

Spatial variation in size and density of adult and post-settlement *Semibalanus balanoides*: effects of oceanographic and local conditions

M. T. Burrows^{1,*}, S. R. Jenkins², L. Robb¹, R. Harvey¹

¹Department of Ecology, Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll, PA37 1QA, UK

²School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, UK

ABSTRACT: Regional oceanographic processes are emerging as strong influences on growth and recruitment of intertidal species, with important consequences for populations. Yet local conditions such as wave exposure are also important. To disentangle these effects for the intertidal barnacle *Semibalanus balanoides*, we surveyed 259 sites around Scotland in July and August over 6 yr (from 2001 to 2006). Scaled digital photographs at 3 shore levels gave sizes and densities of juvenile and adult barnacles for comparison with wave fetch, remotely sensed chlorophyll *a* (chl *a*) concentration and seasonal sea surface temperature (SST). Patterns were also compared with site 'openness': the area of connected open sea <30 km away. Patterns at the 3 shore levels were similar. Hierarchical partitioning (HP) showed that survey year had the biggest effect and improved the predictive power of other variables: wave fetch for adult and juvenile densities, chl *a* for juvenile size and openness for adult size. SST had little effect. Regression models selected using information theoretic measures included positive effects of chl *a*, varying among surveys, on average size of barnacles (R^2 from 0.5 to 0.6), and larger high shore barnacles in greater wave exposure. Population densities of adults and juveniles increased with wave fetch, with chl *a* only influencing density at high shore levels (R^2 from 0.1 to 0.4). Despite temporal and spatial variation in responses to chl *a* and wave fetch among surveys, relationships were consistent with growth and size in *S. balanoides* being limited by food supply, and increased recruitment and adult densities in increased wave exposure. Large-scale ecological patterns in this rocky intertidal species thus result from large-scale oceanographic effects on food concentration with habitat-scale wave-mediated effects on supply of food and larvae.

KEY WORDS: Phytoplankton · Wave exposure · Growth · Recruitment · *Semibalanus balanoides*

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Large-scale ocean circulation patterns play an important role in determining ecosystem structure and functioning in coastal benthic communities and may contribute to observed spatial variability in the relative importance of different processes. Studies of intertidal communities on western continental coastlines in particular, contrasting areas of productive upwelling with interspersed less productive non-upwelling regions, have showed that the structure and dynamics of these

communities are strongly linked to spatial variation in coastal oceanographic features (Menge et al. 1999).

For populations of sessile intertidal invertebrates, the focus of this study, oceanographic conditions have 3 distinct modes of direct effects. (1) Supply of planktonic larvae to the adult habitat depends on physical transport processes. These include tidally driven currents and internal waves which can have an important role in moving larvae shoreward (Pineda 1991). Inter-annual variation in upwelling can affect supply and consequent yearly patterns of settlement along coasts

*Email: mtb@sams.ac.uk

where such features dominate (Gaines & Roughgarden 1985), while local wind-driven flows influence settlement rate (e.g. Hawkins & Hartnoll 1982). Patterns of current flow ultimately result in site-specific transport patterns, as described by dispersal kernels (Aiken et al. 2007), and thus determine population connectivity (Pineda et al. 2007). (2) Oceanographic conditions influence phytoplankton productivity, and this affects feeding success and energy content of dispersing planktotrophic larvae, with continuing effects on post-settlement survival (Emlet & Sadro 2006). In filter feeders such as barnacles, post-settlement growth rates are increased by higher phytoplankton biomass (Menge et al. 1997, Sanford & Menge 2001), while size-specific egg numbers and thus fecundity are also dependent on food supply (Leslie et al. 2005). (3) At ocean scales, current-driven heat fluxes structure regional climates, with consequent effects (e.g. El Niño) that often trump smaller scale influences of oceanographic conditions on coastal marine systems.

On the coast itself, local habitat conditions have a similarly large influence on intertidal populations, evident from variation in community structure. Wave exposure has the most obvious effect: on cold temperate shores, wave-sheltered shores are characterised by large fleshy macroalgae, while wave-exposed shores have algae with tougher, shorter thalli or encrusting forms, and are often dominated by filter feeders (Burrows et al. 2008). While some effects of wave action are obvious, such as physical damage or removal (Gaylord et al. 1994), other effects may be due to modification of species interactions, such as reduction in predation by mobile species (Menge & Sutherland 1987). Species interactions directly affect settling larvae: algae may limit access of barnacle larvae to the substratum (Jenkins & Hawkins 2003), inhibit settlement by sweeping (e.g. Jenkins et al. 1999), while grazers may remove or consume cyprids (Hawkins 1983).

Oceanographic and local influences interact to produce observed patterns of population densities and size structure. Local water flow rates, influenced by wave exposure and coastal tidal currents, combine with the concentration of food and larvae in the water column to determine supply to intertidal communities. Settlement rate is closely related to larval supply (Todd et al. 2006) and may be expected to be higher in areas of higher flows. Flow may thus regulate recruitment and ultimately play a major role in determining adult densities. Juvenile densities reflect levels of settlement and hence differences in larval supply: between habitats (Gaines et al. 1985), along vertical gradients (Grosberg 1982), along gradients of wave exposure (Jenkins 2005), among years of varying coastal upwelling (Roughgarden et al. 1988), among areas with different degrees of flushing (Bertness et al. 1992), and between

periods of wind-driven advection (Hawkins & Hartnoll 1982, Bertness et al. 1996). Flow-related growth effects on filter feeders such as barnacles and mussels are evident. High flow also causes enhanced growth in the barnacle *Semibalanus balanoides* at sites characterised by both low and high ambient chlorophyll *a* (chl *a*) concentrations, with significant effects on population dynamics (Sanford et al. 1994).

Semibalanus balanoides has thus far proved to be a good indicator of the 3 major modes of oceanographic effects: (1) transport and supply of larvae, (2) food supply effects on growth and fecundity and (3) regional climate, which can influence the outcome of competition between northern and southern species (Poloczanska et al. 2008). *S. balanoides* is a near ubiquitous organism on rocky shores in the North Atlantic, with a wide geographic distribution that exposes this species to a wide range of oceanographic conditions. This makes the species a good choice for disentangling local from oceanographic effects on population structure.

Indices of topography derived from coastline data, such as wave fetch (Burrows et al. 2008), have proved powerful predictors of community patterns. Combined with the ready availability of remotely sensed sea temperature and ocean colour data as an indicator of phytoplankton food supply, these indices allow relationships to local conditions to be distinguished from responses to larger scale patterns of temperature and food. We used these indices and remotely sensed measures to develop hypotheses as to the roles of oceanographic versus local determinants of population structure in *Semibalanus balanoides*. We predicted that (1) food supply modified by flow rate would determine growth rate in this barnacle, and that this would result in larger barnacles for a given age and a shift towards larger average size in areas of higher food concentrations and faster flow. (2) Faster flow rate was also predicted locally to enhance larval supply and thus settlement density, with greater density-dependent mortality at high settlement sites (Jenkins et al. 2008) and a potentially faster turnover in these populations.

We exploited the fjordic and island-based geography of the west coast of Scotland to quantify variability in population density and size distributions of adult and juvenile *Semibalanus balanoides* at over 250 sites in contrasting regional and local conditions to test these hypotheses. We used a recently developed model (Burrows et al. 2008) to determine likely wave exposure at our survey sites. An additional consequence of variable shoreline topography as well as small-scale differences in wave exposure is differences in the 'openness' or degree of enclosure of sites which may have important effects on larval dispersal and supply. We aimed to

develop predictive regression models of size and density of adult and juvenile *S. balanoides*. From emerging patterns, we aimed to draw inferences as to the relative roles of population processes acting at spatial scales from local to regional, and to test the generality of previously reported effects of ocean climate on intertidal species.

MATERIALS AND METHODS

***Semibalanus balanoides* population surveys.** *S. balanoides* populations were assessed at 259 sites around Scotland in the summers of 2001 to 2006 inclusive (Table 1). Sites were selected as readily accessible, within 20 to 30 km of other sites to visit on the same low tide, and meeting particular geographical criteria for that year's survey (Table 1). Locations of sites were recorded using handheld global positioning system (GPS) receivers (Garmin GPS76) at mid shore level.

At each site, areas with *Semibalanus balanoides* populations were selected at 3 shore levels, away (>20 cm) from macroalgal plants where possible. Shore levels were chosen as (1) low shore (henceforth LW), just above the lower limit of the barnacle zone, (2) high shore (HW), 10 to 20 cm vertically below the upper limit of *S. balanoides*, and (3) mid shore (MW), midway between low and high levels. Four digital camera images of groups of barnacles were taken at each level at a minimum resolution of 1024 × 768 pixels, always including a scale object of known dimension. Images typically covered areas of from 20 to 120 cm².

Analysis of digital images was made using custom-written image coordinate recording software (using Microsoft Visual Basic™). Depending on the density of barnacles, areas from 4 cm² (>20 barnacles cm⁻²) to 40 cm² (<0.2 barnacles cm⁻²) were randomly located as quadrats within each image. Operculum lengths and species identity of all adult (1+) barnacles in each quadrat were recorded. Juvenile (0+) barnacles were

distinguished from adults (1+) by the absence of shell erosion and fusion of parietes, the lighter colour of newly laid down shell and lack of surficial microalgae (making 1+ *Semibalanus balanoides* appear yellow), and their size (generally smaller than adults) at the time of sampling. *Chthamalus montagui*, *Chthamalus stellatus* and *Elminius modestus* made up <5% of barnacles seen, and, although recorded in the same way as *S. balanoides*, patterns in these species are not described here. Twenty (or fewer, if numbers were insufficient) randomly selected 0+ *S. balanoides* were measured in each quadrat, and the number of unmeasured juveniles was counted. Densities were calculated for each quadrat for adults from the numbers measured and from total counts (measured and unmeasured barnacles) for juveniles.

chl *a* and sea surface temperature from satellite remote sensing. Surface chl *a* concentrations for seas around Scotland were taken from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and Medium Resolution Imaging Spectrometer (MERIS) satellite sensors, and sea surface temperatures (SST) were taken from Advanced Very High Resolution Radiometry/Radiometer (AVHRR) satellite sensors, obtained from web data portals (SeaWiFS and MERIS: European Commission Joint Research Centre Ocean Colour Portal: <http://mersea.jrc.ec.europa.eu/>; AVHRR: <http://podaac.jpl.nasa.gov/>). Inspection of monthly composite images showed that spatial patterns of chl *a* were relatively stable throughout the year, while SST patterns varied seasonally. A 2 km resolution composite chl *a* image was calculated by averaging all monthly composites from January 2000 to December 2006. Average SST images were calculated for February, May, August and November using monthly composite images for the years 2000 to 2006 inclusive. Both these sets of images were supplied processed with a land mask that excluded areas <10 km from the coast, to avoid mistaken assignment of land pixels to sea pixels due to small errors in geolocating images. To spatially match survey sites to

Table 1. Extent and timing of annual surveys of *Semibalanus balanoides* populations around Scotland from 2001 to 2006. Year day: days since the beginning of the year, for the first day of the survey; D: duration of survey in days; +/-: variable measured/not measured

| Year | Extent | Date | Year day | D | No. of sites | Adult size | Adult density | Juvenile size | Juvenile density |
|------|---|--------------|----------|----|--------------|------------|---------------|---------------|------------------|
| 2001 | W coast sea lochs | 19–31 Jul | 200 | 12 | 74 | + | – | + | + |
| 2002 | W coast | 9–17 Jul | 190 | 8 | 43 | + | + | + | + |
| 2003 | W coast | 9–21 Jul | 190 | 12 | 54 | + | + | + | + |
| 2004 | Western Isles | 30 Jun–7 Jul | 182 | 7 | 24 | + | + | – | + |
| 2004 | Orkney | 2–6 Aug | 215 | 4 | 19 | + | + | – | + |
| 2005 | E coast/Solway Firth | 22–26 Jul | 203 | 4 | 20 | + | + | + | – |
| 2006 | W coast/E coast—repeat visit to earlier sites | 9–15 Jul | 190 | 6 | 25 | + | + | + | + |

the SST and chl *a* data, we calculated neighbourhood average maps using 10 km rectangular areas around each pixel, effectively extending the images onto the coast. GIS processing was used to link site locations to SST and chl *a* pixel values. Sites without overlying pixels, at heads of sea lochs for example, were manually matched to the nearest relevant sea pixel.

Wave fetch determination. Wave fetch was determined for all 200 m coastal cells in the study area using the method of Burrows et al. (2008). This gave an estimate of the summed wave fetch in sixteen 22.5° angular sectors, up to a maximum distance of 200 km. Wave fetch thus had a maximum value of 3200 km per cell. Wave fetch values for survey sites were taken from each nearest coastal grid cell.

Coastal topography. Coastal features such as lagoons, estuaries and fjords are often described as semi-enclosed, and the degree of enclosure may have important effects on key ecological processes, particularly dispersal of larvae. We decided to quantify the degree of enclosure using a method analogous to the calculation of cost surfaces in GIS (Burrows et al. 2009) which calculates the area of open sea connected to the site within successively larger distances. A grid of 1 km land or sea cells was created from a vector coastline (GSHHS based on the World Vector Shoreline [NOAA 2006]) projected using the British National Grid. Each survey site was assigned a location at the nearest land grid cell. The first step identified all the sea cells adjacent to the site cell and assigned a distance from the site as the Euclidean separation of their cell centre (1.41 km for diagonals, 1 km for adjacent cells). In the next step, sea cells were chosen next to those cells

whose separation distance was already calculated. For each of these new cells, separation distance ($d_{x,y}$) from the site was assigned as:

$$d_{x,y} = \min_i \left(d_i + \sqrt{\Delta x^2 + \Delta y^2} \right) \quad (1)$$

where i is the set of neighbouring cells for which distance was already calculated, and Δx Δy was the distance separating the centre of the cell from the neighbour cells along the x- and y-axes of the grid. This step was repeated until distance was calculated for all the sea cells (Fig. 1) up to 50 km away from each site. The area of connected sea as a function of distance away gave the 'openness' of the site.

The form of the distance-area function reflected the coastal topography very well (Fig. 1). Open coastal sites had the most connected area for a given distance (Fig. 1A,C), and sites at the head of long fjords had the least (Fig. 1B). The area of open sea within 30 km was used as a measure of openness in analyses.

Statistical analysis. We used multiple regression in 2 ways (Mac Nally 2002) to determine (1) the proportion of variance in each response explained by each of the 5 predictor variables examined (year of observation, SST, chl *a*, wave fetch and openness), and (2) the best predictive model for each of the response variables. Hierarchical partitioning (HP) (Chevan & Sutherland 1991) was used to determine effects of each of the predictors on explained variance (1 above), using the R software package (Walsh et al. 2003). HP compares the fit of all possible models that include the predictor variable, with the fit of all the models that do not. This allows the independent and joint effects of each variable to be mea-

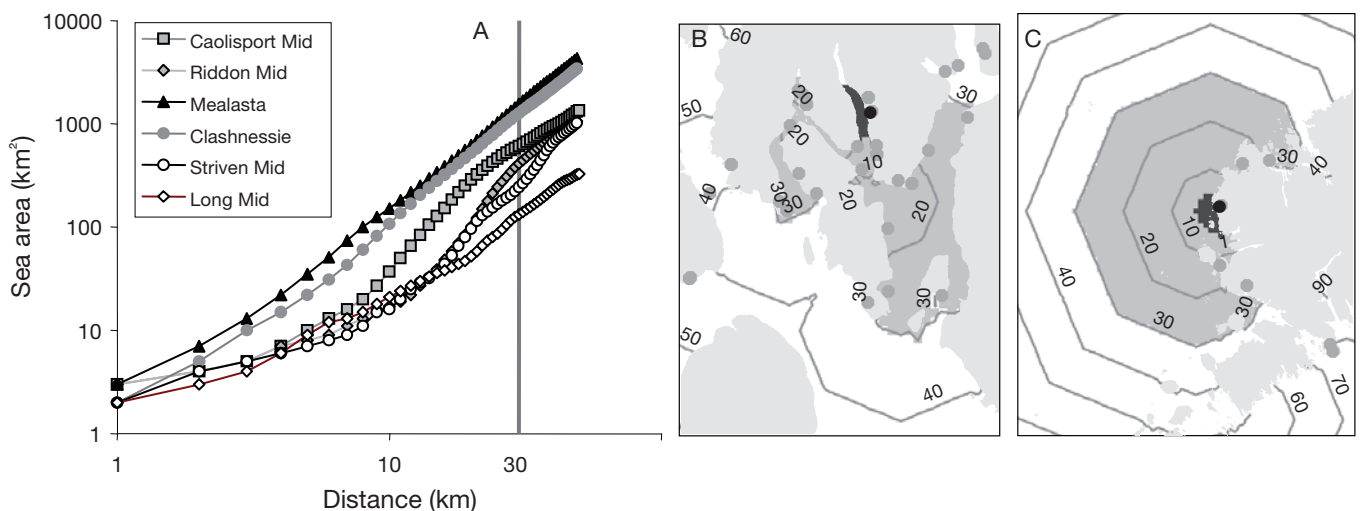


Fig. 1. Openness, the area of sea within a given distance of a coastal site, as a measure of coastal topography. (A) Increase in area of sea within a given distance for 5 sites on the west coast of Scotland. (B, C) Maps with contours showing distance by sea from the sites selected as examples (●) from those sampled (●). Light grey shading is land, mid-grey shading shows the area < 30 km and dark-grey shading < 5 km from (B) an enclosed location in mid Loch Striven in the Clyde Sea, and (C) an open location, Mealasta on Harris in the Western Isles

sured: 'independent' effects as the effect of the variable on its own and 'joint' effects measuring the modifying effect of (or colinearity with) the other variables.

Only those variables emerging from (1) as explaining sufficient variance (>5% of the independent effects) were used in the construction of predictive models (2). The process of selecting the best predictive model for each response involved several steps (Zuur et al. 2007). Candidate models were fitted using generalized least squares (GLS) regression without error variance structure. GLS regression can model the unequal variances associated with different levels of each factor (e.g. years) and with continuous variables (e.g. chl *a*). The set of models included every combination of the main effects, their first-order interactions and the second-order interactions between the continuous variables (SST, chl *a*, wave fetch and openness) and year as a factor. Initial model selection was based on information theoretic measures (Akaike's Information Criterion, corrected for sample size AICc). AICc sets the fit of the model against the number of parameters included, providing the optimal balance between the best fit and the most parsimonious model for that model with the smallest AICc value. This best AICc-indicated model formed the starting point for evaluation of further models that included terms for the underlying variance structure of the data. The best underlying error structure was identified by comparing AIC values of models that included error variance terms for each of the predictors left in the model, fitted using restricted maximum likelihood (REML). If including the error structure significantly ($p < 0.05$) improved the fit of the model over a model without such structure, this error structure was adopted. The final step involved backwards stepwise removal of non-significant terms from the model with the optimal error structure, determined by comparing nested models with and without each term, and fitted using maximum likelihood (ML). The final model was selected once terms could no longer be removed from the model, and subsequently refitted using REML to obtain parameter values. Final inspection of normalised residuals from the model confirmed the assumption of normality.

RESULTS

Oceanographic influences: regional patterns of temperature and food supply

Average surface chl *a* concentrations were lowest (<1 mg m⁻³) in the far north of the study region (Fig. 2) and increased towards the south to >2 mg m⁻³ in the large inlets of central Scotland (Firths of Forth and Clyde). Higher values still occurred in the Solway Firth

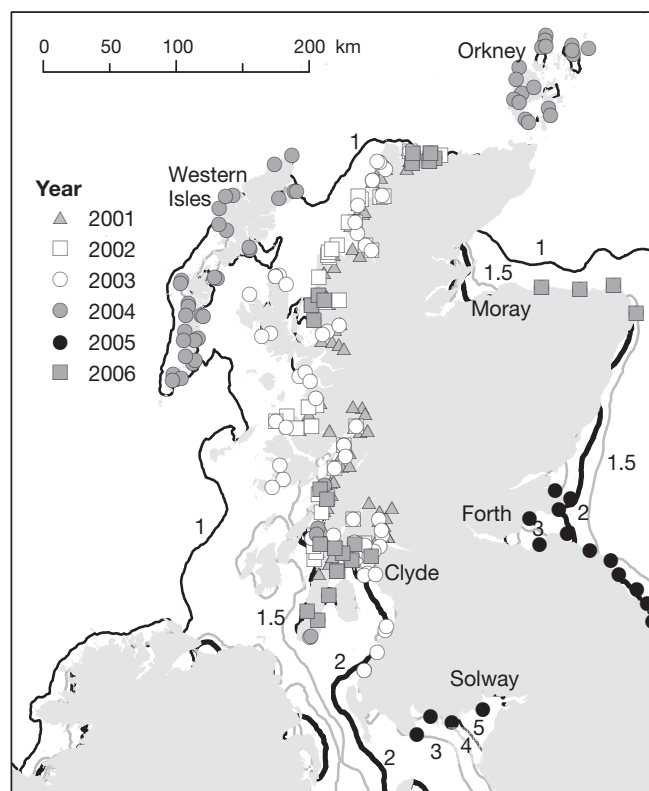


Fig. 2. Location of study sites and contours of average surface chlorophyll *a* (mg m⁻³) from satellite data. Sites in 2006 were returns to previous sites.

(>5 mg m⁻³), though high sediment load may have influenced values in the latter region (Joint & Groom 2000). Patterns of SST changed with the seasons (Fig. 3). In February, SST was highest offshore towards the shelf edge and lowest in inner Firths (Clyde, Forth, Moray, Solway, Fig. 3A). By May (Fig. 3B), SST remained high to the west, but the inner Firths were now warmer than the surrounding coastal regions. Increased SST in coastal regions persisted in August (Fig. 3C), but with warmer temperatures towards the Irish Sea and mid North Sea. By November (Fig. 3D), SST was more uniform. Average chl *a* concentrations at survey sites were positively correlated with patterns of SST in August ($r = 0.629$, $n = 313$ sites), and May ($r = 0.418$), but negatively related to February SST ($r = -0.432$) and not at all with November SST ($r = 0.055$).

Local conditions: wave exposure and coastal openness

Wave fetch and openness at the 30 km scale were positively correlated ($r = 0.619$) as expected, but with considerable variation in summed wave fetch for simi-



Fig. 3. Seasonal patterns of sea surface temperature around Scotland, from 2000 to 2006, derived from satellite data, for (A) February, (B) May, (C) August and (D) November

lar values of openness. Local conditions were relatively independent of regional oceanographic influences. Average surface chl *a* was unrelated to wave fetch ($r = -0.021$) but was negatively related to openness (\log_{10} chl *a* mg m^{-3} , $r = -0.386$). The 2 coastal shape indices (summed fetch, openness) were relatively independent of SST, with only August SST being negatively related to openness ($r = -0.273$).

Relative importance of oceanographic versus local influences

For all but one of the response variables, HP gave the year of the survey as the most important predictor (Fig. 4), having the largest independent effect on deviance. Wave fetch had the second largest independent effect on densities of adult and juvenile barnacles (Fig. 4B). After survey year, chl *a* had the next most important influence on size of juvenile barnacles,

while openness was next for the size of adult barnacles. Of the tested variables, SST effect was never ranked better than third in any comparisons, being >5% of the total independent effects in only 6 of 48 relationships and never >10%.

Independent predictor variables can act in 2 modes: 'additive', where some of the variance explained in the response is shared jointly with other predictors because of correlation among them (colinearity), and 'suppressive', where the predictive power of that variable is improved by the presence of other predictor variables (Hamilton 1987). The sign of joint effects from HP (Fig. 4) shows this. A negative value indicates suppressive mode. Most joint effects were positive (58 out of 96). Joint effects of wave fetch and year on juvenile and adult density were negative, suggesting that the predictive effects of one (fetch) were improved when the other (year) was included in the model. Openness had large positive joint effects on adult size, perhaps reflecting its high correlation with wave fetch.

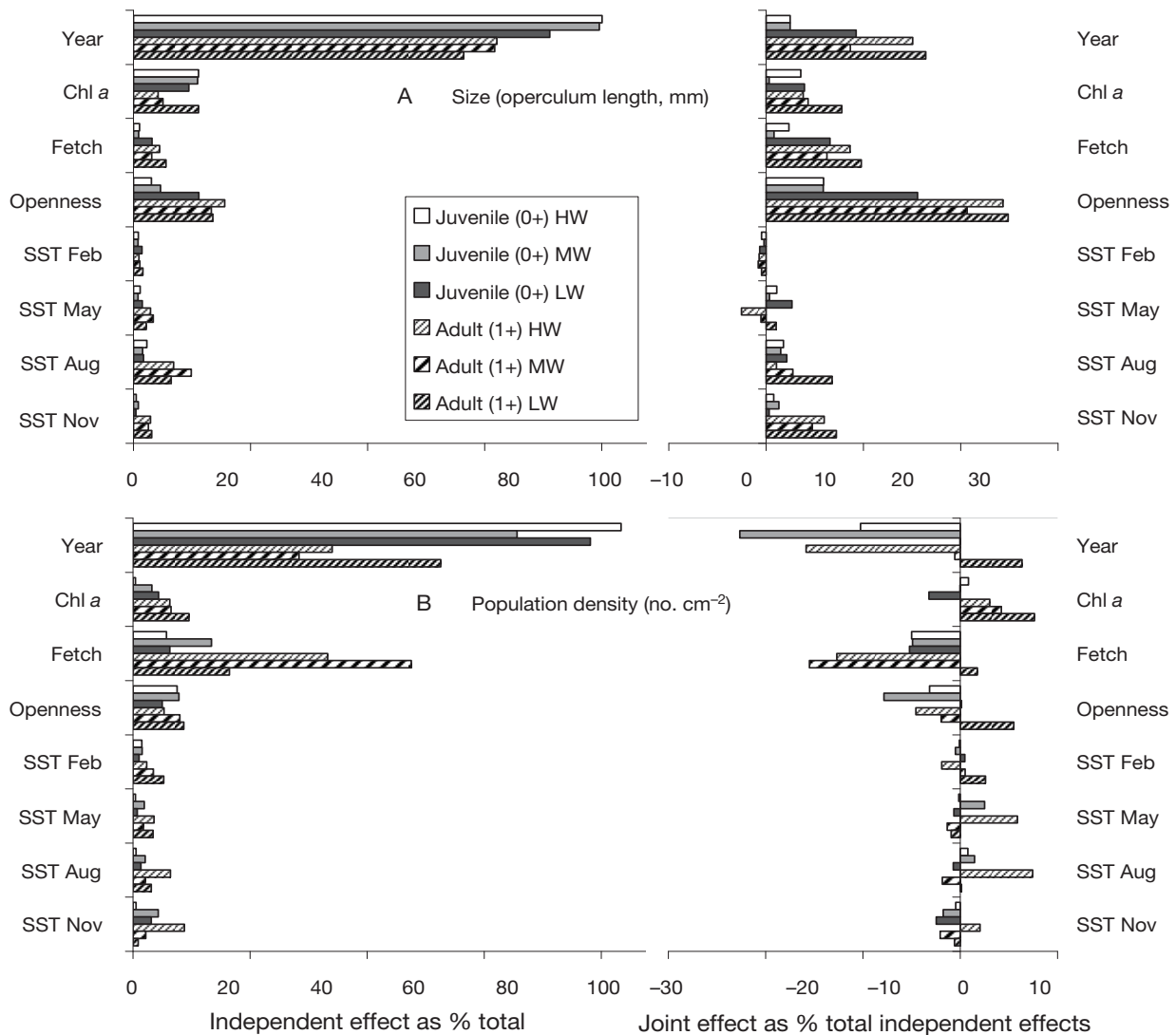


Fig. 4. *Semibalanus balanoides*. Independent and joint effects of predictor variables for each response variable from hierarchical partitioning, as a percentage of the total change in deviance for all variables associated with independent effects. Positive values for joint effects indicate colinearity with other variables (additive mode). Negative values for joint effects mean that including the variable in the model improves the predictive power of other predictor variables (suppressive mode). (A) Size was represented by operculum length (mm), and (B) density by individuals cm⁻². SST: sea surface temperature; HW: high shore, 10–20 cm below upper limit of barnacles; MW: mid shore, midway between HW and LW; LW: low shore, 10 cm above the lower limit of barnacles

Predictive models

Despite the conceptual importance of openness and the strong correlations with response variables, openness was never included in any of the models identified by the selection procedure (Table 2). Sizes of adults and juveniles were best predicted by models including average surface chl *a* and the year of the survey, except at high water where wave fetch had a small modifying influence. Adults (Fig. 5C) and juveniles (Fig. 5D) tended to be larger in areas of high chl *a* concentration, though the trend varied from year to year, being especially strong for adults in 2001. Plots of

barnacle size versus wave fetch showed a negative relationship (Fig. 5A,B), but this was accounted for by the trend for higher levels of chl *a* in areas of low wave fetch. Variance depended on the year of the survey and, for adults at MW and HW, increased with chlorophyll concentrations. Models generally predicted a large proportion of the variance in size among sites (Table 2, R^2 from 0.34 to 0.67).

Population densities of adults and juveniles were best modelled with combinations of terms for wave fetch and chl *a* (Table 2). Adult and juvenile density were always positively related to wave fetch (Fig. 6), but the slope of the relationship between juvenile den-

Table 2. Final structure of selected models for generalised least squares regressions. HW: high shore, 10–20 cm below the upper barnacle limit; LW: low shore, 10 cm above the lower barnacle limit; MW: mid shore, midway between LW and HW; Y: year of survey; C: average surface chlorophyll a (mg m^{-3}); F: summed wave fetch (km); R^2 : proportion of variance in the response explained by the model. Size was represented by operculum length (mm) and density by individuals per cm^2

| Response | Age class | Level | Model terms | Variance structure | R^2 |
|----------|---------------|-------|---|--------------------|-------|
| Size | Juvenile (0+) | HW | Y, C, Y × C | Y | 0.513 |
| | | MW | Y, C, Y × C | Y | 0.464 |
| | | LW | Y, C, Y × C | Y | 0.342 |
| | Adult (1+) | HW | Y, C, Y × C, F, C × F | Y × C | 0.672 |
| | | MW | Y, C, Y × C | Y × C | 0.579 |
| | | LW | Y, C, Y × C | Y | 0.560 |
| Density | Juvenile (0+) | HW | Y, C, F, Y × C, Y × F | Y | 0.339 |
| | | MW | Y, C, F, Y × F | Y × F | 0.237 |
| | | LW | Y, C, F, Y × C, Y × F, C × F, Y × C × F | Y | 0.355 |
| | Adult (1+) | HW | Y, F | None | 0.106 |
| | | MW | C, F, C × F | Y × F | 0.094 |
| | | LW | Y, F, Y × F | Y | 0.148 |

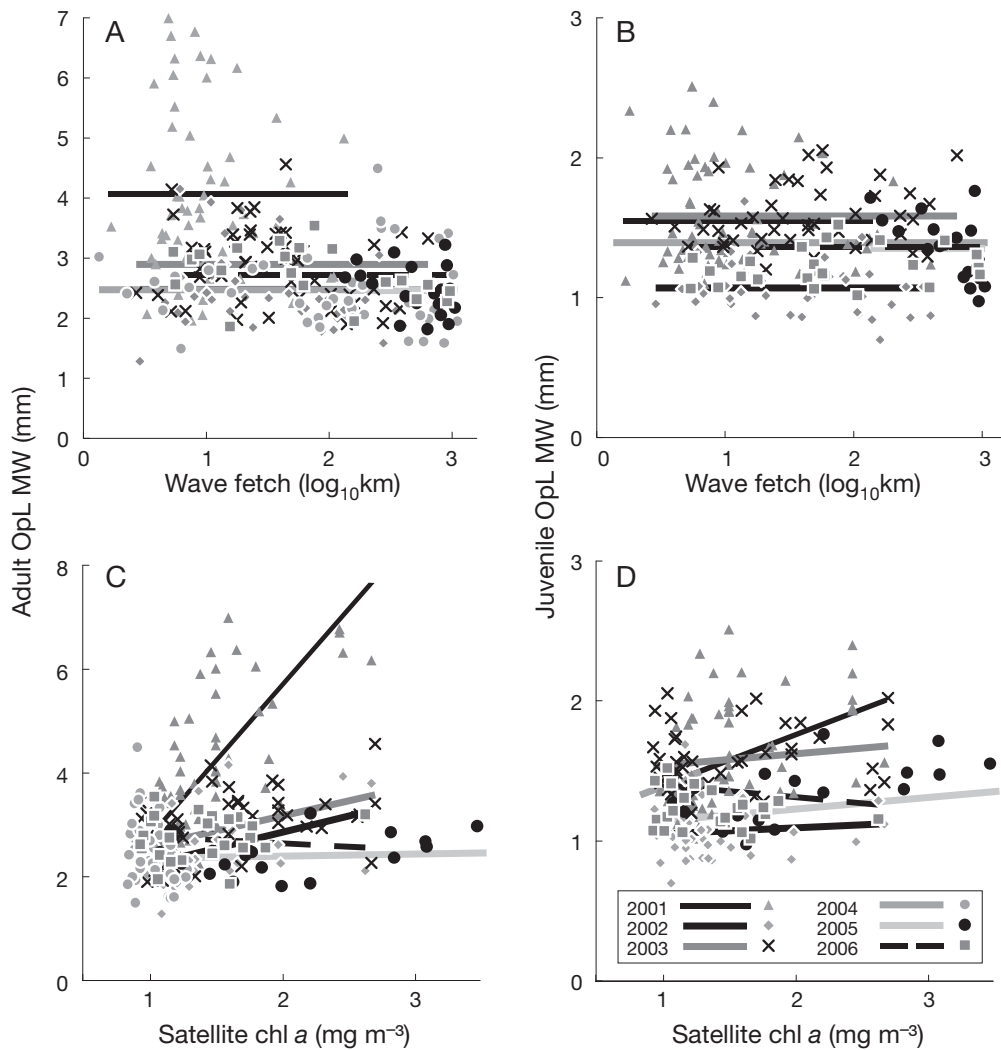


Fig. 5. *Semibalanus balanoides*. Dependence of average size of adults (1+ and older) and juveniles (0+) on summed wave fetch and average chl a concentration (mg m^{-3}) from satellite data. Lines show best fit regression models (Table 2), produced using average values for other predictors. OpL: operculum length, MW denotes mid shore

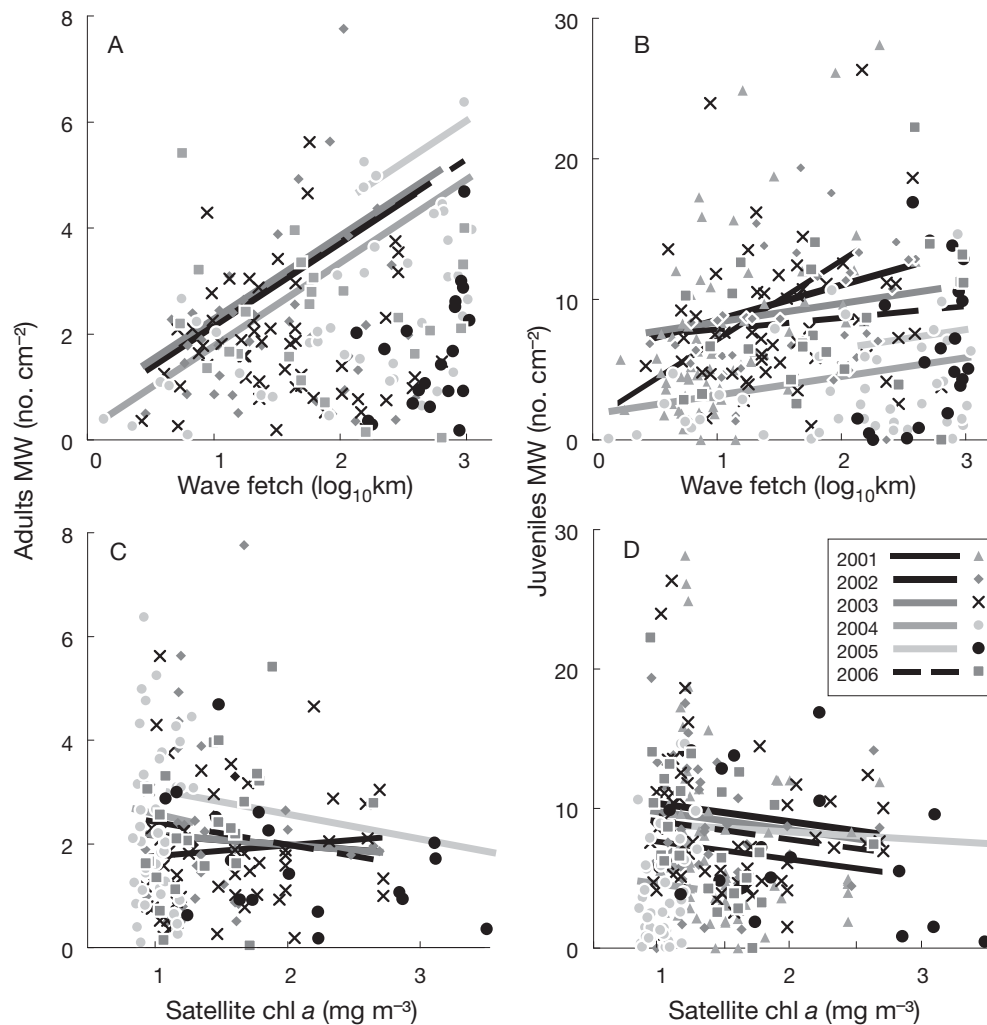


Fig. 6. *Semibalanus balanoides*. Dependence of the population density of (A,C) adults (1+ and older) and (B,D) juveniles (0+) on (A,B) summed wave fetch and (C,D) average chl *a* concentration from satellite data. Lines show best fit regression models

sity and fetch changed between the years of the study (Fig 6B). In extreme wave exposure, densities of juveniles and adults were below the trend line, suggesting that the linear relationship may break down in these conditions (Fig. 6A,B). Chl *a* concentration was not included in final models of adult population density at HW and LW and had only a small and variable negative effect on adults at MW (Fig. 6C) and on juvenile density (Fig. 6D).

Geographical patterns of barnacle demography

An important limitation of this study is the differences in areas surveyed each year. Extending the geographical extent of the study came at a cost: it was not possible to determine whether differences between yearly surveys were due to spatial and/or temporal dif-

ferences in barnacle populations. Some relationships with predictor variables were similar among yearly surveys, such as the relationship between adult density and wave fetch (Fig. 6A), while others varied (MW adult size versus chl *a* concentration, Fig. 5C). Nonetheless, consistent geographical patterns in barnacle size and density emerged. The largest average adult barnacle sizes were found in sea lochs and inner firths (Fig. 7A) and the smallest on the open coasts of the Western Isles and southeast Scotland. Densities of juveniles were lowest in the Western Isles and Orkney, and highest in northwest Scotland and in the Clyde Sea (Fig. 7B).

Repeat visits to sites in 2006 allowed us to test the consistency of the spatial differences using simple correlations (Table 3). Sizes of adults were most consistent between visits to the same sites, with adult densities less so. Patterns of sizes and densities of juveniles

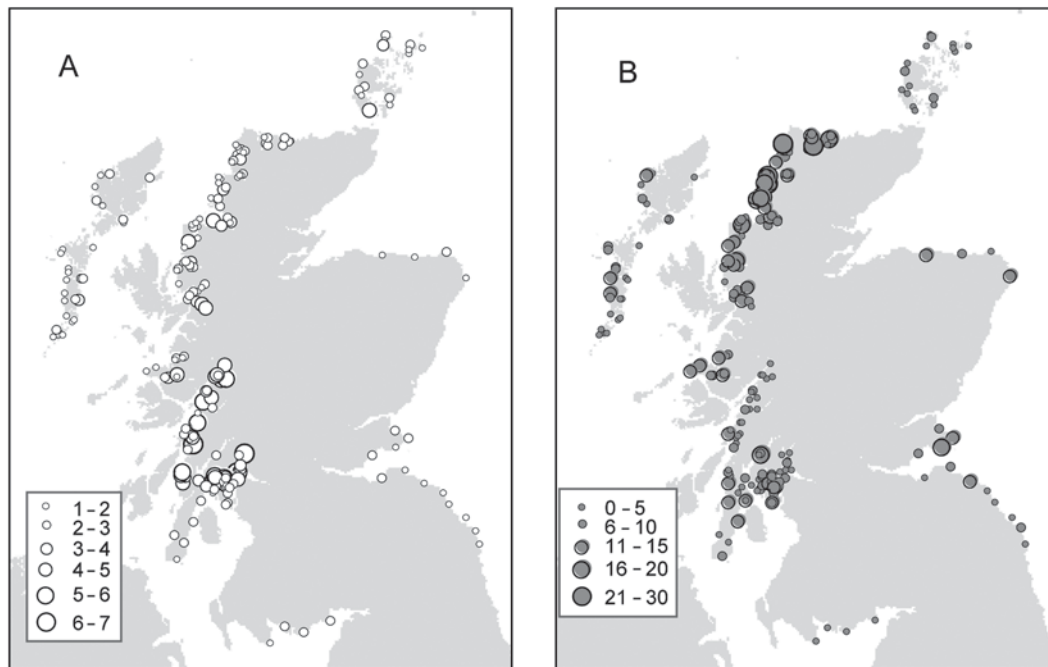


Fig. 7. *Semibalanus balanoides*. Geographical patterns of (A) average size of adults (operculum length, mm) and (B) juvenile density 2001–2006 (no. cm⁻²)

among the resampled sites were not consistent with those in previous visits, suggesting much greater temporal variation in juvenile spatial patterns.

DISCUSSION

Clear spatial associations emerged in this study: barnacles reached larger sizes in areas of high chlorophyll (chl *a*) concentrations, and greater population densities at sites with greater wave fetch. These trends occurred in both adult (1+ and older) and juvenile (0+, 90 to 120 d old) *Semibalanus balanoides*, indicating that the patterns are established early in life. The generalities

Table 3. Correlations between average values for *Semibalanus balanoides* size and density sampled at the same sites in 2006 and previously between 2002 and 2005. Abbreviations: *r*, correlation; *n*, number of sites compared; *p*, 1-tailed probability of *r*, significant correlations in **bold**; HW/MW/LW, see Fig. 4

| | | Size | | | Density | | |
|---------------|----|----------|----------|--------------|----------|----------|--------------|
| | | <i>r</i> | <i>n</i> | <i>p</i> | <i>r</i> | <i>n</i> | <i>p</i> |
| Juvenile (0+) | HW | 0.092 | 17 | 0.362 | -0.064 | 23 | 0.385 |
| | MW | -0.054 | 20 | 0.411 | 0.078 | 23 | 0.361 |
| | LW | -0.093 | 21 | 0.345 | 0.358 | 24 | 0.043 |
| Adult (1+) | HW | 0.519 | 20 | 0.009 | 0.384 | 23 | 0.035 |
| | MW | 0.315 | 23 | 0.072 | 0.311 | 23 | 0.074 |
| | LW | 0.515 | 19 | 0.012 | 0.066 | 24 | 0.380 |

in spatial patterns in these data may not permit definite conclusions as to the underlying ecological processes, but the data set does allow us to assess the plausibility of current explanations for causes of spatial patterns in rocky intertidal communities.

Barnacle size increased in areas of high chl *a*

In the Pacific northwest of the USA, marked differences in rocky shore communities between upwelling and non-upwelling regions of the coast have been linked to differences in nearshore phytoplankton concentrations (Menge et al. 1997). Barnacles in the region (*Balanus glandula*) grew faster, reached larger sizes (Sanford & Menge 2001), and had more reproductive output per individual (Leslie et al. 2005) at sites with higher chl *a*. Similar patterns have been seen in New England, with water flow speed and chl *a* both positively influencing *Semibalanus balanoides* growth at field sites and in the laboratory (Sanford et al. 1994), and adult barnacles reaching larger sizes in sheltered bays with higher chl *a* levels than on open coasts (Bertness et al. 1991).

It seems highly likely that the same mechanisms produced the patterns of size seen in this study. With size well predicted by satellite estimates of chl *a* (R^2 from 0.5 to 0.6), food-limited growth appears to account for most of the large amount of variation in size in Scotland, in

line with our first hypothesis. The apparent decrease in size with increasing wave fetch and openness (see Fig. 5) was entirely explained by the decrease in chl *a* concentrations in exposed areas where wave action was high. If wave action increased the supply of planktonic food through increased water flow (Sanford et al. 1994), we would have expected to see faster growth and larger sizes at wave-exposed sites than at sheltered sites in regions with similar levels of chl *a*, but this expected modifying effect was not seen.

The relationships between size and satellite-estimated chl *a* varied strongly from year to year, albeit always positive. In 2001, for example, when most sample sites were in protected west coast sea lochs, the effect of chl *a* on size was very strong, with extremely large average sizes (>6 mm operculum length) found in regions having the highest chl *a* concentrations (2 to 3 mg m⁻³). In contrast, adult barnacles in the same region in 2003 (at similar levels of chl *a*) were much smaller (from 3 to 4 mm), while in E Scotland in 2005 animals were only around 2 mm. Several explanations seem plausible: (1) Dominant cohorts may have skewed the population average size for some years. The 2000 year class of *Semibalanus balanoides*, for example, was exceptionally strong in the Clyde (Hanson et al. 2003). (2) The satellite-derived estimates of chl *a* concentrations may not reflect the food available for growth. Chl *a* levels in sea lochs were obtained by local averaging and extrapolation from coastal pixels, while elsewhere, such as in the Solway Firth, suspended sediment may result in overestimated concentrations of chl *a* (Case 2 waters, Joint & Groom 2000). Chl *a* from satellites may be a variable proxy for barnacle food, also known to include zooplankton as well as detritus and detached algal filaments (Barnes 1959). (3) Sea and air temperatures may influence feeding (Sanford et al. 1994) and food conversion efficiency. (4) Average size of adults may have been influenced by differential survival. For non-asymptotic growth, enhanced survival might be expected to result in adult populations dominated by larger, older individuals. Our data do not allow us to discount this possibility, but the dependence of the size of 90- to 120-d-old juveniles on chl *a* does suggest that food-limited growth, rather than differential survival, is the proximate cause for the pattern in size.

Barnacle density increased with wave exposure

Population densities of *Semibalanus balanoides* were less well predicted (R^2 from 0.10 to 0.35), but with consistently higher densities in high flow conditions at wave-exposed sites as expected. One possible reason for the reduced predictive power of models relative to

those for average sizes may be that density was much less well characterised by the sampling method than size, with greater variability among photos for densities. Variance to mean ratio was 1.08 for juvenile counts in 2006 and 0.43 for adult counts, while the ratio for average size was only 0.03 for adults and 0.04 for juveniles. The relatively small number of replicates per site will have given less representative estimates of density than size of barnacles.

Observed patterns of population density in *Semibalanus balanoides* reflect either settlement and recruitment or post-settlement and later survival, or both (Hunt & Scheibling 1997, Jenkins et al. 2008). Without repeated censuses in this study, we are unable to discriminate between these processes, but inferences can be made by examination of patterns in juvenile density (which reflect patterns of settlement/recruitment) and the ratio of juveniles to adults (which may reflect post-settlement survival). If we assume barnacle populations are in equilibrium at the regional scale, the relative numbers of adults and juveniles may reflect the level of survival from juveniles to adults. From average log ratios ($S = \log_{10}[N_{\text{Adults}}/N_{\text{Juveniles}}]$), survival appears best in HW populations ($S_{\text{HW}} = -0.19 \pm 0.58$, mean \pm SD), then MW ($S_{\text{MW}} = -0.50 \pm 0.55$) and LW ($S_{\text{LW}} = -0.68 \pm 0.62$), in line with some studies (Burrows 1988) but not others (Jenkins et al. 1999) where post-settlement survival was lower in high shore areas. We did not attempt a systematic analysis of survival inferred from this ratio, but a quick comparison showed that survival (*S*) was strongly positively correlated with the degree of openness of the sites ($S_{\text{HW}} r = 0.32$, $n = 171$; $S_{\text{MW}} r = 0.27$, $n = 179$; $S_{\text{LW}} r = 0.37$, $n = 160$; all $p < 0.001$), but not with wave fetch or chl *a* (all $p > 0.05$), except at HW where *S* was negatively correlated with chl *a* ($r = -0.22$, $n = 171$). If this ratio is indicative, survival appears to be reduced in enclosed areas in this species. This pattern may be mediated by the influence of recruitment on the level of mortality dependent on post-settlement density (Jenkins et al. 2008) since high levels of survival were associated with low numbers of juveniles in open areas.

Coastal topography, as expressed by our openness measure, should influence larval retention and thus larval supply. Populations on open coastlines and headlands should suffer losses of larval output through advection away from the coast into the open sea and through simple dilution effects (e.g. Jenkins 2005), and this could offset the positive effects of increased flow on supply to these wave-exposed sites. This process has been suggested for the progressive loss of *Semibalanus balanoides* from headlands towards its southern limit in Devon and Cornwall (Southward & Crisp 1956) and may be partly responsible for restriction of *S. balanoides* to enclosed areas at the very southern edge

of its range (Wetthey & Woodin 2008). While this may explain the seemingly lower-than-expected densities of juveniles in extreme wave exposure (Fig. 6B), it does not account for the observed low densities in extreme shelter and in enclosed areas in our study. Reduced densities in these areas could be due to low larval retention and supply associated with high flushing rates in enclosed areas, associated with variable river flows (Gaines & Bertness 1992). Larval supply may also be reduced in enclosed areas through low-salinity effects on *S. balanoides* larvae in early spring (Bhatnagar & Crisp 1965).

Biological interactions may also reduce settlement and recruitment of *Semibalanus balanoides* in extreme shelter. Sheltered shores tend to be dominated by macroalgae with less habitat available for barnacles (Burrows et al. 2008), while grazer-mediated loss of macroalgae from more wave-exposed shores may make space available for barnacle recruitment. While we chose our areas for photographs between dense patches of macroalgae, it is possible that physical sweeping and grazer bulldozing effects and lack of cues from adult barnacles reduced settlement and recruitment at algae-dominated sites (Hawkins 1983, Jenkins et al. 1999).

Geographical patterns of recruitment may be further influenced by patterns of fecundity of adults and their contribution to the local pool of larvae (Hughes et al. 2000). *Balanus glandula*, like *Semibalanus balanoides* in this study, has larger adults and produces more larvae per unit body mass in areas of high chl *a* (Leslie et al. 2005). Barnes & Barnes (1968) found 5-fold differences in *S. balanoides* fecundity in our study region: from 800 eggs for a barnacle of 1.5 mg dry weight on the north coast to 5000 eggs for a similar-sized barnacle in the Firth of Clyde, with some evidence for locally enhanced egg production in wave shelter. This trend matches well with the chl *a* gradient, suggesting that food supply may limit biomass-specific egg production. Egg production is also strongly size-dependent (e.g. Burrows et al. 1992), so our observed increase in adult body size with chl *a* should further increase larval supply. Fecundity is also density-dependent in this species, though it is not well established whether effects are always negative or positive in a population-level context (Leslie 2005).

Synthesis: regional population dynamics of a species with widespread larval dispersal

The positive effects of food supply on growth and size in *Semibalanus balanoides*, with the positive effects of wave exposure and slightly negative effects of food supply on recruitment-mediated density in this

region, suggest these mechanisms govern the dynamics of the species over a regional scale (~1000 km). Populations of *S. balanoides* may be influenced by topographical effects on larval retention, and thus inshore concentrations, as expressed by our openness measure, and by local effects of water flow on larval supply. Effects of food supply on adult size and fecundity affect larval production (Leslie et al. 2005). By applying a well-developed modelling approach (Roughgarden et al. 1985, Svensson et al. 2004, Poloczanska et al. 2008) to these space-limited populations in a spatial context over a region such as ours, we should be able to move away from the view of this species as one with demographically open populations in which recruitment is an entirely stochastic process (Svensson et al. 2004) towards one with an explicit understanding of the spatial scale at which the population is demographically closed, where recruitment is linked to adult density. While this may be a considerable task, *S. balanoides* may be the ideal candidate species for such an approach.

Acknowledgements. This study was part of the UK Natural Environment Research Council-funded 'Northern Seas Programme' at the Scottish Association for Marine Science (SAMS) and was also supported by the 'Oceans 2025' Biodiversity Theme. We thank NASA and associated personnel for ready provision of the data used in this research. The Plymouth Marine Laboratory Remote Sensing and Data Analysis Service provided processed satellite data used in earlier versions of the analysis. We also thank various landowners for allowing access to the shore.

LITERATURE CITED

- Aiken CM, Navarrete SA, Castillo MI, Castilla JC (2007) Along-shore larval dispersal kernels in a numerical ocean model of the central Chilean coast. *Mar Ecol Prog Ser* 339: 13–24
- Barnes H (1959) Stomach contents and microfeeding of some common cirripedes. *Can J Zool* 37:231–236
- Barnes H, Barnes M (1968) Egg numbers, metabolic efficiency of egg production and fecundity; local and regional variations in a number of common cirripedes. *J Exp Mar Biol Ecol* 2:135–153
- Bertness MD, Gaines SD, Bermudez D, Sanford E (1991) Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. *Mar Ecol Prog Ser* 75:91–100
- Bertness MD, Gaines SD, Stephens EG, Yund PO (1992) Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *J Exp Mar Biol Ecol* 156:199–215
- Bertness MD, Gaines SD, Wahle RA (1996) Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Mar Ecol Prog Ser* 137:103–110
- Bhatnagar KM, Crisp DJ (1965) The salinity tolerance of nauplius larvae of cirripedes. *J Anim Ecol* 34:419–428
- Burrows MT (1988) The comparative biology of *Chthamalus stellatus* (Poli) and *Chthamalus montagui* Southward. PhD thesis, University of Manchester

- Burrows MT, Hawkins SJ, Southward AJ (1992) A comparison of reproduction in co-occurring chthamalid barnacles, *Chthamalus stellatus* (Poli) and *Chthamalus montagui* Southward. *J Exp Mar Biol Ecol* 160:229–249
- Burrows MT, Harvey R, Robb L (2008) Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Mar Ecol Prog Ser* 353:1–12
- Burrows MT, Harvey R, Robb L, Poloczanska ES and others (2009) Spatial scales of variance in abundance of intertidal species: effects of region, dispersal mode, and trophic level. *Ecology* 90:1242–1254
- Chevan A, Sutherland M (1991) Hierarchical partitioning. *Am Stat* 45:90–96
- Emler RB, Sadro SS (2006) Linking stages of life history: how larval quality translates into juvenile performance for an intertidal barnacle (*Balanus glandula*). *Integr Comp Biol* 46:334–346
- Gaines SD, Bertness MD (1992) Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* 360:579–580
- Gaines S, Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in ecological communities of the marine intertidal zone. *Proc Natl Acad Sci USA* 82:3707–3711
- Gaines SD, Brown S, Roughgarden J (1985) Spatial variation in larval concentration as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67:267–272
- Gaylord B, Blanchette CA, Denny MW (1994) Mechanical consequences of size in wave-swept algae. *Ecol Monogr* 64:287–313
- Grosberg RK (1982) Intertidal zonation of barnacles: the influence of planktonic zonation on the vertical distribution of adults. *Ecology* 63:894–899
- Hamilton D (1987) Sometimes $R^2 > r^2_{yx1} + r^2_{yx2}$: correlated variables are not always redundant. *Am Stat* 41:129–132
- Hansson LJ, Hudson IR, Seddon RJ, Shaw O, Thomason JC (2003) Massive recruitment of the barnacle *Semibalanus balanoides* in the Clyde Sea (Scotland, UK) in the spring of 2000. *J Mar Biol Assoc UK* 83:923–924
- Hawkins SJ (1983) Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). *J Exp Mar Biol Ecol* 71:55–72
- Hawkins SJ, Hartnoll RG (1982) Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977–1981). *J Exp Mar Biol Ecol* 62:271–283
- Hughes TP, Baird AH, Dinsdale EA, Moltschanivskyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology* 81:2241–2249
- Hunt HL, Scheibling RE (1997) Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Mar Ecol Prog Ser* 155:269–301
- Jenkins SR (2005) Larval habitat selection, not larval supply, determines settlement patterns and adult distribution in two chthamalid barnacles. *J Anim Ecol* 74:893–904
- Jenkins SR, Hawkins SJ (2003) Barnacle larval supply to sheltered rocky shores: a limiting factor? *Hydrobiologia* 503:143–151
- Jenkins SR, Norton TA, Hawkins SJ (1999) Settlement and post-settlement interactions between *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) and three species of fucoid canopy algae. *J Exp Mar Biol Ecol* 236:49–67
- Jenkins SR, Murua J, Burrows MT (2008) Temporal changes in the strength of density-dependent mortality and growth in intertidal barnacles. *J Anim Ecol* 77:573–584
- Joint I, Groom SB (2000) Estimation of phytoplankton production from space: current status and future potential of satellite remote sensing. *J Exp Mar Biol Ecol* 250:233–255
- Leslie HM (2005) Positive intraspecific effects trump negative effects in high-density barnacle aggregations. *Ecology* 86:2716–2725
- Leslie HM, Breck EN, Chan F, Lubchenco J, Menge BA (2005) Barnacle reproductive hotspots linked to nearshore ocean conditions. *Proc Natl Acad Sci USA* 102:10534–10539
- Mac Nally R (2002) Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodivers Conserv* 11:1397–1401
- Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am Nat* 130:730–757
- Menge BA, Daley BA, Wheeler PA, Strub PT (1997) Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. *Limnol Oceanogr* 42:57–66
- Menge BA, Daley BA, Lubchenco J, Sanford E and others (1999) Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecol Monogr* 69:297–330
- NOAA (2006) World Vector Shoreline. NOAA Coastal Services Center (www.csc.noaa.gov/shoreline/world_vec.html)
- Pineda J (1991) Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* 253:548–549
- Pineda J, Hare JA, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20:23–39
- Poloczanska ES, Hawkins SJ, Southward AJ, Burrows MT (2008) Modeling the response of populations of competing species to climate change. *Ecology* 89:3138–3149
- Roughgarden J, Iwasa Y, Baxter C (1985) Demographic theory for an open population with space-limited recruitment. *Ecology* 66:54–67
- Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles. *Science* 241:1460–1466
- Sanford E, Menge BA (2001) Spatial and temporal variation in barnacle growth in a coastal upwelling system. *Mar Ecol Prog Ser* 209:143–157
- Sanford E, Bermudez D, Bertness MD, Gaines SD (1994) Flow, food supply and acorn barnacle population dynamics. *Mar Ecol Prog Ser* 104:49–62
- Southward AJ, Crisp DJ (1956) Fluctuations in the distribution and abundance of intertidal barnacles. *J Mar Biol Assoc UK* 35:211–229
- Svensson CJ, Jenkins SR, Hawkins SJ, Myers AA and others (2004) Models of open populations with space-limited recruitment in stochastic environments: relative importance of recruitment and survival in populations of *Semibalanus balanoides*. *Mar Ecol Prog Ser* 275:185–197
- Todd CD, Phelan PJC, Weinmann BE, Gude AR and others (2006) Improvements to a passive trap for quantifying barnacle larval supply to semi-exposed rocky shores. *J Exp Mar Biol Ecol* 332:135–150
- Walsh C, Mac Nally R (2003) The hier. part package. Hierarchical partitioning. R project for statistical computing. URL: <http://cran.r-project.org>
- Wetthey DS, Woodin SA (2008) Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. *Hydrobiologia* 606:139–151
- Zuur AF, Ieno EN, Smith GM (2007) *Analysing ecological data*. Springer, London