In: James G. Wilson (ed.) *The Intertidal Ecosystem: The Value of Ireland's Shores*, 100–114. Dublin: Royal Irish Academy.

# SETTLEMENT AND RECRUITMENT OF THE BLUE-RAYED LIMPET, *PATELLA PELLUCIDA* L. IN GALWAY BAY, WEST COAST OF IRELAND

**David McGrath[1,2] and Helen Foley[1]**

[1]*Department of Life Sciences, Galway-Mayo Institute of Technology, Galway, Ireland*
[2]*Department of Zoology and Animal Ecology, University College, Cork*
Email: dave.mcgrath@gmit.ie

## ABSTRACT

The seasonal occurrence, density and population structure of the blue-rayed limpet, *Patella pellucida,* on crustose coralline algae (CCA) and *Mastocarpus stellatus* are described from an exposed rocky shore at Ballynahown, Galway Bay, Ireland during 1990–1993. Recently settled recruits of *P. pellucida,* i.e. individuals with larval shells still attached, were found on CCA each year and in virtually every month of the year. A marked annual cycle in the abundance of *P. pellucida* on CCA is described, with the largest densities occurring during winter/spring, of up to 15 $cm^{-2}$, falling to minima in the summer months.

Analysis of population structure shows that this pattern is due to a winter/early spring settlement peak. Data from *M. stellatus* suggest that *P. pellucida* may settle directly on this alga, but, if so, at densities two orders of magnitude less than on CCA. The pattern of density change and the population structure on *M. stellatus* support the hypothesis that *P. pellucida* migrates to this alga following settlement on CCA. The larval and developing adult shells are described using SEM photographs.

## INTRODUCTION

The blue-rayed limpet, *Patella pellucida* L., is a mesoherbivorous gastropod which is particularly associated with laminarians (Fretter and Graham 1976; Toth and Pavia 2002), but is also found on a range of other macroalgae (Vahl 1971; McGrath 1992, 1997) and on open rock (McGrath 1997). It is found on all Irish and British coasts (Seaward 1982) and on all Atlantic coasts between Portugal and northern Norway (Graham 1988). The species occurs in the intertidal zone only near LWST and extends sublittorally to 27 m (Fretter and Graham 1976).

Two forms of the species exist. The *pellucida* form, which makes up two thirds of the population of this limpet, is found on the algal frond while the *laevis* form excavates the base of the kelp stipe within the holdfast (Fretter and Graham 1976). *P. pellucida* are annual: two-year-old limpets are mostly the *laevis* form which have recruited to *Laminaria* holdfasts (Fretter and Graham 1976).

*P. pellucida* probably breeds throughout the year at Plymouth (Lebour 1937) and exhibits peak spawning in spring with a short larval life of a few weeks (Fretter and Graham 1976). Azevedo *et al.* (1984) have noted that female *P. pellucida* have early meiotic prophase oocytes in their ovaries by October-December and vitellogenic oocytes in February on the Atlantic coast of Portugal. The shelled larvae are to be found in the plankton at Plymouth in almost any month, sometimes occurring in numbers, and the shell of the late larva is 0.16–0.18 mm across (Lebour 1937). Lebour (1937) figures this late larval stage and notes that there are some differences between it and that of other *Patella* species.

According to Fretter and Graham (1976), the larvae of *P. pellucida* settle all over the shore but only those settling on *Laminaria* spp. survive into adulthood. However, Vahl (1971) failed to find the earliest benthic stages on *Laminaria hyperborea* (Gunn.) Foslie and concluded that settlement of *P. pellucida* occurs on another substratum and is followed by migration to *L. hyperborea*. McGrath (1992) found recently settled *P. pellucida,* with larval shells still attached, on crustose coralline algae (CCA) on the lower shore between February and April at Carnsore Point in south-east Ireland. Analysis of the population structure and density of the species on a range of algae at this site, including *Laminaria digitata* (Huds.) Lamour, *L. hyperborea,* and *Himanthalia elongata* (L.) S.F.Gray, led to the hypothesis that settlement did not occur on these algae but that the juvenile limpets recruited to them following settlement on CCA (McGrath 1992). The situation on *Mastocarpus stellatus* (Stackh.) Guiry was not so clear-cut and McGrath (1992) did not exclude the possibility of settlement on this alga. *P. pellucida* appears to undergo multiple phases of recruitment. Settlement on CCA is followed by recruitment to *Laminaria* spp. and *M. stellatus* (at *c.* 2 mm shell length) and later to *Himanthalia elongata* (at *c.* 3 mm shell length) (McGrath 1992). It also migrates from the frond of Laminaria into the holdfast, generally at 3–6 mm shell length (Graham and Fretter 1947). These phases of recruitment imply a high level of mobility in this species and this has been confirmed by a series of field experiments (McGrath 1997, 2001). However, while the seasonal cycles in the density of *P. pellucida* were described quantitatively for *H. elongata* and *M. stellatus* to support the recruitment model described by McGrath (1992), very little data were supplied on the population dynamics of the limpet on CCA. Furthermore, settlement *per se* was not examined in McGrath's study; he found recruits, which were first encountered when they became visible in the field at a shell length >375 μm (McGrath 1992).

The present study set out to investigate in greater detail the relationship between the earliest study benthic stages of *P. pellucida* and CCA. Sampling by removal of patches of CCA for later microscopic analysis allowed for the detection of earlier recruits than those reported by McGrath (1992). The seasonal occurrence, density and population structure of *P. pellucida* on CCA on the lower intertidal of an exposed rocky shore in Galway Bay, west coast of Ireland over a three-year period 1990–1993 is quantitatively described. Simultaneous examination of the density and population structure of *P. pellucida* on *M. stellatus* was carried out in 1993 to examine the hypothesis that larvae settle on this alga (McGrath 1992).

The generic allocation of this species to *Patella* follows recent molecular and morphological analyses (Ridgway *et al.* 1998, Koufopanou *et al.* 1999).

## METHODS

Samples of CCA were collected at approximately two-weekly or monthly intervals during October 1990 to April 1992 from an exposed rocky shore at Ballynahown in Galway Bay, west coast of Ireland (Irish National Grid Reference L9920). Each sample was composed of a number of small patches of the alga removed haphazardly (Krebs 1989) from the rocky substratum using a knife. Sampling was, however, restricted to relatively thick patches of CCA, often of coarse topography. Three samples were taken on each occasion with two exceptions, when bad weather allowed for the collection of only two. Collection was at or just below the low water spring tide of the day in the upper *Laminaria digitata* zone. The samples were examined under a stereo microscope within twelve hours of collection at a magnification of ×15–×20 and the *P. pellucida* counted, removed and stored in 70% alcohol. The area of CCA examined from each sample was estimated by drawing around each patch on graph paper and numbers found on each sampling trip are expressed as the mean $cm^{-2}$ of CCA. Sample size ranged from 7 $cm^2$ to 42 $cm^2$, mean 21.7±S.D.7.8 $cm^2$.

Three samples of CCA were also examined from the same area of shore at Ballynahown at approximately monthly intervals from February to May 1993. These were either frozen or stored in 70% alcohol prior to examination. The area of each sample was estimated by image analysis. Otherwise samples were treated in the same way as above. Sample size ranged from 14.4 to 67.0 $cm^2$, mean 31.2±S.D.16.6 $cm^2$.

Five samples of *Mastocarpus stellatus* were collected, generally at fortnightly intervals, in 1993, during February to May by cutting the alga from the substratum with a knife. The samples were stored damp in plastic bags at 4°C (up to three days) or at –20°C prior to examination. Sample wet weight (surface blotted dry) ranged from 5.3 to 16.1g, mean 11.2±S.D.3.2g. The algae were scanned microscopically and attached *Patella pellucida* removed and stored in 70% alcohol. Each algal sample was then dried to constant weight (±<2%) at 60°C. The relationship between dry weight and algal surface area was estimated by measuring the surface area of a series of algal samples using image analysis and determining their dry weight as above. A regression analysis of algal dry weight against frond surface area was calculated and used to estimate the surface area of the routinely collected samples. The calculated regression equation was as follows:

Area of frond ($cm^2$) = 31.2*DW (g) + 37.92, $r = 0.55$ ($p<0.05$), $N = 25$.

*P. pellucida* density on *M. stellatus* could therefore be expressed as numbers $g^{-1}$ dry weight or numbers $cm^{-2}$ surface area.

All *Patella pellucida* collected were measured for shell length (maximum dimension) of developing adult shell only to the nearest 25μm below using a calibrated eyepiece in a stereo microscope and were classed into three benthic life history stages:

(i) limpets with larval shell only, or with a developing adult shell

(ii) limpets which had lost the larval shell, but had not developed blue rays

(iii) limpets without a larval shell and with blue rays.

Notes on the identification of the *P. pellucida* recruits:

The smallest recruits found did not have the diagnostic features of the adult shell, *i.e.* characteristic brown colour with blue rays, and are presently presumed to be this species following a number of lines of argument:

- a continuous size series from larval shell only through the various developmental stages has been observed and no discontinuity discerned.
- the larval shell in the smallest stages is similar to that seen on larger shells where some adult shell features are present.
- no other limpet species which might have developed from these larval shells is found as recruits in numbers comparable to *P. pellucida* on the CCA.

In the absence of diagnostic descriptions of the larval shells of all limpet species which might be found in this habitat, proof that *P. pellucida* settles on CCA must await the successful ongrowing of the smallest field collected recruits in the laboratory until the features of the adult shell develop, a diagnostic description of *Patella* species larval shells, or genetic typing of the recruits.

*Patella ulyssiponensis* Gmelin, *P. vulgata* L. and *Tectura virginea* (Muller) are found as adults on the lower shore at Ballynahown in the upper *L. digitata* zone. Observations suggest that recently settled *T. virginea* are readily separable from *Patella*. Single individuals of presumed *P. vulgata* or *P. ulyssiponensis* recruits, with some of the adult shell and colour patterns developed, have been found very rarely on CCA in the lower shore habitat sampled.

The larval shell of *Patella pellucida* appears to be very similar to the light microscope descriptions of *Patella vulgata* (Smith 1935; Lebour 1937) including the presence of minute granulations. Lebour (1937) notes, however, that the larval shells of *P. pellucida* and *P. vulgata* are distinguishable in that those of the former species are smaller, smooth and more symmetrical at the outer lip, the margin overlapping at both sides. This latter feature was not observed in the specimens from Galway Bay and it may be that it is not obvious by the time of settlement. There is, therefore, some disparity between the description of the larval shell of *P. pellucida* as described by Lebour (1937) and the appearance of the larval shell of the recent recruits from Galway Bay.

## RESULTS

The density of *P. pellucida* on CCA during the period October 1990 to April 1992 is shown in Figure 1. A distinct annual cycle is evident. Peak densities occurred in late winter/spring and fell to minima during the summer and autumn. The mean density of *P. pellucida* in the samples ranged from a maximum of 6.84 $cm^{-2}$ in January 1992 to a minimum of 0.01 $cm^{-2}$ in August/September 1991. The maximum density recorded was 15 $cm^{-2}$ on patches of 0.48 and 1.20 $cm^2$ in March 1991 and February 1992 respectively.

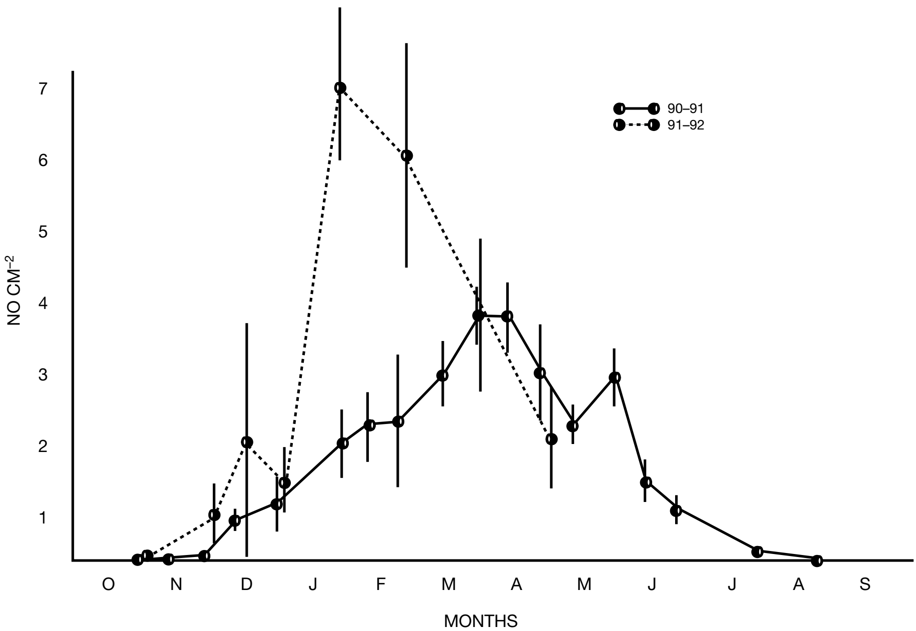



**Figure 1: The density of *Patella pellucida* on the crustose coralline alga, as numbers cm$^{-2}$, from October 1990 to April 1992, on the lower shore at Ballynahown, Co Galway, Ireland. Vertical bars are standard deviations.**

The percentage occurrence of the three benthic life history stages of *P. pellucida* on CCA is shown for 1990–1992 in Figure 2. Recently settled recruits, *i.e.* individuals with larval shells attached, were found each year and in virtually every month of the year, the one exception being September 1991, when only one limpet was found. The highest percentages (>90%) of recent recruits occurred between November and February. The proportion then fell steadily until the summer months when these made up less than 15% of the collections. The number of limpets which had lost the larval shell but had not developed the blue rays characteristic of the adult was at its lowest (<10%) from November to February, increased thereafter and peaked in May (62%) and then decreased again. Individuals with blue rays reached their maximum in July with very low abundances (<5%) from January to April.

Individuals with the adult shell yet to be developed were found in low numbers in the months of October to May on CCA. A mean number of 5 individuals month$^{-1}$ was found over this period. Numbers larger than the mean number were restricted to the months of January to March with a maximum density of 0.47 cm$^{-2}$ in January 1992. The larval shell of these specimens ranged in length from 228 to 252 µm with a mean of 241.35 ± S.D. 6.62 µm (N = 20). The larval shell was generally lost at an adult mean shell length of *c.* 550µm and the blue rays developed at a mean length of *c.* 1 mm shell length. These two length values are calculated as the mean lengths of those limpets in a sample lying between the smallest and largest with a larval shell and without blue rays respectively. Exceptionally, an individual of 450 µm shell length with no larval shell was found on 28 December 1991. The largest limpets on CCA were in the range 1.4 to 2.3 mm.

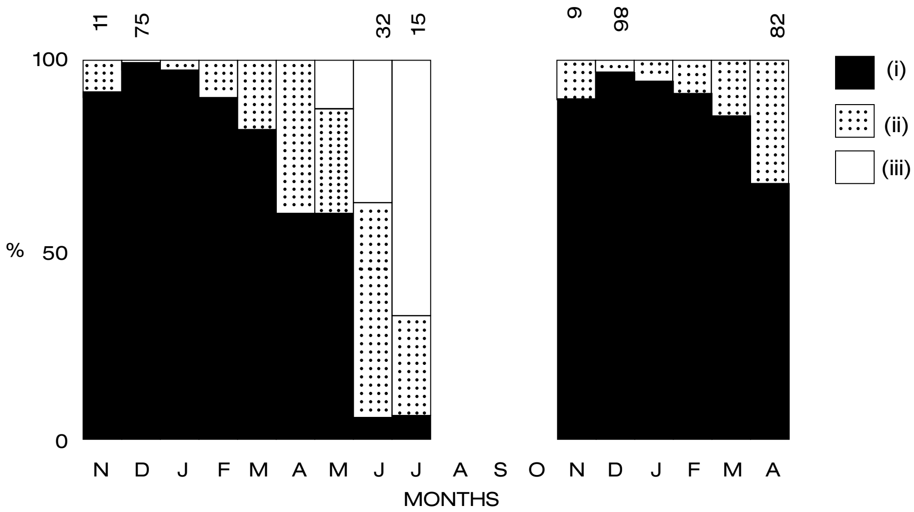



**Figure 2: The relative abundance of three benthic stages of *Patella pellucida* on the crustose coralline alga on the lower shore at Ballynahown, Co Galway, Ireland, November 1990 to April 1992.**

**(i) recruit with larval shell attached.**

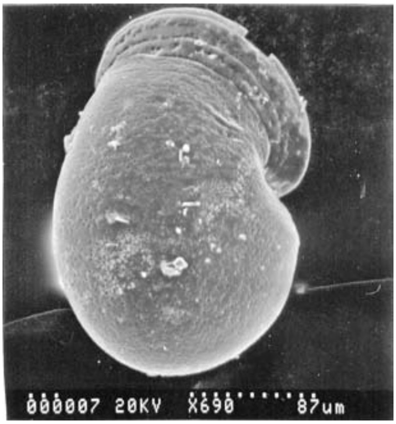
**(ii) without larval shell and without blue rays.**

**(iii) with blue rays present.**

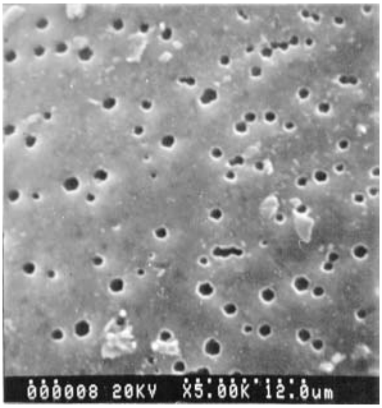
**Numbers from sampling sessions in the same month are combined. Where <100 individuals were assessed, the sample number is shown. No data are available for August to October 1991 as <3 specimens were taken on each occasion.**

The larval shell of *P. pellucida* is shown in Plate 1. It is involute with little external evidence of spiral growth and consists of one and a half whorls. The surface is smooth but with numerous scattered pores or pits (Plate 1). Growth of the adult shell is patelliform and markedly asymmetric with the shell flaring outward to the larval right and the larval shell being displaced from the centre of the growing adult shell before being lost (Plate 1). Following loss of the larval shell, there is a clearly visible shell plate and an indentation on the adult shell posteriorly where the larval shell rested (Plate 1). The growing adult shell differs from the larval shell in that the pores/pits are fewer and there is a suggestion of growth checks (Plate 1).

The length frequency data for *P. pellucida* on the CCA during 1990–1992 are shown in Figure 3 for selected months when more than 60 individuals was collected. The population was generally comprised of a single mode but this tended to be skewed to the right later in the year as the numbers of larger animals increased. Growth is obvious in the population during April/May 1991 with the mode shifting to the right. The population structure was also similar in 1993 with growth in April/May (Figure 3). Growth rates were not estimated from these length data as, given that recruitment was probably prolonged and migration occurred to other macroalgae with increase in size (McGrath, 1992), such rates would be of doubtful value.



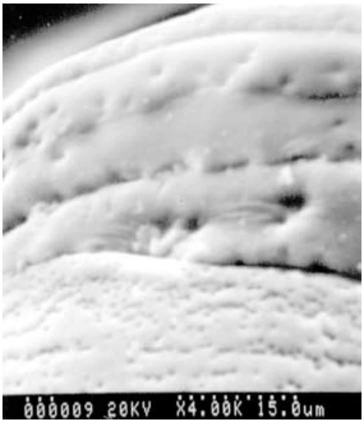

(i)




(ii)


(iii)


(iv)




(v)

**Plate 1: SEM photomicrographs of the juvenile shell of** *Patella pellucida.* **Magnification used and scale are indicated on each photograph. i) The newly settled recruit to show the larval shell: ii) Pits on the shell surface of the larval shell: iii) The developing juvenile shell: iv) The shell plate and larval shell scar: v) The junction between the larval and juvenile shell.**

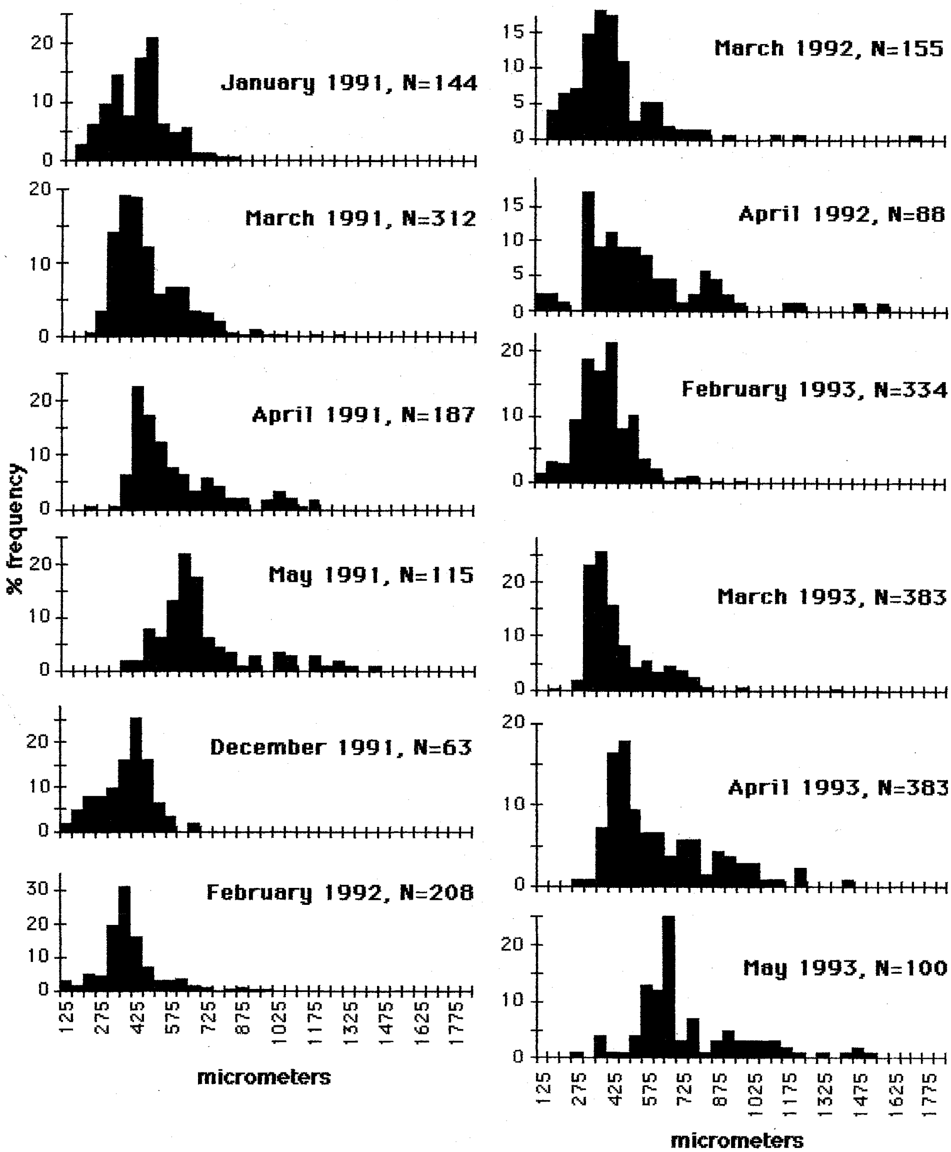



**Figure 3: Length frequency data for *Patella pellucida* sampled on the crustose coralline alga on the lower shore at Ballynahown, Co. Galway, Ireland, January 1991 to May 1993 for selected months where >60 individuals were collected.**

The density of *P. pellucida* on CCA and *M. stellatus* during February to May 1993 is shown in Figure 4. A mean density of 2.37 cm$^{-2}$ on CCA rose to a peak of 4.36 cm$^{-2}$ in March then fell over the following two months to 1.83 cm$^{-2}$. Densities on *M. stellatus* were very low compared to those on CCA with a maximum density of 0.12 cm$^{-2}$ over the four month period. The mean densities over the period on CCA and *M. stellatus* were 2.73±S. D.1.12 and 0.03±S.D.0.04 cm$^{-2}$ respectively. A fall in density on *M. stellatus* from early to late February was followed by a progressive rise from March with the peak density in May. Numbers of *P. pellucida* $g^{-1}$ DW *M. stellatus* ranged from 0.27±S.D.0.24 to 14.48±S.D.4.57, mean 3.62±S.D.5.01.

The occurrence of the three benthic life history stages of *P. pellucida* on *M. stellatus* and CCA for the period February to May 1993 is shown in Table 1. Individuals with larval shells attached were found on *M. stellatus* during March to May, but in very low numbers making up 2.4% of the total found on that substratum (Table 1). This contrasts sharply with the situation on CCA where specimens with larval shells were abundant throughout the period, making up on average 76.9% of the population, while showing a decline in relative abundance from 96.4% to 12.9% from February to May (Table 1). Recruits on *M. stellatus* were dominated by individuals which had lost the larval shell. A comparison between the two substrata shows that recruits on *M. stellatus* were less dense than those

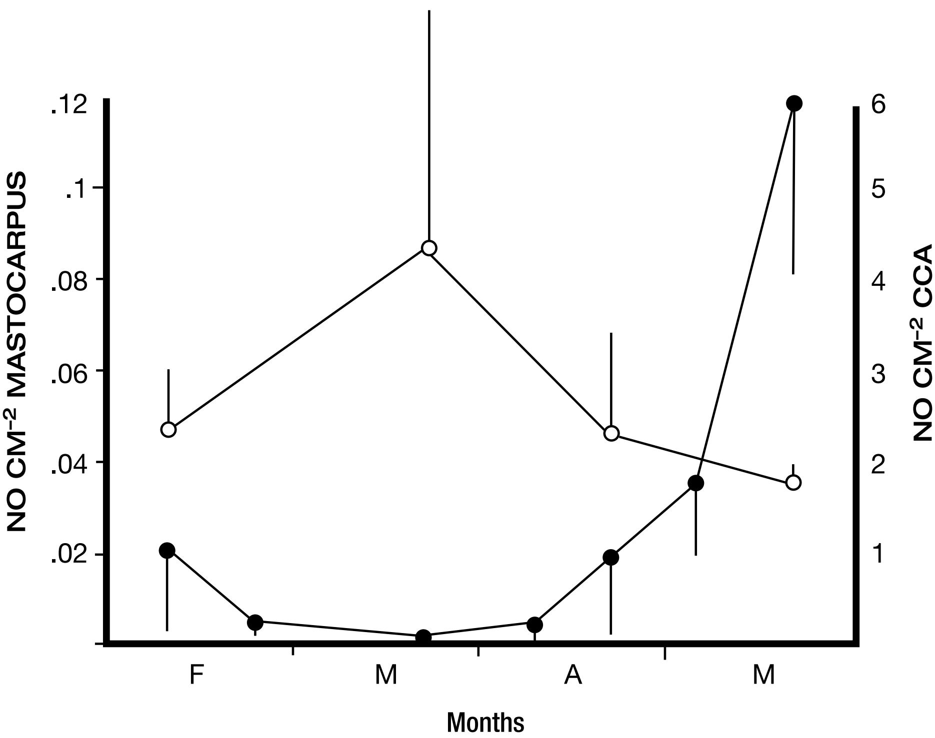



**Figure 4: The density of *Patella pellucida* on the crustose coralline alga (CCA) (o) and *Mastocarpus stellatus* (•) on the lower shore at Ballynahown, Co Galway, Ireland, February to May 1993, as numbers $cm^{-2}$ surface area**

on CCA, increased in density when the density on CCA decreased, and were generally composed of more advanced benthic life history stages (Figure 4, Table 1).

The mean sizes of *P. pellucida* on *M. stellatus* during the months February to May 1993 are listed in Table 2. The range was 375–7360 µm shell length with a mean of 1413.19±S.D.863.66 µm. Mean size fell from February to March, then showed a tendency

**Table 1. Percentages of *P. pellucida* on CCA and *Mastocarpus* during February to May 1993 (February, April, May the replicate *Mastocarpus* samples are combined), on the lower shore at Ballynahown, Co. Galway, Ireland in the three developmental categories as follows:**
**i) With larval shell;**
**ii) Without larval shell and without blue rays**
**iii) Without larval shell and with blue rays**

| | **Mastocarpus** | | | | **CCA** | | | |
|---|---|---|---|---|---|---|---|---|
| | N | i | ii | iii | N | i | ii | iii |
| **February** | 53 | 0 | 0 | 100 | 362 | 96.4 | 3.3 | 0.3 |
| **March** | 4 | 25 | 75 | 0 | 390 | 82.8 | 16.9 | 0.3 |
| **April** | 52 | 9.6 | 67.3 | 23.1 | 141 | 56 | 35.5 | 8.5 |
| **May** | 310 | 1.3 | 41 | 57.7 | 101 | 12.9 | 70.3 | 16.8 |
| **Total** | 419 | 2.4 | 39.4 | 58.2 | 994 | 76.9 | 20 | 3.1 |

to increase until May. The relatively high density of recruits in early February (Figure 4) was composed of larger animals. The data confirm the trend seen in the life history stages in that limpets on *M. stellatus* were larger in any month compare with those on CCA.

## DISCUSSION

*Patella pellucida* recruits were found each year from 1990 to 1993 at Ballynahown on CCA. Later observations also confirm recruitment to CCA in 1994. The smallest recruits encountered during the study were limpets which consisted of larval shells only and these were found during October to May at a maximum density of 0.47 $cm^{-2}$ (January 1992). These had a mean shell length of 241.35±S.D.6.62µm, were involute and consist of one and a half whorls, with a punctate sculpture. Recruits comprised of a larval shell only were rare in the CCA samples. The largest number found was twenty and this made up only 5% of the sample. This may be due to very rapid development of the adult shell. Kay and Emlet (2002) observed that the patellogastropod limpets *Lottia digitalis* (Rathke) and *L. asmi* (Middendorf) initiated adult shell growth 2–4 days after settlement in the laboratory.

McGrath (1992) reported the presence of "recently" settled *P. pellucida,* i.e. limpets with larval shells still attached, at Carnsore Point in south-east Ireland. McGrath (1992) collected visible individuals of *P. pellucida* in the field and the smallest individuals found were 375µm in shell length. These individuals should, more correctly, be termed recruits, settled individuals which have survived some post-settlement time until recorded by an ecologist (Keough and Downes 1982; Connell 1985; Pawlik 1992). In his study, McGrath (1992) gave no data on the length of time these recruits had spent on the shore after settlement and therefore did not define the term recent. Settlement in field situations is

Table 2. Number (N), density ($g^{-1}$ and $cm^{-2}$), mean size (µm) of *P. pellucidum* on *M. stellatus* February to May 1993 on the lower shore at Ballynahown, Co. Galway, Ireland.

| Date | N | $N.g^{-1}$ | SD | $N.cm^{-2}$ | SD | Mean size µm | SD |
|---|---|---|---|---|---|---|---|
| 10/2/93 | 41 | 2.47 | 2.04 | 0.021 | 0.017 | 2447 | 614 |
| 24/2/93 | 12 | 0.66 | 0.42 | 0.005 | 0.004 | 2861 | 1460 |
| 21/3/93 | 14 | 0.27 | 0.24 | 0.002 | 0.002 | 769 | 241 |
| 9/4/93 | 9 | 0.59 | 0.36 | 0.005 | 0.003 | 943 | 577 |
| 21/4/93 | 39 | 2.43 | 2.12 | 0.02 | 0.018 | 865 | 212 |
| 5/5/93 | 96 | 4.43 | 1.7 | 0.037 | 0.014 | 1142 | 476 |
| 20/5/93 | 205 | 14.48 | 4.57 | 0.121 | 0.038 | 866 | 162 |

often inferred from recruitment data measured in days or even weeks after settlement has taken place (Seed and Suchanek 1992). While settlement itself was not observed in the present study, the discovery of individuals with only larval shell, considerably narrows the gap between settlement proper and recruitment.

The larval shell of *P. pellucida* from Ballynahown was lost at *c.* 550µm and the blue rays developed at *c.* 1 mm shell length respectively. These figures are similar to those reported by McGrath (1992). In *Patella vulgata* the shell cap of the post-larva is cut off when the limpet is about 0.5 mm long (Smith 1935). The larval shell of *P. pellucida* appears similar to that of *P. coerulea* (L.). The post-larval shell of the latter species also shows a distinct scar where the larval shell was attached and a second impression where the larval shell lay (Waren 1988). Recent recruits (with larval shell) of *P. pellucida* peaked in relative abundance during November to February. This was followed by a peak in the number of limpets without larval shells or blue rays, which had a maximum in May, then in turn by those with blue rays present which reached their peak abundance in July.

The density of *P. pellucida* on CCA showed a marked seasonal cycle increasing from October/November and peaking in January or March. Analysis of the population structure of the limpets indicates that this density increase was a result of a recent settlement of larvae. The peak abundance of recent recruits coincided with the first months of the density increase. With the decline in density, older life stages became relatively more abundant. The combination of the density data and the information from population structure analysis suggests that the main settlement is a winter/early spring event, peaking in January to March with, perhaps, some differences in timing from year to year. This finding would also suggest a winter/early spring spawning peak in this species. The occurrence of recent recruits in virtually all months of the year on CCA, albeit at times in very low densities, suggests that some settlement occurs throughout the year. While this contrasts with the view of McGrath (1992) who concluded that settlement was completed by May, the main peak of settlement at Ballynahown was complete by May when recent recruits made up <25% of the population. It must also be noted that the studies were done in different years and in different locations. Fretter and Graham (1976) have observed that, while breeding occurs throughout the year in *P. pellucida,* it is maximal in spring. Larvae of this species have been reported from the inshore plankton at Plymouth in February, August, September, November and December (Fretter and Graham 1962). These observations are consistent with the results of the present study.

Because numbers of recruits accumulate following settlement on natural substrata (King *et al.* 1990) and since data on growth rates is lacking, it is not possible to define the settlement peak more precisely. The maximum densities of recruits seen on CCA at Ballynahown of 15 $cm^{-2}$ are of a similar order to those reported by McGrath (1992) of 4 $cm^{-2}$, though predictably larger, because microscopic examination of the Ballynahown samples would discover individuals which would have been overlooked visually in the field at Carnsore Point. The maximum mean densities seen on CCA were of a similar order in the three years 1991–1993 respectively, 3.5, 6.8 and 4.4 $cm^{-2}$ respectively. The possible effect of the non-random sampling method used on estimates of density on CCA is not known.

McGrath (1992) did not exclude the possibility that *Patella pellucida* settles on *M. stellatus.* Recruits with larval shells still attached were found in the present study on this alga in 1993, although in small numbers. Thus, either *P. pellucida* settles on *M. stellatus* or can migrate to it from CCA during the earliest benthic life history stages. If the species settles on *M. stellatus,* then it would appear to be a much less favoured substratum than CCA given the very low densities of recent recruits on this alga during the settlement peak on CCA. In summary, however, the data do not allow rejection of the hypothesis that *P. pellucida* settles on *M. stellatus.* It is possible that the recruits on this alga are "desperate larvae" with reduced settlement substratum specificity (Toonen and Pawlik 1994). McGrath (1992) suggested that *P. pellucida* settled on CCA and then migrated to *M. stellatus,* based on the analysis of the population structure of the limpets on the two algae and the fact that a density decrease on CCA following recruitment was followed by an increase on *M. stellatus.* A similar pattern was observed at Ballynahown. The density decrease on *M. stellatus* in February was comprised of larger animals and was not associated, therefore, with a settlement event. The maximum density of *P. pellucida* on *M. stellatus* at Ballynahown is of a similar order to that seen by McGrath (1992) at Carnsore Point.

Settlement of benthic invertebrates with a planktonic larval stage may be by passive deposition or by active habitat selection, though these processes may not be mutually exclusive, and may both operate in a life history at different spatial and temporal scales (Butman 1987). Passive deposition might result in non-random distribution of recruits intertidally due to differing times of immersion (Minchinton and Scheibling 1991), other hydrodynamic effects (Jeffrey and Underwood 2000) or other factors such as predation (see Ross 2001, for a review). Active habitat selection may involve both positive or negative cues (Woodin 1991). Differential mortality of settlers in different habitats may lead to recruit distribution being trimmed to that of the adult (Connell 1985). Also, the observed distribution of recruits may be established by migration after settlement in another habitat, for example, in some *Mytilus edulis* populations (Bayne 1964).

For *P. pellucida,* settlement is clearly not random, as originally proposed by Fretter and Graham (1976), in that the earliest recruits are absent from habitats occupied by the adult (Vahl 1971; McGrath 1992). Given the very small size of recruits found in the present study on CCA, migration from an earlier settlement site appears unlikely and this strengthens McGrath's (1992) hypothesis that settlement occurs on CCA. The data for *P. pellucida* indicate a non-random process, but whether this is due to larval selection, with CCA as a positive settlement cue, is caused by hydrodynamic delivery of larvae to CCA, or other factors is unknown. The ecology of the earliest benthic stages of the other Irish species of *Patella* is very poorly known. However, *P. ulyssiponensis* recruits also appear to have a close, but non-obligative relationship with CCA, while those of *P. vulgata* appear to be indifferent to it (Delany *et al.* 2002). *P. ulyssiponensis,* however, remains associated with CCA throughout life, while *P. pellucida* uses this habitat as a nursery area prior to migration to adult habitats (McGrath 1992; Delany *et al.* 2002).

## ACKNOWLEDGEMENTS

We wish to thank Martin McNulty for his help with the image analysis, Donncha McGrath for his assistance with computer work and Dr. David Reid, The Natural History Museum, London, for helpful comments on an earlier draft of this paper.

## REFERENCES

Azevedo, C., Castilho, F. and Coimbra, A. 1984. Fine structure and cytochemistry of the oocyte nucleolus in the mollusk *Helcion pellucidum* (Prosobranchia). *Journal of Ultrastructure Research* **89**, 1–11.

Bayne, B.L. 1964. Primary and secondary settlement in *Mytilus edulis* L. *Journal of Animal Ecology* **33**, 513–523.

Butman, C.A. 1987. Larval settlement of soft sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanography and Marine Biology Annual Review* **25**, 113–165.

Connell, J.H. 1985. The consequences of variation in initial settlement *vs.* post settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* **93**, 11–45.

Delany, J., Myers, A. and McGrath, D. 2002. A comparison of the interactions of the limpets *Patella vulgata* and *Patella ulyssiponensis* with crustose coralline algae. *New Survey of Clare Island.* Volume **3**, 79–90. Dublin. Royal Irish Academy.

Fretter, V. and Graham, A. 1962. *British Prosobranch Molluscs*, London Roy Societ.

Fretter, V. and Graham, A. 1976. The Prosobranch Molluscs of Britain and Denmark. Part 1 – Pleurotomariacea, Fissurellacea and Patellacea. *Journal of Molluscan Studies*, Supplement **1**, 1–37.

Graham, A. 1988. British prosobranchs and other operculate gastropod molluscs. *Linnean Society Synopses of the British Fauna* **2**, 1–662.

Graham, A. and Fretter, V. 1947 The life history of *Patina pellucida* (L.). *Journal of the Marine Biological Association of the United Kingdom* **26**, 590–601.

Jeffrey, C.J. and Underwood, A.J. 2000. Consistent spatial patterns of arrival of larvae of the honeycomb barnacle *Chamaesipho tasmanica* Foster and Anderson in New South Wales. *Journal of Experimental Marine Biology and Ecology* **252**, 109–127.

Kay, M.C. and Emlet, R.B. 2002. Laboratory spawning, larval development, and metamorphosis of the limpets, *Lottia digitalis* and *Lottia asmi* (Patellogastropoda, Lottidae). *Invertebrate Biology* **121**, 11–24.

Keough, M.J. and Downes, B.J. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia (Berlin)* **54**, 348–352.

King, P.A., McGrath, D. and Britton, W. 1990. The use of artificial substrates in monitoring mussel (*Mytilus edulis* L.) settlement on an exposed rocky shore in the west of Ireland. *Journal of the Marine Biological Association of the United Kingdom* **70**, 371–380.

Koufopanou, V., Reid, D.G., Ridgway, S.A. and Thomas, R.H. 1999. A molecular phylogeny of the patellid limpets (Gastropoda: Patellida) and its implications for the origins of their antitropical distribution. *Molecular Phylogenetics and Evolution* **11**, 138–156.

Krebs, C.J. 1989. *Ecological methodology.* London, Harper Collins.

Lebour, M.V. 1937. The eggs and larvae of the British prosobranchs with special reference to those living in the plankton. *Journal of the Marine Biological Association of the United Kingdom* **22**, 105–166.

McGrath, D. 1992. Recruitment and growth of the blue-rayed limpet, *Helcion pellucidum* (L.), in south east Ireland. *Journal of Molluscan Studies* **58**, 425–431.

McGrath, D. 1997. Colonisation of artificially cleared *Laminaria digitata* (Huds.) Lamour by the blue-rayed limpet, *Helcion pellucidum* (L.) (Mollusca, Gastropoda). *Biology and Environment: Proceedings of the Royal Irish Academy* **97B**, 245–248.

McGrath, D. 2001. Inter-algal movement of marked blue-rayed limpets, *Patella pellucida* L., between kelps on the lower shore. *Journal of Molluscan Studies* **67**, 398–400.

Minchinton, T.E. and Scheibling R.E. 1991. The influence of larval supply and settlement on the population structure of barnacles. *Ecology* **72**, 1867–1879.

Pawlik, J.R. 1992. Chemical ecology of the settlement of benthic marine invertebrates. *Oceanography and Marine Biology Annual Review* **30**, 273–335.

Ridgway, S.A., Reid, D.G., Taylor, J.D., Branch, G.M. and Hodgson, A.N. 1998. A cladistic phylogeny of the family Patellidae (Mollusca: Gastropoda). *Philosophical Transactions of the Royal Society London* **B 353**, 1645–1671.

Ross, P.M. 2001. Larval supply, settlement and survival of barnacles in a temperate mangrove forest. *Marine Ecology Progress Series* **215**, 237–249.

Seaward, D.R. 1982. *Sea area atlas of the marine molluscs of Britain and Ireland.* Nature Conservancy Council, Peterborough.

Seed, R. and Suchanek, T.H. 1992. Population and community ecology of *Mytilus.* In E. Gosling (ed.) *The mussel Mytilus: Ecology, Physiology, Genetics and Culture,* 87–170. Amsterdam. Elsevier.

Smith, F.G.W. 1935. The development of *Patella vulgata. Philosophical Transactions of the Royal Society, London* **B 225**, 95–125.

Toonen, R.J. and Pawlik, J.R. 1994. Foundations of gregariousness. *Nature, London* **370**, 511–512.

Toth, G.B. and Pavia, H. 2002. Intraplant habitat and feeding preference of two gastropod herbivores inhabiting the kelp *Laminaria hyperborea*. *Journal of the Marine Biological Association of the United Kingdom* **69**, 243–247.

Vahl, O. 1971. Growth and density of *Patina pellucida* (L.) on *Laminaria hyperborea* (Gunnerus) from western Norway. *Ophelia* **9**, 31–50.

Waren, A. 1988. *Neopilina goesi,* a new Caribbean monoplacophoran mollusk dredged in 1869. *Proceedings of the Biological Society of Washington* 101, 676–681.

Woodin, S.A. 1991. Recruitment of infauna: positive or negative cues? *American Zoologist* **31**, 797–807.