of the islet, had moulted and its carapace width had increased from 11 to 14.5 cm.

Table 5. *Cancer pagurus*. Number of tagged crabs recaptured at the study site or less than 0.5 km from the islet in 1980 (1 ♂ in 1982).

Times recaptured	Number recapt. ♀♀	♂♂
1	56	80
2	13	30
3	0	4
4	1	4
5	1	0

Table 4. *Cancer pagurus*. Number and percent of soft-shelled females and males of the total number of the two sexes observed at the study site between late August and December 1980.

Date	♀♀ Total No.	♀♀ Soft-shelled No.	♀♀ Soft-shelled %	♂♂ Total No.	♂♂ Soft-shelled No.	♂♂ Soft-shelled %
28, 29 Aug	131	23	17.6	37	2	5.4
24, 25 Sept	150	40	26.7	59	16	27.2
11 Oct	88	27	30.7	50	22	44.0
31 Oct	11	3	27.3	13	3	23.1
11 Dec	7	4	57.1	21	10	47.6

Table 6. Number of recaptured *Cancer pagurus* and direction and distance in direct line from Prestholmen. (1♀ and 3 ♂♂ with unknown direction are not included.)

	NE		SW		
Distance	♀♀	♂♂	♀♀	♂♂	Total
0.5-5 km	4	3	3	3	13
5-10 km	3	0	5	0	8
10-15 km	2	0	4	0	6
15-20 km	5	0	0	0	5
20-25 km	8	0	2	0	10
25-28 km	1	0	1	0	2
Total	23	3	15	3	44

DISCUSSION

The diurnal vertical movements of *Cancer pagurus* to the shore depend on several factors. Since it is a foraging activity (Dannevig & Gundersen 1982), suitable food has to be present. This was the case at the study site throughout the investigation period. Catching of crabs on summer nights by other people may have influenced the results. However, people in the neighbourhood were asked not to catch crabs at Prestholmen during the investigation period, and thus the number of specimens caught around the islet was probably low.

C. pagurus clearly prefers to forage in shallow water at night as shown by the number of crabs observed during day and night (Fig. 5; Table 2). However, different light conditions at night throughout the year did not seem to influence on the number of crabs (Fig. 4; Table 1). Thus, the nature of the relationship between foraging habits, light conditions, and other factors such as salinity and temperature warrants further studies.

Temperature is an important factor for the feeding of crabs. K.R. Gundersen studied artificial feeding of *C. pagurus* (unpublished compendium, Institute of Marine Research, Bergen 1973). He found that crabs did not eat at all between 0° and 5° C, and that the appetite increased with increasing temperature to a maximum between 16° and 20° C. Although no statistically significant difference was found between number of crabs at night with respect to temperatures and salinities, temperature seemed to be a regulating factor for the crabs' movement to shallow water at Prestholmen in the spring. On 30 March, the surface temperature was 1° C (Fig. 3) and no crabs were observed. In early May, the surface temperature was about 8° C, but crabs were still not observed by the shore. However, the temperature at 10 m depth was below 5° C (Fig. 2), which might have prevented crabs moving into shallower water. On 25 May, when as many as 90 crabs were counted in 1/3 of the study site the night before, the surface temperature was 12.5° C, and at 10 and 15 m the temperatures were 11.5° and 6.7° C, respectively (Fig. 2).

Hallbäck (1972, 1993) who studied the behaviour of *C. pagurus* on the west coast of Sweden over a number of years, found that crabs did not tolerate temperatures above 20° C and salinities below 2 %. During the present investigation rapid changes in temperature and salinity of the surface waters were observed on a few occasions. This was due to shifting wind directions. Between 5 and 7 August when the wind shifted from SW to NE, the salinity of the surface water dropped from 32.0 ‰ to 22.5 ‰. At the same time the temperature of the surface water increased from 15.2° to 18.6° C (Fig. 2). On the same dates, the number of crabs observed, decreased from 52 to 1. The water was calm and there was barely a swell on 7 August. Whether the decrease was due to low salinity is difficult to determine, since as many as 108 crabs were observed at the study site on 10 July when the salinity of the surface water was only 23.1 ‰ (Fig. 2). The same day, the temperature of the surface water was 18.8° C (Fig. 2), which was the highest temperature measured at Prestholmen during the investigation period (Fig. 3).

The number of crabs at the study site was high in June and the first part of July, but decreased in late July and early August. In September and October the number was again high (Table 1). The low number in the first part of August is probably due to moulting and mating behaviour. Bennett & Brown (1983) stated that specimens of *C. pagurus* which are about to moult or have very recently moulted have been observed hiding in shelters.

According to Edwards (1966) and Brown & Bennett (1980), the majority of females moult before males. This difference was believed to be related to the fact that mating only occurs between soft-shelled (recently moulted) females and hard-shelled males. The present results also indicate that the peak period of moulting occurs earlier in females than males (Table 4), and that female moulting probably started in July. Hallbäck (1993) stated that moulting for sexually mature females on the west coast of Sweden occurred in September at the same time as mating, whereas the males moulted about a month later.

According to Edwards (1979), most male crabs over 110 mm carapace width are sexually mature, and most females are mature when they reach a size of 127 mm shell width. It is not clear whether the crabs on the south coast of Norway become mature at the same size as the crabs in British waters. However, the narrow average carapace width of crabs of both sexes observed in July/early August (Fig.7) indicates, that for young crabs which moult more frequently, moulting is not as seasonally dependent as for older crabs.

Ovigerous females were never seen at the study site. This is as expected, since berried *C. pagurus* are believed to spend their six- to nine-month egg-carrying period protecting the egg mass and not feeding (Bennett & Brown 1983).

According to Edwards (1979), the first tagging experiments aimed at obtaining information on the movements of *C. pagurus* were made in 1897-1899 by Williamson (1900) off Dunbar, Scotland. Tagging of *C. pagurus* has been undertaken on the east coast of England since 1903 (Edwards 1979), in the English Channel (Bennett & Brown 1983), on the Brittany shore (Le Foll 1986), and in the Western Channel, the Iroise Sea, and the Bay of Biscay (Latrouite & Le Foll 1989). Gundersen (1979) tagged crabs on the west coast of Norway between 1962 and 1968, and Hallbäck (1972, 1993) carried out tagging of crabs on the Swedish west coast between 1968 and 1973.

The percentage of recaptured crabs (33.9 %) in the present study was nearly similar to the results of Edwards (1965) (36 %) and Hallbäck (1993) (34 %). Gundersen

(1979) released tagged crabs at three different localities near Bergen between 1962 and 1968. Recaptures varied from 20.7 to 81.1 % in the three areas.

Several authors have shown that the movement of male crabs is limited and that female crabs migrate both rapidly and over long distances (e.g. EDWARDS 1979; BROWN & BENNETT 1980). BROWN & BENNETT observed a westward migration of female *C. pagurus* in the English Channel, and pointed out that this could be related to larval distribution. Since the residual current in the Channel is eastwards, the planktonic larval stages of *C. pagurus* hatched off south Devon would be carried east and replenish the crab stocks in the eastern half of the Channel.

Similarly, HALLBÄCK (1993) found that the males were rather stationary, and that females migrated both rapidly and over long distances. Less than 2 % of observed males had moved more than 10 km from the tagging place. Four years and 11 months after tagging, a female crab was caught 225 km away. HALLBÄCK (1993) found that on the Swedish west coast most females moved in the same direction, against the current. He also mentioned that the extensive female movement could be explained by the theory that migration occurs against the current to compensate for larval drift.

LE FOLL (1986) obtained a recapture rate of 8 % along the South Brittany coast, and found that males were relatively sedentary, while the females migrated more. However, she did not find that female migration took place in a certain preferential direction.

The crabs tagged at Prestholmen show the same pattern of movement as found earlier by several authors, with relatively stationary males and migrating females. The crabs moved both NE and SW along the coast. The main current along the southeastern coast of Norway is southwesterly. Unfortunately, the number of recaptures in this study was too low to demonstrate whether or not there is a relationship between female migration in crabs and current direction on the south coast of Norway.

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