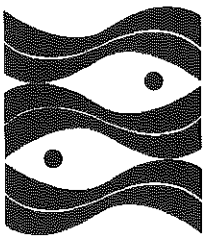
SERIES B (Marine) No.43 1995



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Waleed M. A. Bakir and Brenda Healy

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Roinn na Mara

(Department of the Marine)

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Waleed M. A. Bakir and Brenda Healy

Department of Zoology, University College, Dublin

ABSTRACT

An unfished population of *Necora puber,* in a coastal area just south of Dublin, was sampled monthly between August 1986 and November 1987 using baited creels. The reproductive cycle was analysed using gonad stages, the incidence and size distribution of ovigerous females and developmental stages of the egg masses. Both sexes started to breed at a carapace width of about 50 mm when they were about one year old. Seven ovarian and six testicular stages were recognised, both macro- and microscopically. The ovary underwent continuous cyclical changes and there was no distinct winter resting period. All ovigerous females had developing or ripe ovaries and they may thus produce more than one brood in a season. The main breeding season started in February with the greatest number of ovigerous females found in March-June and a peak in May. Less than 10% of females were ovigerous from August to January. The main periods of larval release were April, June and August. Spawning and recovering males were present throughout the year. Differences between the observed reproductive cycle and those studied in Britain and Spain are discussed.

INTRODUCTION

The portunid crab *Necora puber* (L.) (previously *Portunus, Macropipus,* and *Liocarcinus*) has a wide distribution on rocky coasts of the eastern Atlantic, extending from 61°N in Norway southwards along the coasts of France and Spain to north Africa at 23°N, and in the eastern Mediterranean (Christiansen 1969). It is common all around Ireland and has recently become a commercial species. Data on the biology of the species in Scotland (Kinnear and Mason 1987), south Wales (Choy 1986a, 1986b, 1988), Plymouth (Norman 1989, Norman and Jones 1990, 1992, 1993) and Galicia (González-Gurriarán 1978, 1981, 1985a 1985b, Valdés *et al.* 1991), together with isolated reports from a number of localities on the incidence of berried females and planktonic stages (Jackson 1913, 1914, Lebour 1928, O'Céidigh 1955, Ingle 1980, Martin 1980), indicate that there is much variation in the timing of reproductive events between localities. Thus, information on growth, reproduction and population dynamics, which will be needed for the formulation of stock management policies in Ireland, cannot be inferred from research carried out elsewhere.

The reproductive cycle of a breeding population can be followed by studying internal changes in the gonads, the occurrence of ovigerous females, embryonic development, and larval stages. Gonads undergo seasonal cycles of ripening, gamete release and recovery, usually with a resting phase, which can be recognised by both macroscopic changes in gonad size, shape and colour and microscopic changes in cell sizes and staining and, in the case of ovaries, the accumulation of yolk. In commercial species, the changes correspond to seasonal variations in meat yield and quality as internal resources are shifted between somatic and reproductive tissues. It is customary, particularly when studying fish and crustaceans, to divide the cycles into a number of stages which constitute a gonadosomatic index (GSI). The number of stages recognised varies, the most usual for Crustacea being four or five (Broekhuysen 1936, Hard 1942, Estampador 1947, Meredith 1952, Laulier and Demeusy 1974). However, more detailed study of the tissues, with recognition of more stages, allows distinction between ripening and recovering gonads which is important when dealing with species which produce more than one brood in a season. In previous studies of *N. puber,* only four or five stages were recognised for both ovary and testis ((González-Gurriarán 1985a, Choy 1986a, 1988, Kinnear and Mason 1987, Norman 1989, Norman and Jones 1993). Detailed, illustrated accounts of gonad cycles in other portunids, namely *Callinectes sapidus,* the Americal Blue Crab, (Hard 1942, Cronin 1947), four species of *Scylla* (Estampador 1949) and *Carcinus maenas* (Laulier and Demeusy 1974), provided a useful basis on which we could construct more elaborate indices for both sexes in this study.

Females mate in a soft-shell condition following a moult but copulating males are always hard-shelled (Hartnoll 1968). A peak in the occurrence of soft-shelled females thus indicates increased breeding activity. Following spawning, the eggs are carried on the pleopods of the female until hatching at the zoea stage, as in most decapods. The number of eggs produced (fecundity) varies between species and depends on the size of the female, while incubation time is dependent on temperature. Embryonic development can be followed by observing changes in size, colour and internal appearance of the eggs, while egg remains on the pleopods indicate recent hatching. Four stages of embryonic development are commonly recognised in crustacean studies but as many as 11 or 12 have been distinguished by some authors (e.g. Meredith 1952). Hatching periods may also be deduced from the occurrence of early zoeae in plankton hauls but these were not available for our study. Following release of the larvae, the female may or may not moult, depending on whether she produces a second brood in the season. Males normally moult after mating.

In this study, reproductive events in the annual cycle of *N. puber* have been followed using (1) changes in both macroscopic appearance and microscopic stucture of ovary and testis, (2) the incidence of ovigerous females and (3) the developmental stages of eggs carried by females. Variations in the timing of the breeding season according to age are shown by the size frequencies of ovigerous females. Some observations on moulting and fecundity are also included.

MATERIALS AND METHODS

Sampling. Crabs were collected from various points around Dalkey Island (53°16'N, 6°5'W) between July 1986 and November 1987 and in April and July 1988. There was no commercial fishery for *N. puber* in the area at the time of sampling but a few small boats were fishing lobsters and *Cancer pagurus*. Single samples were also obtained from fished populations at Bantry, Co Cork (July 1986, 204 crabs), Rush, Co Dublin (January 1987, 474 crabs) and Rosslare, Co Wexford (April 1988, 161 crabs). The salinity in the sampling area is approximately 34‰ and the spring tidal range is 3.4 m. There are fairly strong currents in places, especially on the west side of the Island. The substratum in the areas sampled is rocky, with laminarians and red algae.

Monthly samples of about 400 crabs, where possible, were obtained from crab pots (creels) with entry holes 9 cm in diameter and a covering net of 3 cm mesh. Pots were set in 8-pot strings, baited with fish offal, and hauled every one to three days until a sufficient number of crabs was obtained. Sampling depths were 6.5-22m.

External measurements. The number of berried females was noted and all specimens were weighed (live weight to the nearest 1 g) and measured (carapace width, CW, to the nearest 1 mm) as part of a wider programme to investigate growth and population dynamics (Bakir 1990). There was no evidence of parasites or disease on crabs from this or any other locality from which samples were obtained.

Gonad studies. Crabs of both sexes and a range of sizes were taken from monthly samples as available and the carapace removed for examination of the gonads *in situ.* More females than males were examined because both ovigerous and non-ovigerous females were included. The colour of the gonads was noted and the proportion of the body cavity they occupied measured according to their length. A number of male and female gonads, of each of the stages recognised, was kept for histological studies. Portions were fixed in Bouin's fluid and sections stained in haemotoxylin and eosin and mounted in DePeX. A gonad index based on both macroscopic arrearance (size and colour) and microscopic structure (presence, size and appearance of oocytes or spermatocytes, intercellular spaces) was devised for both males and females.

Fecundity. The number of eggs carried by females was estimated by drying an early stage egg mass to constant weight and counting the eggs in a small sample of about 0.05 g (Kinnear and Mason 1987). Egg masses from several age groups were analysed where possible.

Embryonic development. A random sample of up to 50 berried females, as available, was taken from monthly samples and four stages of egg development noted as follows: Stage 1 - before the onset of cleavage, colour orange; Stage 2 - early development, colour brown; Stage 3 - presence of eye pigment and chromatophores, colour dark brown or purple; Stage 4 - presence of head and thoracic appendages, colour grey-black.

RESULTS

Seasonal changes in the catch

Catch sizes varied between 113 and 500, with less than 150 being available for analysis in August 1986 and December 1987. Mean catch per unit effort (CUE = ind.100 pots. 24 hours) was 155, falling below 140 in November-May and reaching over 200 in October 1986 and July-August 2987. In general, catches were highest in summer - early autumn and low in late autumn - early spring. The lower catches are partly due to rough weather but may also be attributed to lower activity at low water temperatures.

Males were predominant in all samples, females never constituting more than 45% of the catch. The highest proportion of females occurred in January-February 1989 and November 1987. The proportion of females was less than 20% in August-September 1986, April-May 1987 and August 1987, and December 1987-January 1988. Few females were obtained in September-November 1987 when sample sizes were small due to rough weather.

Size and growth

The size range of specimens was 45-98 mm CW for males and 48-89 mm CW for females. The size ranges in fished populations were similar i.e. 51-88 mm CW (both sexes) at Bantry and 51-99 mm CW at Rush. The sample from Rosslare was not representative of the total catch.

The size at sexual maturity for both sexes was about 50 mm CW, reached when individuals were about one year old. Females initially grew faster than males but after the first three years female growth was slower and males were eventually larger. The life span is estimated to be about five years for both sexes. Further details of growth and population dynamics are given in Bakir (1990).

Ovarian cycle.

Seven ovarian stages were recognised according to both gross external appearance and microscopic stages. Characters used to distinguish stages from external appearance of the ovaries *in situ* were shape, size and colour (Table 1). The changes were mainly brought about by progressive accumulation of yolk in the oocytes.

Using light microscopy, the seven stages were distinguished histologically as follows:
Stage 1 (immature, virgin). Oogonia, with or without primary oocytes. Oogonia basophilic, spherical or oval, usually in small groups, mean diameter 71 µm ± 0.02 SD, containing large, prominent nuclei, 29 ± 3 µm, with several large, scattered, strongly basophilic nucleoli; cytoplasm scanty, faintly basophilic, without vacuoles.
Stage 2 (developing). Only oocytes present. Secondary oocytes surrounded by a single layer of flattened, follicle cells constituting the theca. Oocytes spherical or oval, 75 ± 26 µm, with large, spherical or oval nucleus, 30 ± 1 µm, containing dispersed, granular chromatin; nucleoli scattered, strongly basophilic; cytoplasm strongly basophilic with some yolk vesicles.
Stage 3 (developed). Primary and secondary oocytes intermediate to large, 113 ± 55 µm, with large, spherical nuclei, 49 ± 13 µm, containing dispersed chromatin and nucleoli arranged peripherally; cytoplasm basophilic with numerous yolk vesicles.
Stage 4 (ripe). Oocytes spherical or oval, of maximum size, 207 ± 79 µm, most without visible nucleus which is masked by numerous acidophilic yolk granules. Some oogonia and primary oocytes may be present.
Stage 5 (spawning). Secondary oocytes, 95 ± 0.03 µm, and some eggs present. Cytoplasm of eggs homogeneous, without distinct yolk globules. Many follicles ruptured leaving spaces in the tissue.
Stage 6 (spent). Oocytes 88 ± 26 µm with homogeneous cytoplasm, some ripe eggs present. Many spaces representing empty follicles.
Stage 7 (recovering). Oocytes only present, 96 ± 47 µm, nuclei 31 ± 16 µm. Empty follicles collapsed inward, zona radiata broken in many places.

Oocytes tended to be deformed in sections of Stages 5 and 6 due to histological processing. The germinal zone appeared first in the centre and periphery of the ovary.

Seasonal occurrence of ovarian stages.

The seasonal distribution of the seven ovarian stages, based on a total of 405 female crabs (Fig. 1), shows that there are continuous cyclical changes in the ovary and no distinct resting period was apparent. There was a predominance of Stages 2 and 3, i.e. developing and developed, from February to July and of Stages 4 to 6, i.e. ripe, spawning and spent, in autumn and early winter. The absence of clear seasonal peaks for spawning and spent stages suggests that spawning activity is poorly synchronised in the population. Spawning, spent and recovering stages were poorly represented in all catches, possibly a consequence of selective sampling (see Discussion), and no reliable conclusions can be drawn from the recorded occurrence of these stages. The incidence of developing and developed stages suggests two cycles per year, one in which the ovary develops from January to March, and a second in which the ovary develops in May and June. This implies a main spawning period starting in spring and a second, involving fewer females, in summer. The poor representation of the immature stage may be explained by the fact that few crabs under 50 mm were obtained for examination.

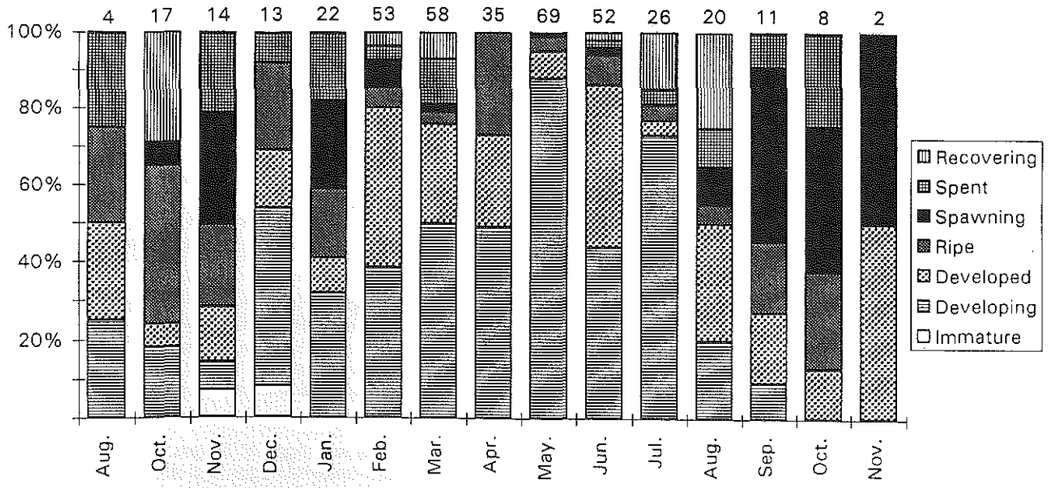

Fig. 1. Seasonal changes in the proportion of seven ovarian stages in crabs collected between October 1986 and November 1987. Sample sizes above the bars.

Size and occurrence of berried females.

Berried females were present in nearly all months, including periods when the water temperature fell to 5-6˚C (Fig. 2). In 1986-1987, less than 10% of females were ovigerous from August 1986 to January 1987 while the greatest number were found from March to June with a peak in May when 73% were ovigerous, the proportion then decreased to 62% in June and fell to 23-24% in July-August. A greater proportion of females remained ovigerous in August than in the corresponding period in 1986. There was no second peak in summer corresponding to a second spawning period as indicated by spawning stages of the gonad.

An examination of the size frequency of berried females (Fig. 3) shows that early spawning individuals are mainly in the older size groups with a modal size in April of 69 mm. These are estimated to be 2 years old or more (Bakir 1990). Younger crabs mostly did not start to breed until May when the modal size of berried females was 63 mm, estimated to belong to the 1+ class.

Fecundity

The mean number of eggs/female was 151,423 for 50-60 mm CW (n=21) and 236,492 for 70-80 mm CW (n=45). The largest brood measured was 743,334 eggs for a 72 mm crab and the smallest was 6215 for a 61 mm crab which may have lost some eggs.

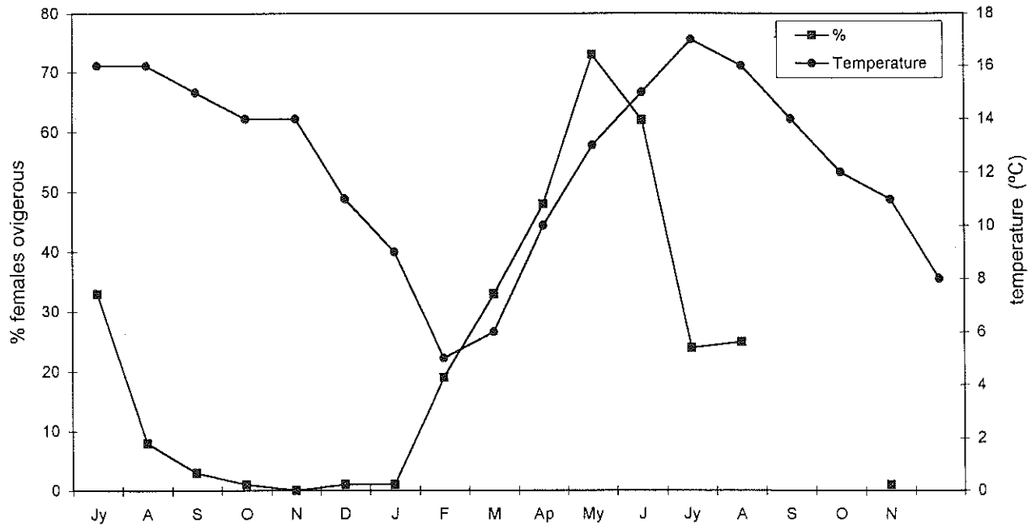

Fig. 2. Ovigerous females as a percentage of the female catch in relation to temperature.

Embryonic development.

The mean diameter of the eggs was 375 µm ± 23 SD for those newly spawned, before the onset of cleavage, and 575 ± 10 µm when ready to hatch. Eggs developed synchronously within the mass in the early stages but later development was less well synchronised.

The number and proportion of females with eggs at different stages of development was used to indicate periods of spawning and larval release (Fig. 4). The highest proportion of females with egg masses at Stages 1 or 2, suggesting recent spawning, occurred in February-March, May and July, with a peak in May. The three peaks are poorly defined, however. Relatively few egg masses at Stage 1 were found although in aquaria cleavage could be delayed for up to two months (Bakir 1990). A possible explanation is that spawning and recently spawned females were not entering baited pots.

The main periods of larval release, indicated by a high proportion of females with eggs at Stages 3 or 4, were April, June and August, suggesting a developmental period of 2-3 months for early-spawned eggs and about one month for eggs spawned in May or later. If this is the case, females which spawn early in the year would have ample time to spawn and hatch a second brood. However, few Stage 4 egg masses were found before June so some early spawners may fail to carry eggs to the hatching stage. Larger samples taken over several years would be needed to verify these indications.

Ovary development in berried females.

All ovigerous females with eggs at an early stage of development had developing or developed ovaries and some with eggs close to hatching had ripe ovaries. All females, therefore, may be capable of producing a second brood in the season and early spawners may even hatch a third brood. Size frequency data (Fig. 3) suggest that females which spawned in February-March could have produced second broods in May-June while the 1+ cohort, which mainly spawned later in April-May, could have produced second broods in June-July.

Testicular cycle.

Six developmental stages were recognised according to both external appearance of the gonad and microscopic changes. Changes in colour, shape and size were used to distinguish stages *in situ* (Table 2).

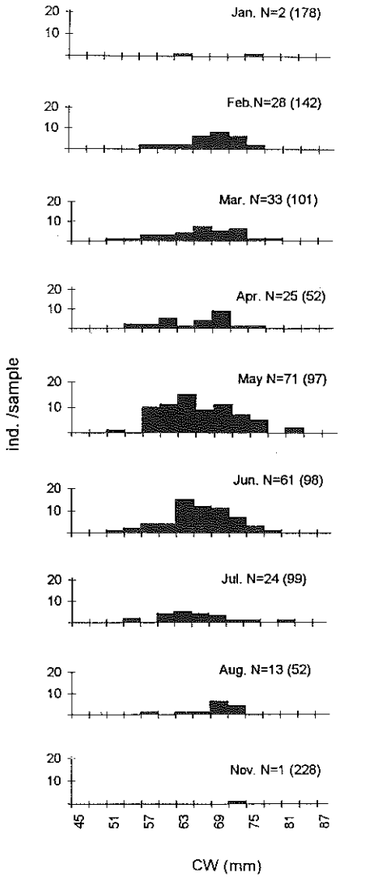

Fig. 3. Number of ovigerous females in 3 mm carapace width size classes in given months. Figures in brackets are total females.

Histological studies distinguished changes in the seminiferous tubules ending in rupture to release the spermatozoa, followed by recovery.
Stage 1 (immature). Spermatogonia spherical or oval, in small groups, at different stages of development.
Stage 2. (developing). Primary and secondary spermatocytes and spermatids packing the tubules, their nuclei staining more intensely than those of the spermatogonia. A few spermatozoa present, recognised by their deep blue colour.
Stage 3. (ripe). Spermatozoa abundant in the lumen of the tubule.
Stage 4 (spawning). Walls of the tubules become stretched and finally break, releasing spermatozoa and leaving spaces.
Stage 5 (spent). Tubules ruptured, more spermatozoa released leaving many spaces in the tissue.
Stage 6 (recovering). Tubules with spermatogonia in different stages. The presence of spermatids and undischarged spermatozoa distinguish recovering from developing testes.

Season occurrence of testicular stages.

Sample sizes were smaller than for females with only 187 males analysed and the data were insufficient to deduce spawning peaks with any confidence. Stages 4 and 5, i.e. spawning and spent, were present in all months (Fig. 5) indicating that some males mate, or are capable of mating, throughout the year. However, spermatogenesis is not continuous but cyclic, i.e. nearly all sperm are discharged into the vasa deferentia with rupture of the seminiferous tubules and the germinal tissue must then redevelop to produce another generation of spermatozoa. There are indications in Fig. 5 of greater spawning activity in the periods November 1986-February 1987 and June-October 1987, while the recovery stage, which could correspond to a moulting phase, was most frequent in October 1986 and February-April 1987.

It was thought that some further indications of moulting periods might be apparent from the incidence of epifauna on the shell. Barnacles were present on 10-40% of both males and females in September 1986-February 1987 and July-September 1987 but occurred on less than 5% of both sexes in March-May 1987. This suggests a main moulting period in spring but this cannot be confirmed as there is no available information on the settlement period of the barnacles concerned.

Observations on moulting.

Soft-shell crabs were rare in the samples. Soft males were taken in April (3), May (1), June (5) and July (1), and soft females in May (3), June (1), July (1) and August (1), suggesting a possible later moulting period for females.

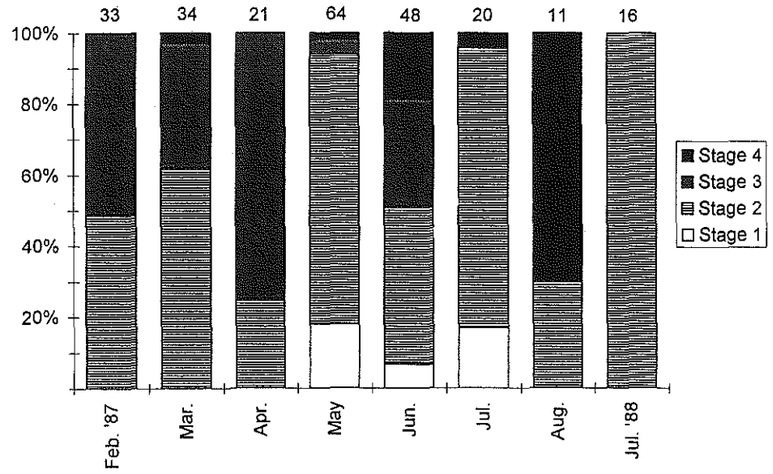

Fig. 4. Seasonal changes in the proportion of four embryonic stages carried by ovigerous females. Sample sizes above the bars.

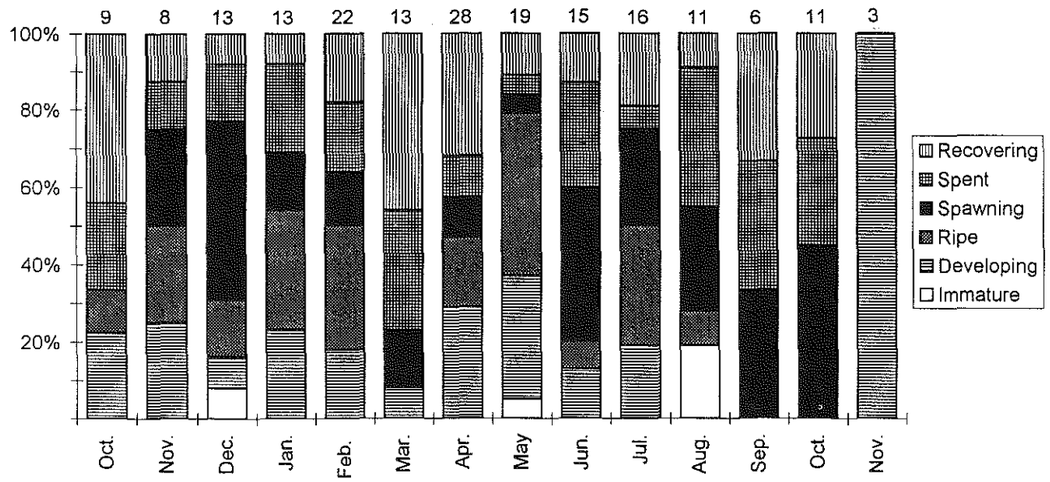

Fig. 5. Seasonal changes in the proportion of six testicular stages in crabs collected between October 1986 and November 1987. Sample sizes above the bars.

Reproductive cycle.

There is no clearly defined annual cycle for either sex. Gonads undergo cycles of ripening, gamete release and recovery, and there may be resting phases, but the cycles are poorly synchronised in the population, making it difficult to delimit peak seasons of mating, spawning, larval release or moulting. Peaks of moulting, and of mating which occurs at the female moult, could not be distinguished because few moulting individuals were obtained. Results from the three methods used to trace the female cycle, i.e. gonad index, occurrence of berried females and embryological staging, taken together, indicate a main season of spawning lasting from January-February to August, but the peaks in spawning, determined by the different methods, do not always coincide. Females carrying late stage embryos were present throughout the period February to August in 1987 and no spawning peaks could be detected using this method. Some of the difficulty results from some small samples, the proportion of females in the catch sometimes falling below 20%, but it is believed to be the overlapping cycles of the different year classes, which themselves overlap, which is mainly resonsible for the absence of distinct peaks of spawning and larval release. In the male, peaks in ripening and spawning stages in the testis were also unclear and data were insufficient to allow further analysis e.g. by the separation of year classes.

DISCUSSION

The use of baited pots produced large samples which were useful for age and growth analyses and were representative of commercial catches. However, the method introduces a bias towards individuals which are feeding at the time of sampling and this must be borne in mind when interpreting data on reproduction, especially when comparing the Dalkey population with those studied elsewhere where other methods were used, e.g. at Plymouth where the population was intertidal (Norman 1989, Norman and Jones 1993), and in S. Wales (Choy 1986a, 1988) and Galicia (González-Gurriarán 1985a) where samples were obtained by trawling. Moulting crabs, for example, rarely enter pots because they normally remain inactive until feeding is resumed at the paper-shell stage (Norman and Jones 1992).

In the present study, crabs were often kept for several days in holding boxes until a large enough sample was obtained and this may explain why some soft-shelled individuals were recorded. Similarly, the scarcity of females with ovaries at the ripe or spawning stage, or with newly laid eggs, may be attributed to a reduced feeding rate during this phase (Choy 1986a), difficulty in entering pots when carrying large egg masses, or the deterrent behaviour of already captured large crabs, especially males. However, it is also possible that females migrate to sand or mud to spawn since many crabs apparently need a soft substrate for successful attachment of the eggs (Crothers 1969, Wear 1974, Edwards 1979).

In an aquarium where both rocks and sand were available, it was observed that berried females generally remained buried in sand with only their eyes and antennae protruding. Kinnear and Mason (1987) found that the proportion of females in creel samples fell during the period when ovigerous females were most frequent and Choy (1986a) reported that ovigerous females were less likely to be caught in trawls. In an intertidal population at Plymouth (Norman 1989), foraging behaviour was less marked in ovigerous females, and especially in those which had recently hatched broods. It is thus likely that the proportion of spawning and ovigerous females was underestimated in this investigation. Moreover, sampling bias may be responsible for the low proportion of both females and immature specimens in all catches. *Necora puber* is known to be a very aggressive species and it has been suggested (Kinnear and Mason 1987) that the poor representation of juveniles and the 1+ class in creel catches may be due to their reluctance to enter pots in which large crabs are already present.

It is worth noting, in the context of possible sampling bias, that *N. puber* is an omnivorous feeder and that algae are an important component in the diet, especially in older crabs (Choy 1986b, González-Gurriarán 1978, Norman and Jones 1990, 1992). Stomachs of individuals obtained from Dalkey by divers contained 75% algae in June but in November one third were empty and the remainder contained only 48% algae. Seasonal variation in the amount of algae consumed was also observed by González-Gurriarán (1978) and Norman and Jones (1992) but it is not known whether the proportion of the different food items varies with reproductive condition or whether individuals ever feed exclusively on algae. In choice experiments under laboratory conditions (Bakir 1990), *N. puber* always selected fish pieces in preference to algae or live invertebrates such as mussels, thus it seems unlikely that any feeding individuals would fail to respond to fish bait in the field.

The general pattern of reproduction in *N. puber* is typical of portunid crabs in that mating takes place while the female is still in a soft-shelled condition following ecdysis, and sperm transfer, ovulation and oviposition are independent events. Following rupture of the seminiferous tubules, sperm is stored in the vasa deferentia for extended periods and can be used for several inseminations, especially in larger males (Norman 1989). Sperm are also stored in the spermathecae of the female, which generally has unripe ovaries at the time of mating, and the stored sperm, which are protected by sperm plugs, can be used to fertilize successive clutches during an intermoult or may even be retained though a moult (Warner 1977, González-Gurriarán 1985a). Thus, mating can occur at any time, independently of gonad development, and great flexibility in the timing of reproductive events is possible.

Moulting seasons could not be delimited in this study but as moulting normally occurs after the main breeding season, it probably takes place in late summer and early autumn. The female moult occurred from late July-mid November at Plymouth (Norman 1989) and from August-September in S. Wales (Choy 1986a) but two periods, in February-April and June-September, were reported in Galicia (González-Gurriarán 1985b).

The recognition of six testicular and seven ovarian stages made it possible to distinguish between recovering and developing gonads and between ripe and spawning, distinctions not made using the usual index of four stages for this species (González-Gurriarán 1985a, Choy 1986a, Kinnear and Mason 1987, Norman 1989, Norman and Jones 1993). With practice, the stages can be distinguished by macroscopic features alone and thus a rapid analysis of the reproductive state of a population is possible. Analysis of monthly samples showed that breeding was poorly synchronised in the Dalkey population, all gonad stages being present throughout the year. As all ovigerous females had ripening ovaries, many, if not most, females may produce two broods in a season, and some may even produce three. This is supported by reports from other localities. Two broods per season, for crabs two years old or more, seem to be usual in British populations (Choy 1986a, Norman 1989) while in Galicia, some females may spawn three times in a season (González-Gurriarán 1985a).

The occurrence of ovigerous females is the most obvious indication of spawning periods, although the proportion of females which are breeding may be underestimated if creels are used for sampling. All studies of reproduction in *N. puber* so far show an extended spawning period, the length of which is related to latitude, being as short as five months in NW Scotland (Kinnear and Mason 1987) but as long as ten months at Plymouth (Norman and Jones 1993) and Galicia

(González-Gurriarán 1985a) A shorter breeding season with greater synchronisation within the population is typical of crustacean species at high latitudes (Jones and Simons 1983, Sastry 1983, Healy 1990), while in warmer water, breeding is generally less well synchronised and may be almost continuous. In spite of the fact that sampling was by creels in both E. Ireland and NW Scotland, the maximum proportion of the population which was ovigerous was nearly the same as in S. Wales where trawls were used (Choy 1986a) and Plymouth where the population was intertidal (Norman 1989) i.e. 60-70%, whereas in the warmer waters of Galicia, sampled by trawling, the maximum was 45% (González-Gurriarán 1985). In Scotland, all ovigerous females in June carried eggs at the hatching stage and no ovigerous females were taken between July and January, but at Dalkey, Plymouth and S. Wales, ovigerous females were only absent for one or two months in early winter, while in Galicia, a small proportion of berried females occurred throughout the year. The onset and peak of breeding do not seem to vary with latitude, however. The main breeding period, i.e. spawning, was observed to start in December in S. Wales and Plymouth, in January in Galicia, in January-February in E Ireland and in March in NW Scotland, while the peak of ovigerous females occurred in January-March in Galicia and S. Wales and in April-June at Dalkey and Plymouth, but it also occurred in April in Scotland in spite of the higher latitude (58°N) of the locality.

There may be genetic differences between these populations but there are many other possible explanations for observed variations in the timing of reproductive events, for example differences in sampling methods, date of sampling, sampling error (e.g. small samples in bad weather), and variation from year to year at the same locality. No long term studies beyond two years are available which show the extent of annual variation in breeding of *N. puber* but its reproductive strategy allows for great temporal flexibility, thus it might be expected that individuals could respond not only to small changes in water temperature but also to other environmental changes.

The rate of gonad ripening is probably related to temperature but could also be influenced by other factors, especially feeding rate and diet. Egg development after spawning, however, is directly related to water temperature (Wear 1974, Choy 1986a, 1991, Valdés et al. 1991). Embryonic development of N. puber raised in the laboratory at 8°C took 125 days (Choy 1986a) while at 15°C hatching occurred after only 42-48 days (Choy 1986a, 1991). Similar results were obtained by Valds et al. (1991) who demonstrated a lower threshold temperature for embryonic development of 4°C, and incubation times of 76 days at 10°C, 40.7 days at 15°C and 17.6 days at 25°C. The incubation time for early spawners at Dalkey is thus likely to be 2-3 months while eggs spawned in June, when the water temperature is about 15°C, could hatch in 5-6 weeks. It would be possible, therefore, for females which spawned in April to produce and hatch a second brood. Those which did not release larvae until July probably did not spawn again as there were very few ovigerous females after August.

The protracted breeding season of *N. puber,* by comparison with a season of about three months for *Cancer pagurus* (Edwards 1979), has important implications for both the marketing of commercial catches and fishery management. Ovigerous females had lower yields of white meat during the main spawning period but the yield of brown meat remained high throughout the breeding season although it never exceeded 18% of total meat (Bakir 1990). A higher yield of 68% brown meat in *C. pagurus* may be explained by its contracted breeding season and high fecundity relative to body size, females producing up to three million eggs (Edwards 1979). Berried velvet crabs are, in fact, acceptable at market outlets, both in Ireland and abroad, although their export has now been halted. Experience has shown that velvet crab populations are very vulnerable to overfishing and both imposition of a minimum marketable size and prohibition of the sale of berried females may be needed to conserve stocks.

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Table 1. Ovary stages determined by appearance and proportion of the body cavity occupied by the gonad.

Stage	Shape	Colour	Body cavity occupied
1. Immature, virgin	small, thin	white, translucent	1/7
2. Developing	swollen	light yellow-pale orange	1/3
3. Developed	swollen	yellow-orange	1/2
4. Ripe	swollen	orange-red	2/3
5. Spawning	collapsed, shrunken	deep orange	1/4
6. Spent	small, shrunken	orange-brown dark brown	1/8
7. Recovering	small, not swollen	white, pale green, yellow or orange	1/6

Table 2. Testis stages determined by appearance and proportion of the body cavity occupied by the gonad.

Stage	Shape	Colour	Body cavity occupied
1. Immature	small, slender	white, translucent	1/10
2. Developing	large, swollen	creamy white	1/5
3 Ripe	large, coiled	pale orange-orange	1/4
4. Spawning	small, shrunken shrunken	blood-shot	1/6
5. Spent	small, shrunken	blood-shot	1/7
6. Recovering	small, shrunken	white	1/9

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