

# Massive recruitment of the barnacle *Semibalanus balanoides* in the Clyde Sea (Scotland, UK) in the spring of 2000

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In April 2000 a massive recruitment of the barnacle *Semibalanus balanoides* was observed in the Clyde Sea. At one location 700 cyprids  $l^{-1}$  of this species were recorded. This is  $\sim 3500$  times more abundant than previously recorded, and resulted in metamorphosis of some cyprids whilst still in the plankton, as well as massive settlement, with recruits found on adults and in the splash zone. The maximum density recorded was 109 settlers  $cm^{-2}$ . Over the next 60 d mortality averaged 85%, resulting in a mean density of 8.4 recruits  $cm^{-2}$  in June 2000. Recruitment varied spatially at the km and m scale (site, shore height) but there was no evidence that it was affected by the presence of adult conspecifics.

In the Clyde Sea the acorn barnacle, *Semibalanus balanoides* (L.), is abundant on intertidal rocks from the confluence with the Irish Sea as far up the estuary of the River Clyde to the east of Dumbarton. The growth of Clyde barnacles can be fast, and fecundity is the highest recorded in Europe, with up to 8000 eggs per 1.5 mg of adult somatic tissue (Barnes & Barnes, 1968). With only 3–4 weeks between release of nauplii and cyprid settlement, and restricted flows over the shallow sill at the southern end, it is likely that many of the offspring are retained within the Clyde Sea. This frequently leads to heavy settlement of cyprids in the spring, which has made the Clyde Sea a focus for research on barnacles for the past five decades. Such appearance of a massive cohort of one species can have strong ecological impacts on a whole community. In the spring of 2000, recruitment intensity of *S. balanoides* was surprisingly high, and we here report on this extraordinary recruitment event.

The first observations were made on 10 April 2000 during a visit to a rocky shore 2 km north of Largs (Figure 1A). The rocks were at that time covered with non-metamorphosed cyprids. The concentration of cyprid larvae near Largs on 14 April was estimated from three 1-l water samples collected (along 50 m shore line) from the upper 30 cm of surface water during high tide. Larvae were identified to *S. balanoides*. The mean density was  $700 \pm 420$  (SD) cyprids  $l^{-1}$ , which compares with previously reported maxima of 6 cyprids  $l^{-1}$  for *Balanus crenatus* (Grosberg, 1982) and only  $< 0.2$  cyprids  $l^{-1}$  for *S. balanoides* (Gaines & Bertness, 1993). Thus cyprid density of *S. balanoides* in the Clyde Sea estimate was  $\sim 3500$  times greater than found elsewhere.

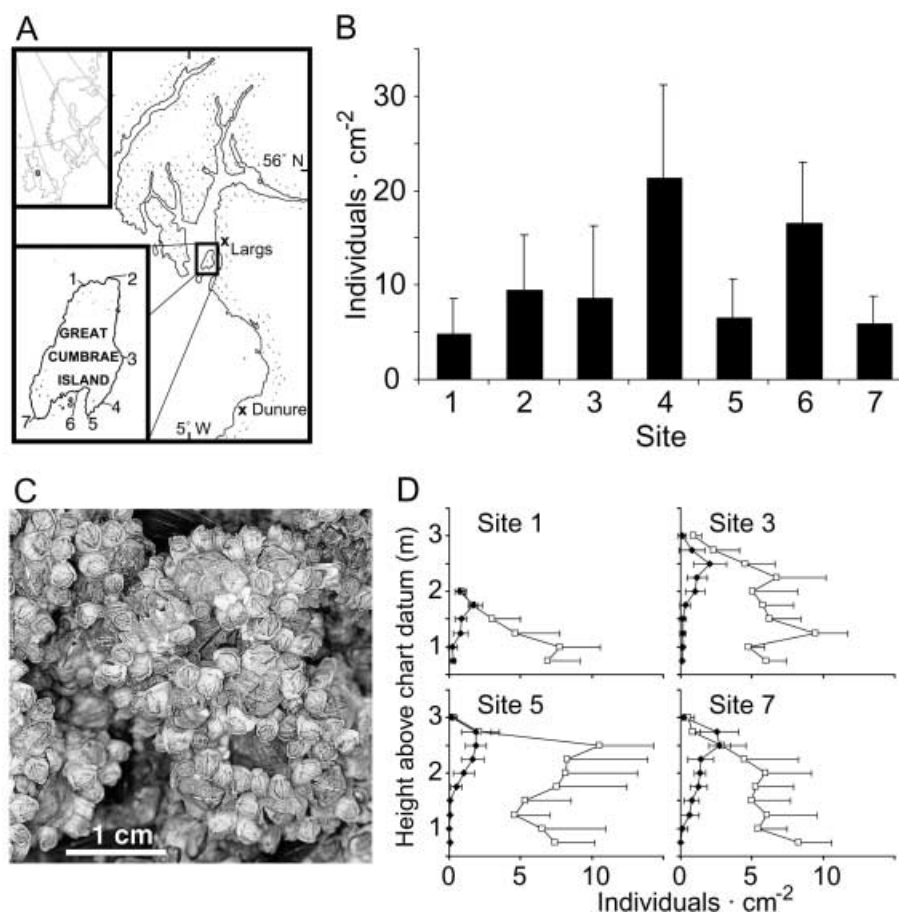
A very high, albeit not quantified, concentration of planktonic cyprids was observed as far south as Dunure, 48 km south of Largs (Figure 1A), and we believe that the density estimates may be representative for the eastern coastal waters of the Clyde Sea. However, considering the low plankton sampling frequency, we can only speculate about total abundance in the area. Average abundance of sexually mature barnacles (here defined as  $> 1$ -year old) in the barnacle zone was  $0.8 cm^{-2}$  (Figure 1D). These produce approximately 5000 eggs  $ind^{-1}$  (Barnes & Barnes, 1968). The number of offspring from these barnacles would thus only be sufficient to fill a 3 m (which was the vertical distribution

of barnacles in the intertidal zone) deep water body, reaching 57 m from the shore, with the observed 700 cyprids  $l^{-1}$ . An accumulation of cypris larvae near the shore at the time for metamorphosis therefore seems likely, emphasizing the important, but largely unknown, accumulation and retention of intertidal planktonic larvae close to the shore at the time for metamorphosis (Warner & Cowen, 2002). Winds and intensity of the spring diatom bloom have long been regarded as causative factors for the annual variation of cyprid larvae in the Clyde Sea.

With such high near-shore densities, it was not surprising to note intense competition for space, with larvae settling well up in the splash zone and on conspecific adults (Figure 1C). We recorded up to 14 recruits  $cm^{-2}$  on adults in June 2000. Lack of available space intensifies settlement rates, and in this case appears to override some physical and chemical cues governing larval choice. We even noted metamorphosing unattached cyprids in the plankton samples: presumably individuals unable to find available space prior to metamorphosis.

Density of newly settled cyprids in Largs was recorded from photographs taken of rocks with a ruler as a reference. The number of settlers in 10 to 27  $cm^2$  was counted. Mean abundance on 18 April below the zone of adult barnacles ( $\sim 1.3$  m above chart datum (acd)) was  $32.9 \pm 7.1$  settlers  $cm^{-2}$ , while within the adult barnacle zone, but on rock surfaces void of adults ( $\sim 2.3$  m acd) it was  $80.5 \pm 40.8$  settlers  $cm^{-2}$ . In this zone we found a maximum density of settlers of 109.3 settlers  $cm^{-2}$ . This is higher than any previous report of *in situ* settler or recruit density that we have found. During a revisit to the Largs site on 15 May 2000 the rocks  $\sim 2$  m acd were covered with metamorphosed recruits with a mean density of  $34.3 \pm 3.4$  recruits  $cm^{-2}$ .

In mid-June 2000 the density of *S. balanoides* recruits was quantified at seven sites around the Isle of Cumbrae,  $\sim 10$  km from the mainland Largs site (Figure 1A). Recruits were enumerated in 10, 25  $cm^2$  quadrats at 1.5 m acd. Overall mean density was  $8.4 \pm 7.4$  recruits  $cm^{-2}$ , with a maximum density of 35.9 recruits  $cm^{-2}$  at Keppel Pier (Figure 1B). There was a significant difference in recruitment densities between sites (square-root transformed data, one-way analysis of variance (ANOVA),  $F_{[1,6]}=18.9$ ,  $P < 0.001$ ). Mortality rates over the 60 d from April to June was



**Figure 1.** (A) Map of sites surveyed in the Clyde, 1, Stinking Bay; 2, Tomont End; 3, Clashfarland Point; 4, Keppel Pier; 5, Farland Point; 6, Kames Bay; 7, Portachur Point; (B) densities (mean  $\pm$  1SD) of *Semibalanus balanoides* recruits at the seven sampling sites on Isle of Cumbrae (Longitude 4°55'W Latitude 55°46'N); (C) recruits of *S. balanoides* on conspecific adults; and (D) densities (mean  $\pm$  1SD) of *S. balanoides* adults (filled) and recruits (open) by height above chart datum for four of the sites.

85%, or 1.4% of initial density per day, equivalent to 0.8 recruits  $\text{cm}^{-2} \text{d}^{-1}$ , assuming a constant linear mortality rate. Such mortality rates are common for benthic invertebrates.

The vertical distribution of both adults and recruits was also quantified at four of these sites in June, 2000 by enumerating 10, 25  $\text{cm}^2$  quadrats at stations with 25 cm vertical separation from 0.75 to 2 m a.c.d. There was no significant correlation between adult and recruit densities ( $r = -0.18$ ,  $P = 0.28$ ), but there was a highly significant difference in recruit densities by site (Figure 1D, two-way ANOVA, square-root transformed data,  $F_{[3,216]} = 12.4$ ,  $P < 0.001$ ), height ( $F_{[5,216]} = 5.7$ ,  $P < 0.001$ ), and height  $\times$  site ( $F_{[15,216]} = 5.0$ ,  $P < 0.001$ ). Similarly there were highly significant differences for adult densities by site ( $F_{[3,216]} = 28.0$ ,  $P < 0.001$ ), height ( $F_{[5,216]} = 47.7$ ,  $P < 0.001$ ), and height  $\times$  site ( $F_{[15,216]} = 5.5$ ,  $P < 0.001$ ). Thus, adult densities vary by site and shore height, but recruitment densities, although varying by site and height do not correlate with adult numbers. Presumably, massive settlement intensification overrides spacing behaviour in settlers. However, extreme settlement does not result in extreme adult densities, as high-density recruitment can lead to the formation of hummocks containing elongate barnacles that are extremely fragile (Barnes & Powell, 1950), resulting in very high mortality between recruitment and adulthood.

These data show that the Clyde Sea has the highest reported densities of planktonic cyprids. This huge number of potential settlers results in larval behaviours that appear to override 'normal' settlement cues and behaviours, and this results in

extreme settlement. Such high settlement densities are known to be potentially deleterious, resulting in very high adult mortality and low fecundity.

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