

Doses of darkness control latitudinal differences in breeding date in the barnacle *Semibalanus balanoides*

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This paper reports the first study of breeding in the boreo-arctic barnacle *Semibalanus balanoides* in which latitudinal variation in timing of egg mass hardening has been examined simultaneously over the geographical scale involved, thereby excluding temporal confounding of the data. The timing of autumn egg mass hardening on the middle shore was established in 2002 and 2003 at ten stations ranging latitudinally from Trondheim (63°24'N) to Plymouth (50°18'N). To assess variation at local scale (<10 km), breeding was studied on three shores at each of two Irish locations (Cork and Galway). At Oban (Scotland) and Cork, the effect of shore height on timing of breeding was investigated. A strong influence of latitude and day length on timing of breeding was found in both 2002 and 2003. In both years, barnacles bred much earlier (when day length was longer) at high rather than low latitudes. No significant effect of environmental temperature or insolation on timing of breeding was detected. Shores no more than 10 km apart showed minimal difference in middle shore breeding date (<4 days). However, upper shore barnacles bred significantly earlier (by 7–13 days) than middle shore animals. The data indicate that breeding is controlled by period of daily darkness, with high shore animals encountering longer effective 'nights' because of the opercular closure response to emersion (which will reduce light penetration to tissues). Predictions concerning the effects of global changes in climate and cloud cover on breeding and population distribution are made. It is suggested that increased cloud cover in the northern hemisphere is likely to induce earlier breeding, and possibly shift the present southern limit of *Semibalanus* southwards.

INTRODUCTION

The boreo-arctic intertidal barnacle *Semibalanus balanoides* (L.) releases its nauplii in spring/summer, when they are able to take advantage of the phytoplankton bloom. *Semibalanus* produces a single brood each year and the eggs and nauplii develop over the autumn and winter during a prolonged period of anecdyosis (Rainbow, 1984). There is extensive literature on the breeding of the species (see Klepal, 1990; Anderson, 1994 for reviews). Whereas naupliar release in spring/summer varies considerably in timing (by several weeks at a single location and by many months over the species distribution), the autumn onset of breeding (gonad maturation and fertilization of the egg masses) apparently varies at a given location only by a few days (King et al., 1993).

The environmental control of gonad maturation and fertilization is still unresolved, though Tighe-Ford (1967) showed that constant light inhibited the process, while Barnes & Stone (1972) showed that penis development (a necessary prerequisite to copulation) is inhibited by light. Davenport & Crisp (unpublished data from Menai Bridge,

Wales) found that experimental exposure to either constant darkness, or 6 h light: 18 h dark photoperiods induced autumn breeding in *Semibalanus*. They also confirmed that very low continuous light intensities (little more than starlight) inhibited breeding. However, it is not known whether there is any thermal modulation of the process. It is a general feature of ectothermic animals that gonad and egg development takes longer at lower temperatures. Our study aimed to elucidate environmental control, and determine whether time of egg mass hardening might be a useful tool for monitoring response to climate change (comparable perhaps to the shifts in breeding times shown for some passerine birds; Sanz, 2002). It is easy to distinguish solid ('hard'), fertilized egg masses from soft, developing ovaries; this is an all-or-nothing endpoint and requires minimal skill to monitor.

MATERIALS AND METHODS

First, the proportion of hard (=fertilized) egg masses was monitored in the autumn of two years (2002/2003) at

Table 1. Latitude and longitude of sampling sites.

Site	Latitude	Longitude
Trondheim	63°24'N	10°25'E
Bremanger	61°50'N	4°52'E
Bremanger S*	61°48'N	4°58'E
Bergen*	60°17'N	5°14'E
Kristineberg	58°15'N	18°35'E
Oban	56°27'N	5°29'W
Menai Bridge	53°12'N	4°10'W
Galway	53°12'N	9°3'W
Cork	51°42'N	8°28'W
Plymouth	50°18'N	4°10'W

*, sites sampled in 2002 only.

sites (Table 1) readily accessible to the project participants over as wide a range of latitude as possible, and at which the *Semibalanus* were distributed densely enough to permit cross fertilization. During 2002, at each of ten sites, 50 barnacles scraped from rocks on the middle shore at weekly intervals were assessed from August until all egg masses were hard. Once some egg masses were hard, the frequency of monitoring was increased as convenient to participants. The time (Julian day) corresponding to 50% of the barnacles exhibiting egg mass hardening was estimated to the nearest day by probit analysis (Finney, 1971). During 2003 the exercise was repeated, but operational problems reduced the number of sites to eight, while monitoring was not started until one month prior to the critical dates recorded in 2002 (to reduce observer effort). In 2002 and 2003 surface seawater temperatures at the time of breeding were ascertained from ORAD satellite data for nearby offshore waters (source: website 1). In 2003 these temperature values were supplemented by surface water temperatures collected from nearby inshore waters by the study participants.

Second, at two sites (Oban and Cork; Table 1) the effect of shore height on time of egg mass hardening was assessed in 2003. In this case 50 *Semibalanus* were also scraped from rock at the uppermost limit of distribution on each of the sampling occasions when middle shore animals were studied.

Third, at two sites (Galway and Cork, Table 1) the effect of relatively small geographical distances on time of egg mass hardening was assessed in 2003. In this case three different shores within a total distance of < 10 km were selected at each site. At Galway the shores were: Furbo (main reference site: 53°14.947'N 9°13.353'W), Spiddal (53°14.601'N 9°17.975'W) and Barna (53°14.927'N 9°09.016'W). At Cork the shores were: Kinsale Harbour (the main reference site: 51°41.805'N 8°30.895'W), Sandy Cove (51°40.628'N 8°31.426'W) and Bullens Bay (51°38.584'N 8°33.052'W).

Relationships (using untransformed data) between Julian date corresponding to 50% hardness and latitude, day length, temperature and insolation (calculated from Pidwirny, 1999–2004) were investigated by polynomial regression analysis (MINITAB) at linear, quadratic and cubic levels. Quadratic equations invariably gave better fits (higher R^2 values) than linear regressions, but cubic equations yielded negligibly better fits, and poorer visual correlations with data. The relationship between day

Table 2. Significant relationships between variables.

A. 2002.	
a) Latitude	$y = 1076 - 24.5x + 0.19x^2$ $r^2 = 81.7\%$ $P = 0.0026$
where y = Julian day corresponding to 50% egg mass fertilization	x = latitude (°)
b) Day length	$y = 615 - 47.9x + 1.53x^2$ $r^2 = 64.4\%$ $P = 0.0269$
where y = Julian day corresponding to 50% egg mass fertilization	x = day length (h)
B. 2003.	
a) Latitude	$y = 870 - 16.5x + 0.12x^2$ $r^2 = 96.8\%$ $P = 0.0002$
where y = Julian day corresponding to 50% egg mass fertilization	x = latitude (°)
b) Day length	$y = 1679 - 273x + 13.38x^2$ $r^2 = 94.8\%$ $P = 0.0006$
where y = Julian day corresponding to 50% egg mass fertilization	x = day length (h)
c) Latitude and day length	$y = 2.94 + 0.108x$ $r^2 = 89.0\%$ $P < 0.0001$
$\log y = 0.668x - 0.215$ $r^2 = 88.1\%$ $P < 0.0001$	
where y = day length (h) corresponding to 50% egg mass fertilization	x = latitude (°) corresponding to 50% egg mass fertilization

length corresponding to 50% fertilization and latitude corresponding to 50% fertilization was similarly investigated, using both logged (\log_{10}) and non-logged data. Julian dates for 50% hardness were compared between Cork and Galway sites and were compared using Student's *t*-test.

RESULTS

A strong influence of latitude on timing of *Semibalanus* breeding was found in both 2002 and 2003. (Table 2, Figure 1). In both years, barnacles bred much earlier at high rather than low latitudes. Given a Julian date and latitude it is possible to calculate theoretical day length on that date for a given site (source: website 2). When the relationship between day length and timing of egg mass hardening was investigated, strong relationships were again revealed in both years (Table 2, Figure 2). In this case, breeding took place when day length was longer at high latitudes than it was at low latitudes. For example: in 2003 50% egg mass hardening was recorded on 16 October (Julian day 289) at Trondheim when day length

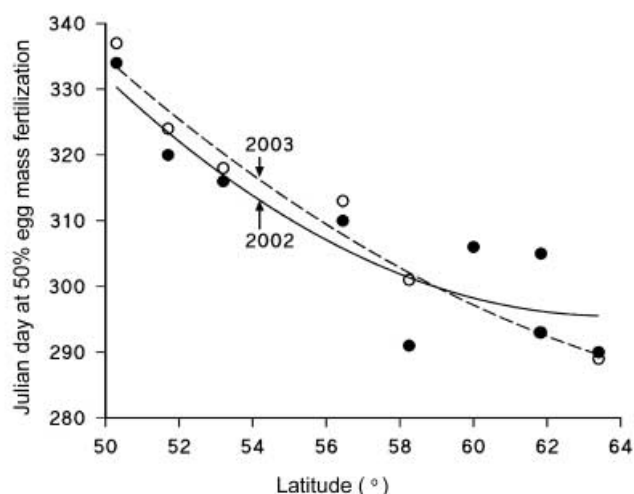


Figure 1. Relationship between latitude ($^{\circ}$ North) and time of breeding in *Semibalanus balanoides*. Closed circles, 2002; open circles, 2003.

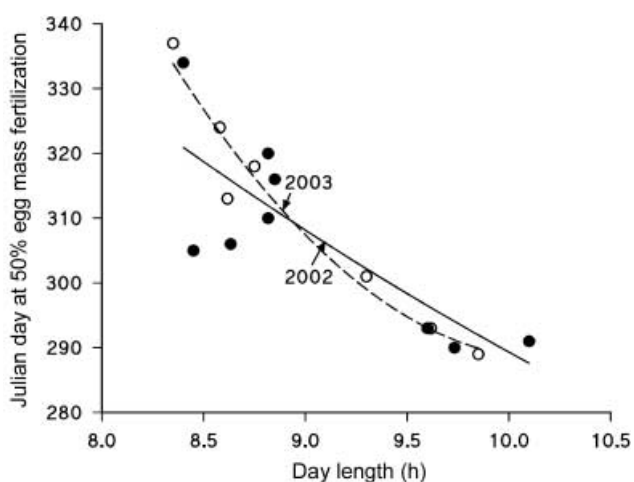


Figure 2. Relationship between day length and time of breeding in *Semibalanus balanoides*. Closed circles, 2002; open circles, 2003.

was 9.85 h, while at Plymouth the same stage was not reached until 2 December (Julian day 337) when the day length was 8.35 h. The relationship between day length and latitude corresponding to 50% egg mass hardening was investigated for 2003 (Table 2). There was a highly significant linear relationship ($P < 0.0001$) whether data were log transformed or not.

Insolation (intensity of solar radiation; affected by a combination of day length and sun angle above the horizon) decreases with Julian date in temperate northern latitudes (see Figure 3). However, although day length clearly had a significant influence on breeding time, insolation values calculated from Pidwirny (1999–2004) did not (2002: $r^2 = 30.7\%$, $P = 0.277$; 2003: $r^2 = 59.4\%$, $P = 0.105$).

In 2002 surface seawater temperatures at the time of breeding were ascertained from ORAD satellite data for nearby offshore waters. There was no significant correlation between Julian date corresponding to 50% egg mass hardening and environmental temperature (polynomial

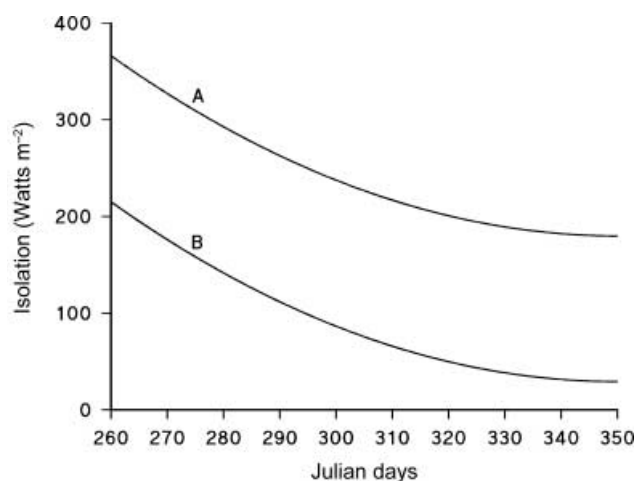


Figure 3. Relationship between insolation and Julian day at (A) 50° N and (B) 60° N (calculated from Pidwirny 1999–2004, and from Lalli & Parsons, 1997).

[quadratic] regression: $r^2 = 34.3\%$, $P = 0.230$). In 2003 this calculation was repeated with similar results ($r^2 = 37\%$, $P = 0.306$). In 2003 surface temperatures collected from coastal waters as close as possible to the study sites revealed a similar picture. Temperatures at the time of 50% egg mass hardening ranged from 1°C (Bremanger), to 12.4°C (Plymouth). There was no significant correlation between Julian date corresponding to 50% egg mass hardening and environmental temperature (polynomial [quadratic] regression: $r^2 = 38.5\%$, $P = 0.128$). It should be noted that temperature also varied greatly over short periods and was subject to local influences (e.g. at Bremanger cold freshwater input was apparently responsible for low surface temperatures).

Table 3 shows the influence of shore height on timing of breeding. At the Oban and Cork sites barnacles on the upper shore showed 50% egg mass hardening several days before those on the middle shore (Oban: 7 days difference, Cork: 13 days). In each case the difference was statistically significant (probit analysis (Finney, 1971); $P < 0.05$).

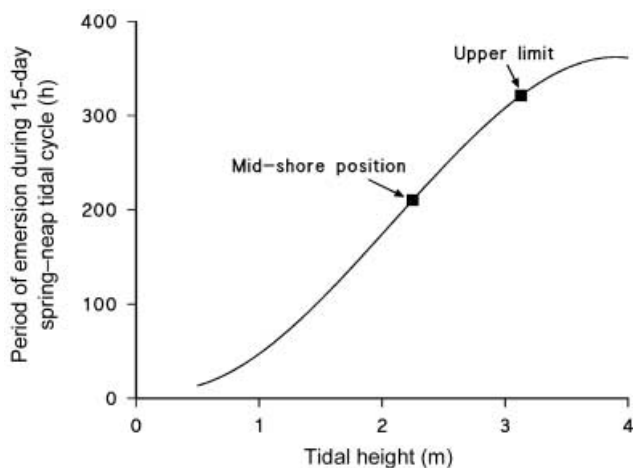
Table 4 shows egg mass hardening dates for *Semibalanus* collected from three closely-located shores (< 10 km) at each of two Irish sites. While there was a significant difference in mean egg mass hardening date between the

Table 3. Timing of egg mass hardening in *Semibalanus balanoides* on upper and mid-shores at two sites in 2003.

Site	Julian day corresponding to 50% egg mass fertilization
A. Oban	
a. Upper shore	306
b. Middle shore	313
B. Cork	
a. Upper shore	311
b. Middle shore	324

Table 4. Timing of egg mass hardening in *Semibalanus balanoides* at mid-shore level at locations in Galway and Cork in 2003.

Site	Location	Julian day corresponding to 50% egg mass fertilization
A. Galway shores		
Furbo	53°14.947'N 9°13.353'W	318
Spiddal	53°14.601'N 9°17.975'W	322
Barna	53°14.927'N 9°09.016'W	319
B. Cork shores		
Kinsale Harbour	51°41.805'N 8°30.895'W	324
Sandy Cove	51°40.628'N 8°31.426'W	327
Bullens Bay	51°38.584'N 8°33.052'W	323

**Figure 4.** Relationship between shore position of *Semibalanus balanoides* and period of emersion during September 2003 spring–neap tidal cycle at White Bay, Isle of Cumbrae (55°46'N 4°55'W). Upper limit is mean of three transects. Emersion time at upper limit = 321 h; emersion time at midshore position = 210 h.

Galway and Cork sites (t -test; $P=0.042$), dates for the shores at each site varied by only four days in each case.

DISCUSSION

This study was essentially correlative. While correlation does not equal causation, our data and analysis, in combination with previous observations (Tighe-Ford, 1967; Barnes & Stone, 1972; Davenport & Crisp, unpublished data), indicate that breeding onset in *Semibalanus* is controlled primarily by light/dark regimes that are dependent on latitude. Temperature appears to have no significant influence. Because daily insolation is not correlated with breeding, yet day length is, it seems probable that it is the period of darkness rather than the period of light that is effective. However, there will obviously have to be a threshold of light intensity that the barnacles perceive as 'dark'. It is inevitable that the timing of attaining this threshold will be influenced by cloud cover and physical

topography (aspect, shelter). Variations in these latter factors (not considered in the present study) may be responsible for 'noise' and inter-year variability in our results. We predict that barnacles will breed earlier in crevices or on the undersides of rock than upon surfaces receiving more light. Breeding on north-facing shores will probably be earlier than on south-facing shores. It is likely that breeding will be earlier on sheltered shores with algal cover than upon exposed shores with stunted and sparse macroalgae. Tidal range would be expected to affect the interval between first and last breeders on a given shore; we would expect the interval to be greater on shores with greater tidal range.

The period of darkness needed to trigger breeding is longer (i.e. shorter day length) at lower latitudes (Table 2). This may be a manifestation of the Weber–Fechner Law (that to increase the intensity of sensation in an arithmetic progression, it is necessary to increase the intensity of the stimulation in a geometric progression). As the autumn progresses, the rate of change of day/night length progressively decreases. At high latitudes at the beginning of autumn, night length increases more rapidly than it does at low latitudes later in the year. Sensory systems are normally sensitive to rate of change in variables as well as to absolute values. It is suggested that a longer dose of darkness is required to stimulate breeding in *Semibalanus* at lower latitudes because the rate of change of night length is lower. Further study to test this hypothesis more rigorously would be desirable.

A breeding system triggered wholly by declining day length/increased length of darkness has a fundamental limitation—breeding onset must be accomplished by 21 December (Julian day 355) when day length is shortest. By extrapolation from the relationships between latitude and time of breeding onset shown in Table 2, we can predict that the southern European limit for breeding in *Semibalanus* would be around 42°N (using the 2002 equation) or 48°N (using the 2003 equation). These values encompass the southern part of the Bay of Biscay and the coast of northern Spain. This coincides reasonably well with published data for the southern limit of intertidal distribution in *Semibalanus* (Southward et al., 1995).

If one assumes that reduced day length/increased night length triggers egg mass hardening, then it might be expected that hardening would start earlier in the upper part of the distribution of the barnacle on the shore than lower down, simply because seawater absorbs light so that 'night' starts and ends earlier lower on the shore. Yet the data collected from Oban (Scotland) and Kinsale Harbour, Co. Cork (Ireland) showed that the reverse is the case—barnacles on the upper shore exhibit hardened egg masses some days before those sampled on the middle shore (Table 3). The explanation probably lies in the response of *Semibalanus* to emersion. All intertidal barnacles respond to emersion by closure of the opercular plates which presumably reduces the quantity of light penetrating to light sensors. Some species display a pneumostome at intervals, which would let light in, but *Semibalanus* usually does not (Davenport & Irwin, 2003). Presumably the tissues of emersed barnacles are exposed to longer periods of low light intensities perceived as 'darkness' than are immersed barnacles. Figure 4 shows that there is a strong influence of height of distribution on the

shore and period of emersion in *Semibalanus*. It seems probable that the longer period of emersion higher on the shore offsets the higher light intensities encountered by high shore *Semibalanus* during immersion.

Why should *Semibalanus* rely on darkness cues for initiation of breeding rather than temperature signals? Breeding in the species is apparently arranged so that fertilized eggs develop over the winter period so that competent nauplii are available whenever the spring bloom occurs (see Rainbow, 1984). Energy accumulated during the spring and summer is used for gonadal development in advance of autumn breeding. Increasing length of darkness is a much more predictable signal than temperature, particularly if the threshold of darkness is set at a low light intensity, so that night length varies relatively little between clear and cloudy conditions. In contrast, autumn spells of cold or warm weather can markedly, and often unpredictably, influence exposure temperatures, particularly in a species such as *Semibalanus* that encounters both air and seawater temperatures. In many ways this situation is analogous to that seen for a variety of mammals that enter hibernation in autumn in response to relatively stable light cues rather than variable temperatures (see Davenport, 1992 for review). Clearly the earlier onset of breeding at higher latitudes (coupled with a tendency towards later spring blooms) means that egg and naupliar development in *Semibalanus* takes substantially longer at high latitudes. This is consistent with the generally slower processes of development at high latitude that result from lower average temperatures.

The results of our study suggest that timing of breeding in *Semibalanus* will not be directly influenced by global seawater temperature changes to any significant extent. However, global climate change is likely to involve changes in cloud cover, and hence effective length of nights. Indeed, there is some evidence that significant reductions in global radiation (~10%; predominantly due to increased cloud cover) have already taken place in the last few decades ('global dimming'; Stanhill & Cohen, 2001; Liepert, 2002; Roderick & Farquhar, 2002). There is currently a consensus that global warming will be accompanied by increased storminess in the northern hemisphere, which will also tend to produce increases in average cloud cover over the distributional range of *Semibalanus*. If *Semibalanus* does not adapt to changing regimes fast enough, we would predict a trend towards earlier breeding in the species, because the duration of perceived darkness will be extended. If this prediction proves to be correct, we would also expect breeding to be possible further south than at present. This opens up the paradoxical possibility of global warming extending the range of an arcto-boreal species southwards.

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