

Response of intertidal barnacles to air temperature: long-term monitoring and *in-situ* measurements

Colin Little¹, Cynthia D. Trowbridge², Gray A. Williams³, T.Y. Hui³, Graham Pilling⁴, David Morritt⁵, Penny Stirling¹

¹*Beggars Knoll, Long River Road, Westbury, BA13 3ED, UK;* ²*Oregon Institute of Marine Biology, University of Oregon, Charleston, OR 97420 USA;* ³*The Swire Institute of Marine Science and School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong SAR, China;* ⁴*The Pacific Community (SPC), B.P. D5, 98848 Noumea Cedex, New Caledonia;* ⁵*School of Life Sciences and the Environment, Royal Holloway University of London, Egham, Surrey TW20 0EX, UK*

ABSTRACT

A twenty-five year (1994–2018) survey at 10 rocky sites within Lough Hyne Marine Reserve (SW Ireland) showed that, despite considerable spatial and temporal patchiness, three barnacle species (*Chthamalus stellatus*, *Semibalanus balanoides*, and *Austrominius modestus*) declined in overall abundance in the early 2000s, particularly at three sites. There was no clear response of *A. modestus* or *C. stellatus* to the cold winters of 2010 and 2011. In 2004, however, *S. balanoides* declined suddenly, but showed a slight recovery after the cold winter of 2010 to maintain sparse populations in the lough, but remained abundant outside the lough. A fourth species, *Chthamalus montagui*, showed a different pattern, with wide fluctuations in abundance but no overall decline. Changes in the Atlantic Multidecadal Oscillation may have influenced the overall composition of barnacle populations. Rising maximum air temperatures, resulting in high body temperatures recorded for *A. modestus* even during mild days, are suggested to have impacted the barnacle populations as a result of the prolonged aerial exposure times caused by the lough's asymmetric tidal pattern.

Keywords:

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1. Introduction

Long-term investigations of intertidal communities have demonstrated that the drivers of seasonal and/or annual variations of populations need to be viewed against a background of fluctuations and changes that may occur over decades (e.g. Dayton, 1971; Menge, 1976; Southward, 1991, 1995; Dye, 1998a, b; Menge et al., 2011a, b; Schiel, 2011). In many areas, long-term changes in the composition of intertidal communities have been linked to changing temperature regimes resulting from climate change (e.g. Southward, 1967, 1991; Sagarin et al., 1999; Hiscock et al., 2004; Mieszkowska et al., 2014), and these have wide ranging implications for management and conservation (Elliott et al., 2015).

One way of inferring the effects of temperature change has been via correlative studies to investigate the movement of intertidal species' ranges towards or away from the poles. Schiel (2011), for example, followed intertidal communities in New Zealand for 17 years, revealing marked annual changes in dominant species, but no overall poleward drift of species. Local, physical variables such as sea surface temperature (SST) and wave height did, however, account for 10–20% of the variation in community assemblages. In the northern hemisphere, Barry et al. (1995) and Sagarin et al. (1999) monitored changes in intertidal communities over 60 years along the west coast of the USA. During this time, many 'southern' species increased while 'northern' species decreased, concomitant with the rise in mean SST. On the east coast of the USA, Jones et al. (2012) showed that the southern limit of the northern species, *Semibalanus balanoides*, had moved 350 km northwards between 1963 and 2007. In Europe, however, there have been a number of conflicting studies. For example, Simkanin et al. (2005), comparing the distribution of intertidal species around Ireland in 2003 with that in 1958, found that both northern species and southern species showed significant changes, but not all in accord with a poleward shift with warming temperatures. In contrast, the classic study by Southward (1991) which followed barnacle populations near Plymouth, U.K. from 1951 to 1990 showed that the changing proportions of barnacle species were correlated with

changes in the temperature of local seawater. A later 10-year study (Herbert et al., 2007) further demonstrated the importance of changes in water temperature in determining distributional changes of barnacle species on the south coast of England.

Although explanations based on correlations of species' distributional changes with changing SST are probably too simplistic, interactions between temperature and other large-scale factors are clearly important (e.g. Sagarin et al. 1999, Poloczanska et al. 2008). The effects of low-frequency oceanic climate variability such as the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) have also been emphasized in determining species' distributions (Alheit et al., 2014; Mieszkowska et al., 2014; Drinkwater and Kristiansen, 2018); whereas extreme effects such as severe cold winters may have shorter term, acute effects than gradual trends of warming or cooling (Crisp, 1964; Wethey et al., 2011).

The impacts of these large-scale drivers interact with the physiological tolerance of a species to changes in local conditions, which ultimately will determine its success and distribution (e.g. Barnes, 1963; Somero, 2010; Power et al., 2011). For example, the retreat of the southern limit of the northern barnacle *Semibalanus balanoides* on European shores by 15–50 km per decade is related to an intolerance of high winter SST which inhibits breeding in this species (Barnes, 1958, 1963; Wethey and Woodin, 2008). In contrast, the southern species *Chthamalus stellatus* and *C. montagui* breed only when SST rises to 10°C (O'Riordan et al., 1995). The Australasian species, *Austrominius modestus* (formerly *Elminius modestus*), can breed over a wide range of temperatures (Barnes, 1963; O'Riordan, 1996; O'Riordan et al., 2020).

Accordingly, models based on long-term environmental data have been used to predict how barnacle assemblages may change in the future (Hawkins et al., 2009) and the ratio between different barnacle species has been used as a 'Warm Index' (i.e. the ratio between *Chthamalus* spp. and the total of *Chthamalus*-plus-*Semibalanus*, Southward, 1991). Researchers have, however, also considered the influence of changes in other aspects of temperature, such as aerial temperatures during emersion. Both Barnes (1958) and Lewis (1964) noted that falling air temperatures may allow *S. balanoides* to breed, even though sea temperatures are above the required maximum, and that winter aerial temperatures that are too high to allow gonad maturation may act as a geographic barrier. Distribution patterns are also affected by differences in settlement, which can vary immensely from day to day, site to site and at different tidal levels (Wethey, 1985; Morgan, 2001; O'Riordan et al., 2004; O'Riordan et al., 2020). Mortality of newly settled cyprids may be as high as 90% and this

may be significant in determining distribution patterns (Wetthey, 1985; Power et al., 1999; Jenkins et al., 2000; Delany et al., 2003). Other temperature-related factors such as desiccation may also affect the settlement of cyprids, and thus determine the southern limit of distribution of species such as *A. modestus* (O’Riordan et al., 2020). Temperature may interact with other factors such as pH to impact growth rates of postlarvae which can vary widely (Jenkins et al., 2001; Findlay et al., 2010). In addition, tolerance of low food levels by cyprids may be affected by changing temperatures (Griffith et al., 2021). Thermal stress on the shore is thus often not directly predicted by latitude, but rather an integration of all the factors that define intertidal microhabitats (e.g. substrate type, duration of emersion, tidal height, aspect, etc.; Helmuth et al., 2002, 2006, 2014; Schneider and Helmuth, 2007; Power et al., 2011; Dong et al., 2017; Wang et al., 2020). In particular, solar heating (a non-climatic heat source) may underlie thermal adaptation in many intertidal animals (Marshall et al., 2010). In the tropics, for example, high air temperatures and solar heating can lead to summer heat stress and mortality of adults of *Tetraclita japonica*, when body temperatures are considerably higher than rock temperatures (Chan et al., 2006; Wong et al., 2014). Even eurythermal species such as *A. modestus* may have their local distribution determined by the degree to which they are exposed to direct sunlight (O’Riordan et al., 2020).

The overall importance of air temperature, and the influence of solar heating on barnacle body temperatures have not, as far as we know, been investigated on temperate barnacles (but see Wang et al., 2020 who investigated temperatures of barnacle biomimetics across a temperate-tropical gradient). Lough Hyne, a sea lough in southern Ireland, supports populations of four intertidal acorn barnacles (*Semibalanus balanoides*, *Chthamalus montagui*, *C. stellatus* and *Austrominius modestus*). Lough Hyne is a model site to examine the effects of variation in aerial temperatures as shores in the lough experience long emersion times because of its asymmetrical tidal regime, and it is located near the biogeographic interface of warm Lusitanian and cold-temperature boreal species (e.g., Rogers, 1991). In the present study, we assessed long term variation in barnacle populations over a 25-year period in relation to environmental temperatures. We hypothesized that with increasing SST the boreal species (i.e. *S. balanoides*) would decline, the more southerly *C. montagui* and *C. stellatus* would increase, while the eurythermal *A. modestus* would not change. Secondly, we examined the relationship between body temperatures of barnacles and daily air temperatures during emersion to determine if aerial temperatures during long emersion periods could be a major factor affecting the observed variation in barnacle populations.

2. Materials and methods

2.1. Site description

Lough Hyne is a semi-enclosed sea-lough in southwest Ireland (Fig. 1A–B) which is connected to the sea by narrow Tidal Rapids (Bassindale et al., 1948). The lough is $\sim 1 \text{ km}^2$, and, as a result of its small fetch, all its shores are relatively sheltered (Kitching, 1987). Because of the restricted inflow at the Tidal Rapids, the tidal cycle is asymmetric and of low amplitude, with tides restricted to about 1 m, so the intertidal area is compressed, with the mid-shore often emersed for long periods (Rees, 1931, 1935; Bassindale et al., 1948; Little, 1991). The upper barnacle belt (50–70 cm above Standard Level, approx. the level of low water, see Bassindale et al., 1948), where barnacle body temperatures were measured, is at the top of the fucoid zone, *Ascophyllum nodosum* and *Fucus vesiculosus*, and is usually dominated by *Chthamalus montagui* and *A. modestus* (Little et al., 1988; Little, 1991). On spring tides, the 50 and 70 cm levels are out of water for 6 and 8 h, respectively; but on neap tides the 50 cm level is not covered at high tide, and so could be out of water for 24 h or longer (Kitching, 1987).

Much of the intertidal is either bedrock or shingle and varies from nearly vertical to shallow slopes (Ebling et al., 1960; Williams et al., 1999). The fauna and flora of the rocky intertidal zone were first quantitatively surveyed in 1955 by Ebling et al. (1960) who established 20 rocky shore monitoring sites around the lough (and additional ones outside the lough). Ebling and co-workers recorded the location of these photographically so that they could be precisely relocated. References to other areas in the lough are based on shore sectors, topographically distinct stretches of the shore, as defined by Renouf (1931, Fig. 1C).

2.2. Monitoring sites

To cover as wide a range of the lough's rocky shores as possible and enable assessment within a logistical time constraint of 2 weeks, ten out of the 20 sites initially surveyed by Ebling et al. (1960) were selected for annual monitoring (Fig. 1C). Each site consisted of a 10 m length of shore marked at each end with a stainless-steel plate. For the monitoring surveys, each site was subdivided into five, 2 m-long, sections ($\Sigma N = 10 \text{ sites} \times 5 \text{ sections} = 50 \text{ sections}$). Surveys were carried out from 1994 to 2018 in the last week of August and first week of September. In 2018, surveys were extended to cover all 20 sites in the lough

surveyed by Ebling et al. (1960), and also at two sites outside the lough in Barloge Creek: North Nita and Southern's Point (Fig. 1C).

2.3. Barnacles

Four species of acorn barnacle were present in the intertidal: the invasive *Austrominius modestus*, the northern species *Semibalanus balanoides*, and the southern species *Chthamalus stellatus* and *C. montagui*. *Verruca stroemia* and *Balanus* spp. were also found under low intertidal to shallow subtidal rocks but were not monitored. Barnacle species were assessed by counting the numbers of individuals in 10, haphazardly located, 1 cm² quadrats along the entire barnacle belt within each 2 m section. Quadrats were placed on the open rock surface excluding crevices, and all four species were counted in each quadrat. These counts provided an assessment of the proportion each species contributed to the overall barnacle assemblage. Overall barnacle density (% cover) in the sections was estimated by eye as this approach is rapid and has been shown to be both more efficient for small areas and more accurate, allowing more replicates within a fixed time, than random-point quadrats (e.g. Dethier et al., 1993; Benedetti-Cecchi et al., 1996). Abundance of each species was expressed as % cover and calculated from the overall % cover and the relative proportions of each species in the 1 cm² quadrats.

To allow direct comparison with the 1955 results of Ebling et al. (1960), counts of barnacles were also made in 2018 according to the historical, categorical method used by Ebling et al. with density assessed as 0, < 10, 11–500, or > 500/100 cm² in the appropriate zone. It should be noted that while the method using abundance categories was better at identifying low densities of barnacles because wider areas of substratum were scanned, the % cover method gave more insight into differing abundances because it was not limited by the very broad abundance categories.

2.4. Temperatures of barnacles and rock surfaces

To investigate the temperatures experienced by barnacles during emersion, we measured body temperatures of the most common species, *Austrominius modestus*, using a digital thermocouple (K-type thermocouple approx. 0.7 x 0.9 mm; Tecpel digital thermometer), calibrated in water against a standard mercury thermometer. Barnacles selected were solitary, large enough to accommodate the thermocouple, and located between 50 and 70 cm above

Standard Level. Barnacle temperature was measured by inserting the thermocouple through the opercular plates (after Chan et al., 2006). Rock surface temperature was measured ~1 cm from individual barnacles by placing the thermocouple on the rock while shading. Air temperatures were measured at the same level, ~10 cm from the rock, in shade. Ten replicate measurements of barnacles and adjacent rock surfaces were made every hour. On 4 Sep 2015, measurements were made from 14.00 to 19.00 at South Castle and SE Labhra (chosen for convenience of access, Fig. 1C) where barnacles were directly exposed to the sun. On 5 Sep 2015, measurements were made at SE Labhra from 14.00 to 19.00, with barnacles either in sun or shade, to compare the effects of direct sunlight with indirect effects of rising air temperature.

2.5. Regional and local air and seawater temperatures

Temperature data were obtained from five different sources. First, hourly air and sea surface temperatures were obtained from Ireland's Buoy M3 (51.215956°N, 10.54821°W) off SW Ireland (Fig. 1B; accessed on 10 Dec 2019 for Jul 2002 to Dec 2019). Although there were two shortcomings of this data set as it only started in 2002 and there are missing data due to sensor malfunctions (particularly in 2015 and 2016, $\Sigma N = 118,715$), it is the highest-quality dataset available due to the standardized hourly collection at one location.

Using the M3 datasets, we adopted two statistical approaches to evaluate any inter-annual warming trends: Spearman's rank correlations (which evaluate monotonic inter-annual warming trends but cannot detect seasonal or diurnal cycles) and autoregressive integrated moving average (ARIMA) analyses. For the former, we used hourly data. For the latter, we grouped the hourly data into average daily temperatures, and then fit a seasonal ARIMA for M3 air and SST temperature time series. The results are expressed in ARIMA notation $(p,d,q)(P,D,Q)[s]$, with the terms in the first bracket indicating the non-seasonal ARIMA component: p = order of autocorrelation; d = order of differencing; q = order of moving average. The second terms indicate the seasonal ARIMA component: P = order of seasonal autocorrelation; D = order of seasonal differencing; Q = order of seasonal moving average, while s = the seasonal time period. Such ARIMA models can detect periodicity between years (the seasonal component) and characterize the time structures of temperatures within years (the non-seasonal component). Time series models were assessed based on corrected Akaike Information Criteria (AICc), with the model with the lowest AICc selected as the best model.

Second, additional SST data were obtained from the ICES oceanographic data portal for regional and local seas (<http://www.ices.dk/marine-data/data-portals/Pages/ocean.aspx>), using Winkler bottle data for sites in the area of 50–52°N and 8–10°W, with salinities > 30. Data were accessed on 10 Dec 2019 for Mar 1990 to Feb 2019 (N = 25,842, note this portal contains contributed data from multiple sources with no overall quality control and extreme spatial and temporal variability in data collection). Annual mean, maximum, and minimum temperatures in summer (Jun to Sep) and winter (Dec to Mar) were extracted from the ICES SST as the extreme values may set the species' survival or reproductive limits (i.e. cold winters could kill southern barnacles and hot summers could kill northern species).

Third, monthly maximum air temperature data were obtained from Met Éireann for the Sherkin Island meteorological station (the coastal station closest to the lough) and used in barnacle analyses (section 2.7) because of its longer duration, having started in 1974. Fourth, sea surface temperatures were also measured manually in the lough with a thermometer at Glannafeen Quay and/or North Promontory (Renouf sectors S4 and N11, respectively; Fig. 1C) every few days during annual Aug/Sep surveys.

Fifthly, from 2013 to 2019, HOBO oxygen/temperature sensors (U26-001) were deployed for 6-mo periods at various shallow subtidal sites to measure seawater temperature (see Trowbridge et al., 2019). A subset of the HOBO data was compared to the M3 Buoy data to assess variation in seawater temperature inside vs. outside the lough seasonally based on when HOBO data were available from two monitoring sites (North Labhra and East Goleen) and the M3 SST sensor was functioning in winter 2014/2015 and spring/summer 2019.

2.6. North Atlantic Oscillation (NAO) & Atlantic Multidecadal Oscillation (AMO) indices

Regional atmospheric and oceanographic data indices were obtained from NOAA. Monthly data of North Atlantic Oscillation and the Atlantic Multidecadal Oscillation were downloaded from <https://www.esrl.noaa.gov/psd/data/timeseries> on 10 Dec 2019 and annual means calculated for each index.

2.7. Time series analyses: barnacle abundance vs physical variables

To test if the temporal fluctuations of the four barnacle species can be explained by the temporal variations in physical variables (SST, air temperatures, NAO, AMO), time series analyses were conducted separately for each species. For each, their abundances through time

from 1995 to 2018 were fitted with a regression model with an ARIMA error structure. Such regression models can explain the annual barnacle abundance (the response variable) by both the physical variables of interest (the explanatory variables) and the time structure of responses (i.e. ARIMA error structure; autocorrelations in the response and its error). Seven ARIMA models were fitted for each barnacle species, with the external regressor being, in each model, annual time series of AMO, NAO, year, Lough SST, ICES SST and minimum and maximum air temperatures of the Sherkin land-based records. A model without external regressors (explaining the response only by the autocorrelations in itself and its error) was also fitted for each species, leading to a total of nine candidate time series models for selection.

Time series models were assessed based on AICc as above. Such model comparisons were then repeated with ARIMA models of differing order equal to one ($d = 1$) to accommodate models that were not meeting the stationarity assumption when the differencing order was zero ($d = 0$). Residuals from all ARIMA models selected were not autocorrelated (Ljung-Box test, all $P > 0.05$). If the model with year as the best regressor (i.e. indicating a temporal trend) or without external regressors was selected, change point analyses were conducted to further examine the temporal patterns. All time-series and change point analyses were performed using the packages ‘forecast’ (Hyndman and Khandakar, 2008) and ‘EnvCpt’ (Beaulieu and Killick, 2018) in R (R version 3.5.2; R Core Team, 2018).

3. Results

3.1. Air and seawater temperatures

Based on the Irish M3 Buoy data (Fig. 2), mean monthly SST (averaged hourly values calculated for each month from 2003 to 2019) peaked in July (15.8°C) with mean August and September values slightly lower (15.6°C). Maximum SST values occurred in June and July (18.6°C) with August and September values slightly lower (18.5°C). Minimum SST values were in February (9.5°C) with January and March just slightly warmer (9.7 and 9.6°C, respectively). There was no significant difference in SST during these 16 years (Spearman rank correlation, $r_s = 0.011$, $P > 0.05$, $N = 108,011$).

An ARIMA analysis of mean daily SST from the same dataset indicated a strong annual cycle but no inter-annual trend, with the best model revealing complex autocorrelations between daily temperature differences (5,1,0)(0,1,0)[365] (see above for model notation).

Based on August data (ICES and our measurements), the average regional and local SST showed an apparent declining trend during the 25-year study; over a longer timescale (e.g. 27 y), however, there was no apparent decline in summer temperatures (Fig. 3B). The lough seawater temperatures were warmer than the nearshore coastal ones in summer (Fig. 3B, Fig. 4A), whereas the lough water was slightly colder than nearshore water in the winter by several degrees (Fig. 4B).

Despite daily and seasonal variations, air temperatures at the M3 Buoy did not vary significantly over 17 years (Spearman correlation, $r_s = 0.003$, $P > 0.05$, $N = 113,264$). An ARIMA analysis of mean daily air temperature from the same dataset indicated a strong annual cycle but no inter-annual trend, with the best seasonal ARIMA identified as $(4,0,1)(0,1,0)[365]$, indicating within-year temperature autocorrelations of up to the past four days. Maximum air temperature at Sherkin Island did, however, increase significantly over the period of 1975 to 2019 (Little et al., 2020).

3.2. Temporal patterns of the four barnacle species

Whilst overall barnacle cover fluctuated widely at some sites, it showed a significant general decline in Lough Hyne over the 25-year period (Fig. 5). Although the decline was most noticeable after 2000, the pattern of decline varied between sites, and was strongly influenced by sites where barnacle abundance was relatively high. At the most abundant barnacle site, North Island, overall cover declined, and similar trends were shown at Westwood North and North Labhra, whereas at the other sites, no overall temporal pattern was seen (Supplemental Fig. 1).

The overall decline in barnacle % cover (Fig. 5A) reflected different temporal patterns in abundance of the four species from 1995 to 2018 (Fig. 5B–E). The introduced barnacle *Austrominius modestus* declined over the 25 years but % cover fluctuated greatly (Fig. 5E). A peak in abundance was seen in 1999, while lowest numbers were seen in 2004, 2006, 2013 and 2014. There were considerable differences between sites (Supplemental Fig. 2), with many supporting abundant populations in the late 1990s and early 2000s (SE Labhra, Boundary Bay), while others showed a progressive decline (North Island, North Labhra, Westwood North), or no clear, overall trend (Westwood South, East Castle).

Chthamalus stellatus also showed an overall decline (Fig. 5C). Inter-annual changes showed no significant relationship with the increasing air temperatures recorded at Sherkin (Table 1). For this species, a change in temporal structure was detected before and after 2013,

when the autocorrelation of the barnacle % cover changed from positive to negative (Table 1). Between 1994 and 1995, the population at North Island rose to over 25% cover, and then fell to less than 10% cover in the 25-year period. However, there were considerable differences between sites (Supplemental Fig. 4).

Semibalanus balanoides also declined over time but was positively correlated with its % cover in the previous year (Table 1, AR1 coefficient = 0.50, $P < 0.01$). The change in % cover consisted of three different phases: before and after 2004, when the mean % cover in 2004 suddenly dropped by 65% compared to 2003; and before and after 2011, when the % cover recovered by 76% in 2011 compared to 2010. The recovery comprised some settlement after the unusually cold winter and was most evident at North Island but was similar at five other sites (Supplemental Fig. 3). Outside the lough, the species remained abundant in 2019 (pers. obs.).

Chthamalus montagui increased with the SST estimated from the ICES Winkler bottle data, with residuals having an autoregressive structure positively correlated with the value from the previous year (AR1 coefficient = 0.49, $P < 0.01$, Table 1). In contrast to the other three species, *Chthamalus montagui* showed wide fluctuations: peaking during 2007–8, then declining to its lowest numbers in two decades during 2013 and subsequently recovering by 2016. The decline in 2013 was similar at the three sites of greatest barnacle cover (North Island, SE Labhra, and Boundary Bay; Supplemental Fig. 5).

3.3. Barnacle temperatures

Measurements of barnacle body temperatures when emersed on 4 Sep 2015 (weather: hazy sun and a light northerly breeze) showed differences between the two sites (Fig. 6A), both of which faced approximately southwest. At South Castle, initial temperatures were near those of air, but after three hours they rose to be $> 10^{\circ}\text{C}$ higher. At this time, barnacle temperatures were also higher than those of the rock. At SE Labhra, barnacle temperatures were also consistently higher than those of the rock and air (Fig. 6B).

At SE Labhra on 5 Sep 2015 (weather: full sun, very slight breeze), on both sun exposed and shaded rocks, temperatures of rocks and barnacles rose rapidly after initial readings, taken just after emersion (Fig. 6C–D). Temperatures of barnacles rose faster than those of rock and maintained higher values (mean ca. 29°C in those exposed to the sun: more than 10°C higher than air temperature, Fig. 6C) for at least 5 hours. Even in the shade, maximum barnacle temperatures were $> 5^{\circ}\text{C}$ higher than air temperatures.

3.4. Warm Index, NAO, and AMO

The Warm Index of barnacles (Fig. 3A) varied from 0.8 to almost 1.0 over the 25 years. The index decreased in 1996, 2001–3, and 2014 (Fig. 3A). The North Atlantic Oscillation (NAO) fluctuated between -0.5 to +0.5, with an exceptionally low value in 2010, and a slightly more positive value in 2015 (Fig. 3A). The Atlantic Multidecadal Oscillation (AMO) rose from values as low as -0.2 to values above +0.3 and showed a long-term fluctuation from positive in 1950–60, to a negative phase from 1965 to 1995, and positive again from 2000 to 2018 (Fig. 3C).

4. Discussion

4.1. A historical view: 1955 to 2018

The first quantitative surveys of barnacle populations in Lough Hyne were undertaken in 1955 (Ebling et al., 1960) and recorded only two intertidal species: *Semibalanus balanoides* and *Chthamalus stellatus*, with the latter more widespread (Fig. 7, first column). This simple picture was later complicated with the realization that early descriptions of *C. stellatus* included a second species, *C. montagui* (e.g. Southward, 1976, 1991). The Australasian invasive *Austrominius modestus* was first recorded in the lough in 1980 (Holmes, 1980), and by 1987 was described as ‘occasional’ (Little et al., 1988). *A. modestus* was, however, almost certainly present earlier than 1980 as it was recorded outside the lough in 1956 (Beard, 1957).

By 1990, the situation had changed dramatically (Fig. 7, second column; Little et al., 1992). *A. modestus* was widespread around the lough, as were the two *Chthamalus* species, and *S. balanoides* had also spread more widely, so that most shores had mixed populations of all four species.

For approximately the first 10 years of our survey, 1994–2004, the four species continued to be widespread, but populations were dominated by *A. modestus* (as noted in 2001 by Lawson et al., 2004). In 2000–2003 *A. modestus* accounted for the majority of barnacle recruitment in the lough (Watson et al., 2005), mirroring its spread around the shores of Ireland (O’Riordan, 1996; Allen et al., 2006). *S. balanoides* generally maintained its populations until 2003/4 after which it declined abruptly although it was still abundant outside the lough in Barloge Creek in 2001 (Lawson et al., 2004).

The second half of our survey, from 2005 onwards, showed a continued dominance by *A. modestus*, although densities at many sites fell between 2005 and 2013 before rising again (Gallagher et al., 2017; Fig. 7 third column). Cover of *S. balanoides* generally declined for the first 10 years of the survey, remaining low in the lough until 2011, when abundance rose slightly for 3 years before falling again (Supplemental Fig. 3). The final survey of 2018 showed that this species was still abundant outside the lough in Barloge Creek (Fig. 7).

Overall barnacle abundance in the lough has decreased over time. The causes of these long-term changes, as in other marine populations and communities, are varied (e.g. Southward, 1991; Dye, 1998b), being influenced directly or indirectly by biological processes (e.g. Denley and Underwood, 1979; Menge et al., 1986) or related to abiotic processes such as climate, anthropogenic disturbances and stochastic events (Southward, 1967; Foster and Schiel, 2010). Whilst this combination of direct physical influences and biological interactions is traditionally investigated via short-term experimental approaches (e.g. Underwood, 1985; Paine, 1994; Dye, 1998a), here we consider the evidence generated by the long-term monitoring approach used in Lough Hyne.

4.2. Influence of abiotic processes

There is considerable evidence that increasing water temperatures have allowed the northward and eastward spread of *Chthamalus* spp. in Europe, while decreasing the numbers of *S. balanoides*, mediated through its influence on species' reproduction (Southward, 1991; Herbert et al., 2007; Wethey and Woodin, 2008). Understanding the climatic factors that control reproduction and larval supply is thus a major key to understanding adult barnacle distribution and abundance. However, climatic factors such as temperature act in complex ways: directly affecting reproduction in barnacles but also indirectly affecting the timing of the spring phytoplankton bloom, on which barnacle larvae depend for food (Svensson et al., 2005; Scrosati and Ellrich, 2016; Crickenberger and Wethey, 2017). We evaluate the identified trends in barnacle abundance in relation to potential climatic influences.

4.2.1 Oceanic climatic cycles

NAO-related changes in climate have been linked with changes in several marine ecosystems (Ottersen et al., 2001). However changes in the NAO did not explain changes in barnacle populations of Lough Hyne, nor did they explain changes in those on the southern

shores of England (Mieszkowska et al., 2014). Mieszkowska et al. (2014) also investigated the Atlantic Multidecadal Oscillation (AMO), which reflects long-term variability in sea surface temperature in the north Atlantic oscillating from cool to warm phases and showed a clear relationship between the Warm Index and the AMO index, which was strongest for a time lag of 2 years. During our 25-year survey, which is short in relation to the periodicity of the AMO, the AMO has risen from negative values around -0.2 to positive values up to nearly +0.4, which coincided with a fall in the abundance of *S. balanoides*. This result suggests that although local SST has not risen since the survey began, there could have been some influence of rising sea temperature in the wider Atlantic. Alternatively, however, since the AMO also affects air temperatures (Dima and Lohmann, 2007), the correlations could reflect a rise in air temperature.

Over the longer term, the AMO has cycled from positive in the 1950s to negative in 1970–1990 before rising during the period of the survey. From the data of Ebling et al. (1960), *S. balanoides* was relatively rare in the lough in 1955, being present at only 7 out of 20 sites. The barnacle species increased in abundance to be present at all 20 sites by 1990 (Little et al., 1992) and its decline during the current survey could, therefore, be seen as a cyclical return to the situation in 1955 rather than a progressive change, with an overall negative relationship to the AMO over a 63-year period.

4.2.2. Seawater and air temperatures

Three species of barnacles showed major changes in lough populations over the monitoring period. In the early 2000s, *A. modestus* showed a gradual decline at many sites, a decline further exaggerated in 2013, after the cold winters of 2010/11, 2011/12 and 2012/3. Thus, the fall in populations demonstrated by Gallagher et al. (2017) after the unusually cold winters was from a population that had already declined, although the causes of the initial decline are unknown. Earlier cold winters in Europe in 1946 and 1947 may have affected the northern limits of this species (O’Riordan et al., 2020). Some authors have regarded *A. modestus* as a warm-adapted species (Witte et al., 2010; Gallagher et al., 2017), although others have termed it eurythermal (O’Riordan and Murphy, 2000; O’Riordan et al., 2020). Although water temperatures within the lough have not been shown to decline significantly in the early 2000s, they have shown a great deal of variation, with low temperatures recorded in 2008 (Little et al., 2012). These may have reduced breeding success in *A. modestus*, although

there is, confusingly, evidence that high temperatures can also reduce breeding success of this species in some instances (O’Riordan and Murphy, 2000).

The second change has been a decline in *C. stellatus*. This southern species might have been expected to increase its populations as maximum air temperature has risen. However, it was found primarily low on the shore, below 35 cm above Standard Level (Little et al., 1988), and consequently is only emersed for short periods. Given the lack of a clear trend in water temperature within the lough, which appears unlikely to have driven changes, its decline remains unexplained.

The third major change seen has been the decline of *S. balanoides* in the second decade, with a slight recovery in 2011/12. The decline parallels those shown at the species’ southern limits on east-coast USA (Jones et al., 2012) and continental Europe in recent years (Wetthey and Woodin, 2008; Wetthey et al., 2011), declines ascribed to an increase in sea temperatures. However, the decline in *S. balanoides* in Lough Hyne in the early 2000s does not seem to be directly related to any overall change in summer SST. The low abundance of *S. balanoides* inside the lough, where tidal cycles are asymmetric, was highlighted by Gallagher et al. (2017), and contrasted with high abundance outside, where tidal cycles are symmetric. This species has remained abundant outside the lough throughout our study, emphasizing the difference between populations inside and outside the lough. Populations of *S. balanoides* inside the lough may thus provide an advance warning system of the effects of climate change.

The small increase of *S. balanoides* in 2011–13 parallels a similar phenomenon in continental Europe (Wetthey et al., 2011). By 2010, populations of this species increased in northern France and spread further south than its earlier limits in 2005–07. These changes were interpreted by Wetthey et al. (2011) as a response to the unusually cold winters of 2008–09 and 2009–10, which allowed higher fertilization success. In Lough Hyne, the winter of 2009–10 was particularly cold, with ice covering part of the Goleen (Fig. 1C) for a considerable time (T. Kearney, pers. comm.). The 2010 to 2015 winters were appreciably colder than pre-2009 winters (Little et al., 2020: supplemental figure) with minimum air temperatures well below 10°C, the upper limit required for *S. balanoides* reproduction. Despite the maximum air temperatures being slightly greater than 10°C, the northern barnacle’s populations rebounded briefly.

In summary, our predictions in terms of water temperature were upheld only with regard to *C. montagui*, which has remained relatively constant as water temperature has remained stable and *A. modestus* which has declined, possibly in response to cold winters. For *S.*

balanoides and *C. stellatus*, populations have declined despite the low variation in water temperature, whereas we would have predicted no change in their populations. Indeed, in terms of responses to climate change, although *S. balanoides* was predicted to decline, *C. stellatus* would have been predicted to increase. Thus, we assume that drivers other than long-term trends in water and air temperature in the lough must have been important.

4.2.3. Non-climatic warming

While seawater and air temperatures are common variables considered when assessing temperature effects, the actual temperatures experienced on the shore may be quite different (Helmuth et al., 2002, 2006). Temperatures of the barnacle *Tetraclita japonica* were, for example, consistently higher than those of the rock, and the barnacles experienced considerable physiological stress on tropical shores (Chan et al., 2006; Wong et al., 2014). Barnacles experienced temperatures up to 10°C above air temperature in the lough, which is similar to Southward's (1958) records at Plymouth where, even earlier, Moore (1935) recorded body temperatures of 36.3°C for *Chthamalus* sp. In Lough Hyne, where the tidal cycle is asymmetric, such stress may be prolonged (Power et al., 2011) and species are emersed in air for much longer periods than on 'normal' shores (see Methods; Bassindale et al., 1948; Kitching, 1987), creating a more harsh thermal environment for species to tolerate (Foster, 1971; Power et al. 2011). So, could high temperatures caused by solar radiation be lethal for barnacles in Lough Hyne? Historically, Southward (1958), reviewing work on the Isle of Man and at Plymouth, UK, concluded that most species appear capable of withstanding even exceptional conditions, but that for *S. balanoides* the detrimental effects of heating up in the sun may contribute to its geographical limit. LT₅₀ values obtained by Southward (1955, 1958) and Foster (1969) for continuously submerged specimens varied from 35 to 40°C for *S. balanoides*, and 37°C for *A. modestus* and Davenport and Davenport (2005) recorded a LT₅₀ of 34.9°C for *S. balanoides* in air. Comparing mortality in water and air is problematical, but it is thus likely that while a body temperature of 30°C may affect physiological processes including reproduction, it is unlikely to cause mortality. However, Lewis (1964) reported that air temperatures of 20–25°C resulted in the deaths of juvenile *S. balanoides* on the north-east coast of the USA. Further investigation is required to determine to what extent the internal temperatures of barnacles could rise to lethal levels in the temperate zone. In southern New England, USA, Wethey (1984) has reported mortality of *S. balanoides* during summer heat, so the same may apply in Europe.

Even if high air temperatures and the direct effects of solar radiation were not lethal for *S. balanoides*, the effects of rising air temperatures may counteract that of falling seawater temperatures. Over the last two and a half decades, locally recorded maximum air temperatures have increased, with maximum monthly temperatures above 20°C being more common (Little et al., 2020, Supplemental figure S1; this paper). We suggest that this rise in air temperature, allied with the effects of increased solar radiation, may have been responsible for the decrease in *S. balanoides* populations in the lough, exacerbated by the asymmetrical tidal regime resulting in longer emersion times.

4.3 Influence of biological processes

Beyond the potential influences of abiotic processes such as climate, biological processes may also contribute to trends in barnacle abundance within the Lough. Predation of barnacles within the lough is low compared to other locations. Key predators of barnacles such as the dogwhelk, *Nucella lapillus* (e.g. Connell, 1961a; O’Riordan et al., 2010) which predate *S. balanoides* in preference to *A. modestus* (O’Riordan et al., 2020) are relatively rare within the lough (Ebling et al., 1964; Kitching et al., 1966), and numbers did not change significantly during our survey (Little et al., unpub. data). Other predators (e.g. the nudibranch *Onchidoris bilamellata* (Thompson and Brown, 1984), or fish (e.g. Monteiro et al., 2005) are either also rare (Nunn et al., 2006), or barnacles represent a very minor part of their diet (Deady and Fives, 1995).

The competitive interactions for space between *S. balanoides* and *Chthamalus* spp. have been well documented by Connell (1961b), and the influence of SST on these interactions has been emphasized by Poloczanska et al. (2008), but the competitive influence of *A. modestus* has not been established experimentally (Watson et al., 2005; Gallagher et al., 2015). However, modelling of the colonisation of space by *S. balanoides* and *A. modestus* under different scenarios (Gallagher et al., 2020) has demonstrated that the timing of reproduction is the key factor in determining whether the two species can co-exist, and this may change as climate warms. In addition, growth and settlement of cyprids of *S. balanoides* were depressed by food limitation as temperature increased, while that of *A. modestus* was unaffected (Griffith et al., 2021). A rise in temperature could therefore lead to an increase in dominance by *A. modestus* if there is a mismatch with phytoplankton supply. In Lough Hyne, the introduced *A. modestus* is now the dominant intertidal barnacle, and it is pertinent to ask whether it has taken over space previously occupied by other species. *C. montagui* and *S.*

balanoides primarily occupy the same zone and whilst the former has maintained its populations at most sites, *S. balanoides*, which is close to its southern range edge, has declined greatly since 2004. During this period, however, *A. modestus* has also been in low densities, so increased interspecific competition is unlikely. In a study at several sites in southwest Ireland, Gallagher et al. (2016) also concluded that there was generally enough free space for coexistence of native barnacle species and the invasive *A. modestus*.

Fucoid cover is known to inhibit barnacle settlement (Hawkins and Hartnoll, 1983; Hartnoll and Hawkins, 1985), and consequently when fucoid canopies increase, *S. balanoides* decreases, albeit with a time lag. In Lough Hyne there was no clear relationship between % barnacle cover and limpet-fucoid cycles (Little et al., 2017), perhaps because *A. modestus*, the dominant barnacle, appears quite tolerant of fucoid cover (pers. obs.). However, there was an inverse correlation between cover of *S. balanoides* and *Fucus vesiculosus* (Little et al., 2017).

Finally, larval supply could play a key role as Lough Hyne is connected to the open ocean by only a narrow channel. At the same time, this relative isolation could lead to larval retention, boosting autochthonous larval numbers. Barnacle larvae show extremely variable concentrations in the incoming and outgoing phases of the tide (Rawlinson et al., 2005), with no overall bias in one direction, and little mortality (Jessopp, 2007). Since the densities of larval barnacles in Lough Hyne were all higher than outside (Jessopp and McAllen, 2007), larval retention may thus influence settlement within the lough, as already proposed for two species of mollusc (Trowbridge et al., 2008; Little et al., 2020). However, since there were also examples of overall import of *C. stellatus* and *A. modestus* larvae into the lough (Jessopp and McAllen, 2008), changes in the supply from external populations may be important.

4.4 Summary

Overall, the changes in barnacle populations in Lough Hyne over a 25-year period appear to have been related more to changes in physical conditions such as air temperature and solar radiation than to biological interactions such as competition and predation. These changes may well have been exacerbated by the lough's unique, asymmetric tidal regime. The physical changes in Lough Hyne have not entirely paralleled those seen on other coasts in Europe: while maximum air temperatures have indeed risen (see Little et al., 2020), there is no evidence that seawater temperatures in either the lough or the neighbouring coastal areas have changed significantly (Bishop, 2003; Little, pers. obs.). In the UK, regional sea temperatures have remained relatively stable or declined over the period 2002–2018

(Mieszkowska et al., 2020). Changes seen in barnacle populations in Lough Hyne have, therefore, been more involved with changing aerial conditions than with sea water temperatures.

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Table 1. Time series analyses on the temporal patterns of the four barnacle species (*Chthamalus montagui*, *C. stellatus*, *Semibalanus*, *Austrominius*) and their overall changes from 1995 to 2018. Regression models with ARIMA errors were fitted to the time series of each species with differencing order (d) of either 0 or 1. Numbers indicate the regression coefficients of the regressors (bracketed variables, see main text for abbreviation) selected from the best model, and bold numbers indicate the ARIMA error structure expressed in (p,d,q) form, where p = order of autoregression, d = differencing to achieve stationarity and q = order of moving average. * indicates $P < 0.05$; *** indicates $P < 0.001$. No $d = 1$ models were selected for *C. montagui* and *Austrominius* (hence the symbol /); no regressors were identified for the $d = 1$ model of *Semibalanus* and the overall barnacle cover (hence the symbol /). Change point analyses were further conducted for *C. stellatus*, *Semibalanus*, *Austrominius* and the overall barnacle abundance as ‘year’ was selected in the best models (lower panel of the table). Y_t indicates the barnacle abundance at the year t , which was identified as a function of t and/or the barnacle abundance of the past two years (Y_{t-1} and Y_{t-2}). No change points were identified for *Austrominius* and the overall barnacle cover (the temporal patterns from 1995 – 2018 could be described using a single regression model), while a change point was identified between 2012 and 2013 for *C. stellatus*, and two change points were identified for *Semibalanus* between 2003 – 2004 and 2010 – 2011 (multiple regression models were needed to describe the temporal changes in *C. stellatus* and *Semibalanus*).

	Differencing order	<i>C. montagui</i>	<i>C. stellatus</i>	<i>Semibalanus</i>	<i>Austrominius</i>	Overall
Best model	$d = 0$	0.51 *** (ICES SST) (1,0,0)	-0.13*** (year) (0,0,0)	-0.12*** (year) (1,0,0)	-0.23* (year) (0,0,0)	-0.46*** (year) (0,0,0)
	$d = 1$	/	-0.16 (Sherkin Max) (0,1,1)	/	/	/
Change point analyses						
<i>C. stellatus</i>		From 1995 – 2012: $Y_t = 1.36 + 0.35Y_{t-1} + 0.14Y_{t-2}$ From 2013 – 2018: $Y_t = 3.17 - 0.48Y_{t-1} - 0.40Y_{t-2}$				
<i>Semibalanus</i>		From 1995 – 2003: $Y_t = -0.57 + 0.34t + 0.10Y_{t-1} + 0.50Y_{t-2}$ From 2004 – 2010: $Y_t = -0.85 + 0.07t + 0.17Y_{t-1} + 0.25Y_{t-2}$ From 2011 – 2018: $Y_t = 2.21 - 0.07t - 0.12Y_{t-1} - 0.12Y_{t-2}$				
<i>Austrominius</i>		From 1995 – 2018: $Y_t = 12.53 - 0.22t + 0.28Y_{t-1} - 0.10Y_{t-2}$				
Overall		From 1995 – 2018: $Y_t = 25.03 - 0.42t + 0.24Y_{t-1} - 0.16Y_{t-2}$				

FIGURE CAPTIONS

Fig. 1. A. Regional map of the British Isles and Atlantic France, indicating the surrounding water bodies, location of the Irish M3 Buoy off SW Ireland, and Lough Hyne. B. Detail of SW Ireland including Lough Hyne and nearby islands and bays. C. Map of Lough Hyne, showing long-term monitoring sites (10 m wide on shore) that were surveyed annually for 25 years. Annual site (closed symbols) names are abbreviated as follows: BB, Boundary Bay; CB, Codium Bay; EC, East Castle; EG, East Goleen; GY, Graveyard; NI, North Island; NL, North Labhra; SEL, South West Labhra; WVN, Westwood North; WWS, Westwood South. Historical site (open symbols) names are abbreviated as follows: BH, Bohane Harbour; GC, Glannafeen Quay; NC, North Castle; NN, North Nita; NWC, Northwest Castle; RN, Rookery Nook; SC, South Castle; SL, South Labhra; SP, Southern's Point; WC, West Concrete; WL, West Labhra; WP, Whirlpool Point.

Fig. 2. Temporal variation of air temperature and sea surface temperature from 2003 to 2019 from buoy M3 in SW Ireland. Data recorded every hour (except during periods of sensor malfunction).

Fig. 3. A. Warm Index based on ratio of the *Chthamalus* species to total native species (excluding *Austrominius modestus*) from 1994 to 2018. NAO (North Atlantic Oscillation) index based on NOAA data publicly available online. B. Mean of 2 to 3 surface seawater temperature readings in Lough Hyne, measured in Renouf sectors N11 and S4, from 1993 to 2019 and SST measured at M3 Buoy. C. Interannual variation in AMO (Atlantic Multidecadal Oscillation) from 1948 to 2019. Arrows indicate timing of key studies at Lough Hyne Marine Reserve.

Fig. 4. Comparison of seawater temperature inside Lough Hyne in the shallow subtidal habitat at two monitoring sites (North Labhra and East Goleen) and outside the lough at the M3 buoy. Data periods were selected when HOBO data were available for two study sites and when the M3 buoy sensor was fully functional (A, 2019; B, 2014–2015).

Fig. 5. Temporal patterns of the (A) overall mean percentage cover of acorn barnacles and (B–E) the four species. Black-filled dots indicate the mean percentage covers over all 10 study sites within the lough from 1995 to 2018. White open dots are the best ARIMA model fits (see Table 1) with differencing order = 0; grey-filled squares are the best ARIMA models with differencing order = 1.

Fig. 6. Temperatures of *Austrominius modestus* and adjacent rocks at Lough Hyne on 4 Sep 2015 (A, B) and 5 Sep 2015 (C, D). Sample size was 10 measurements for barnacles and rock surface and 1 for air. Error bars are ± 1 SE.

Fig. 7. Distribution of acorn barnacle species in Lough Hyne in 1955, 1990, and 2018. Data are based on counts per 100 cm². The 1955 data are from Ebling et al. (1960); 1990 data from Little et al. (1992).

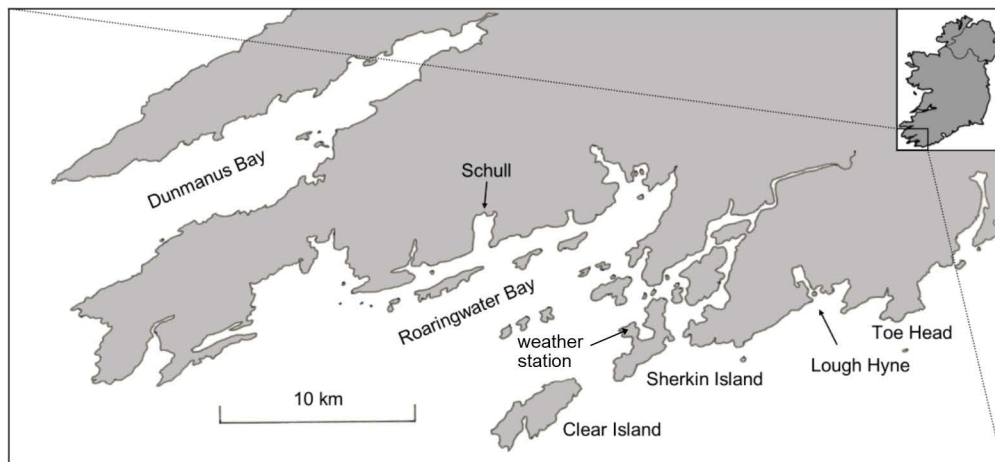
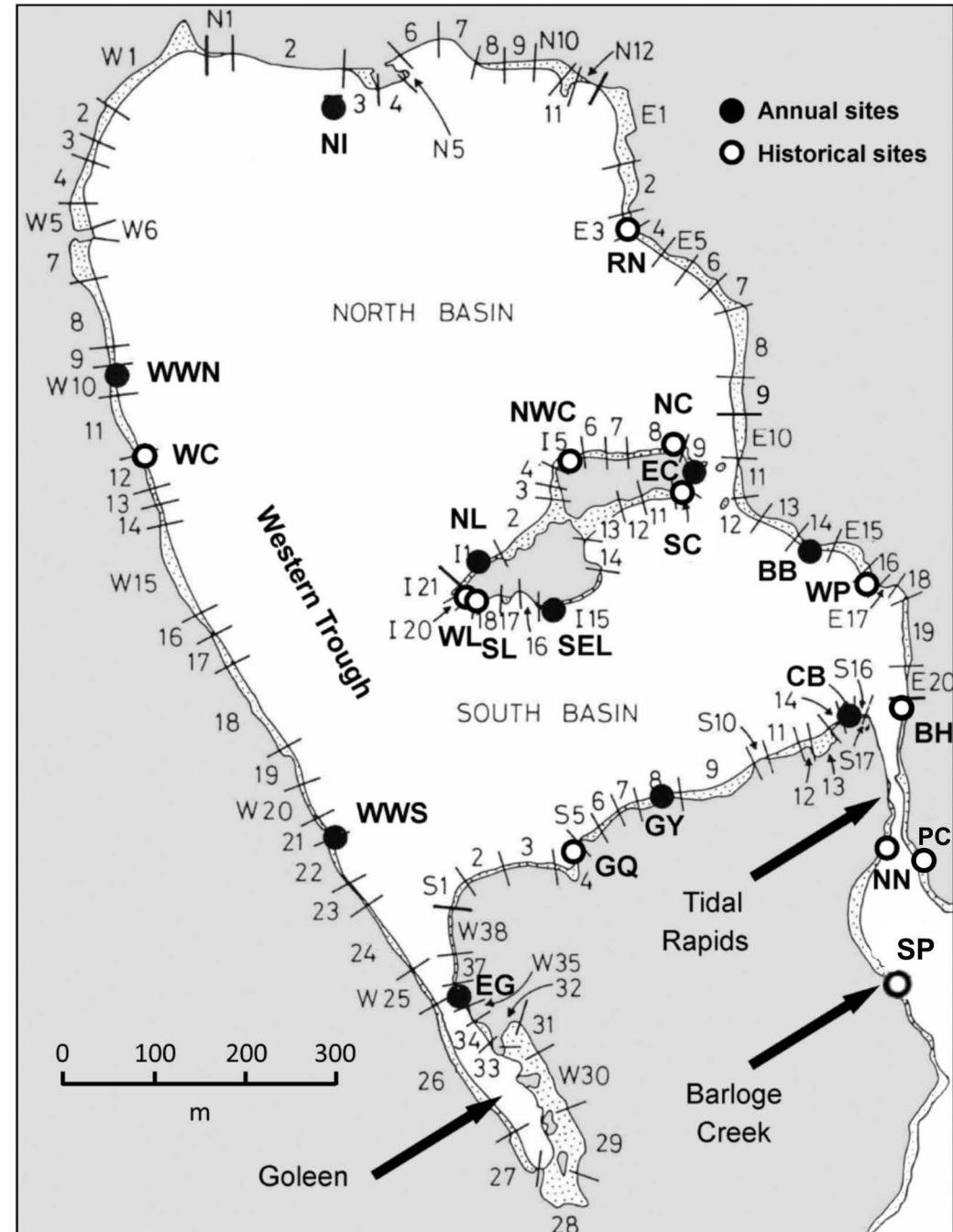
Supplemental Fig. 1. Temporal cycles of intertidal acorn barnacles (over all four species) in Lough Hyne Marine Reserve, SW Ireland. Error bars denote ± 1 SE.

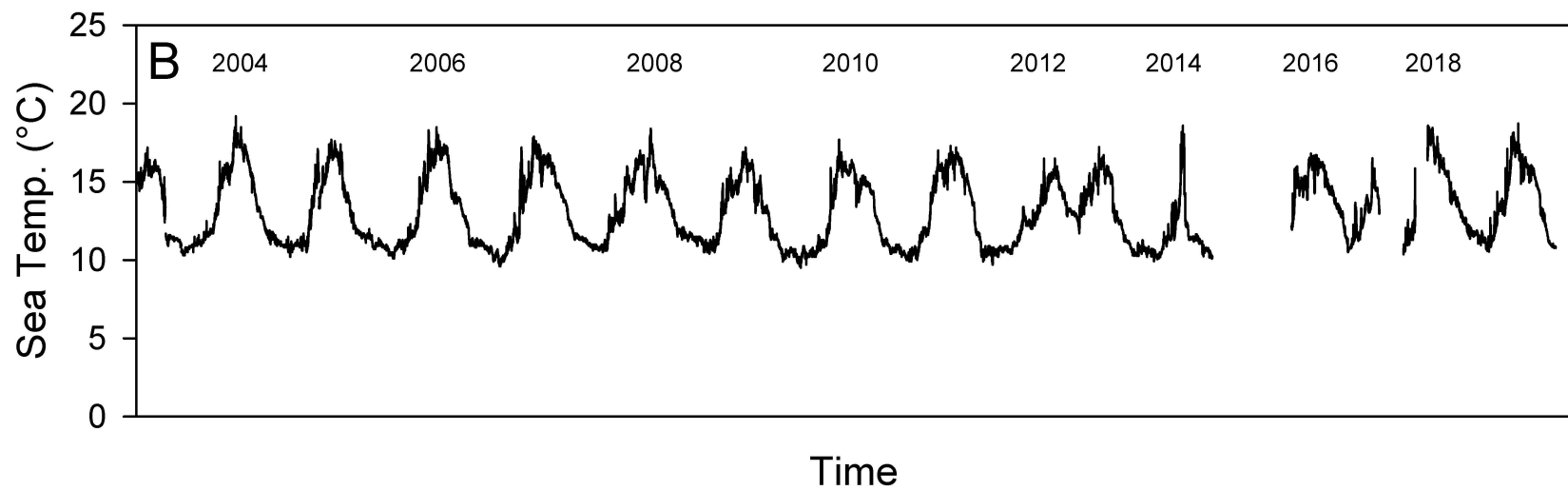
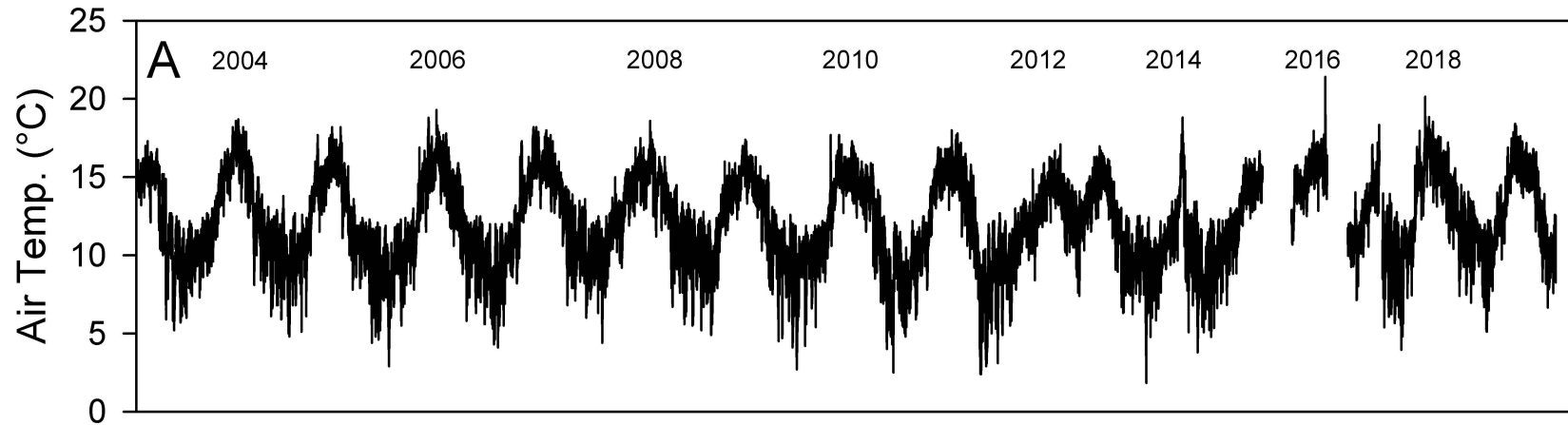
Supplemental Fig. 2. Temporal cycles of *Austrominius modestus* in Lough Hyne Marine Reserve, SW Ireland. Error bars denote ± 1 SE.

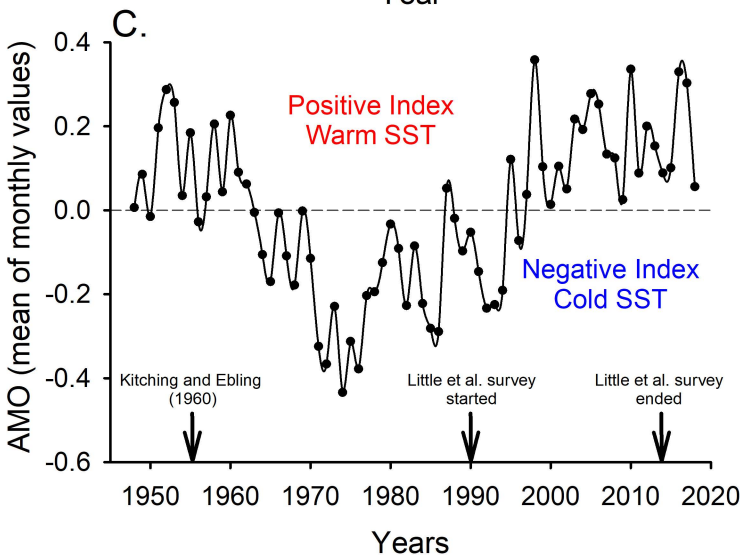
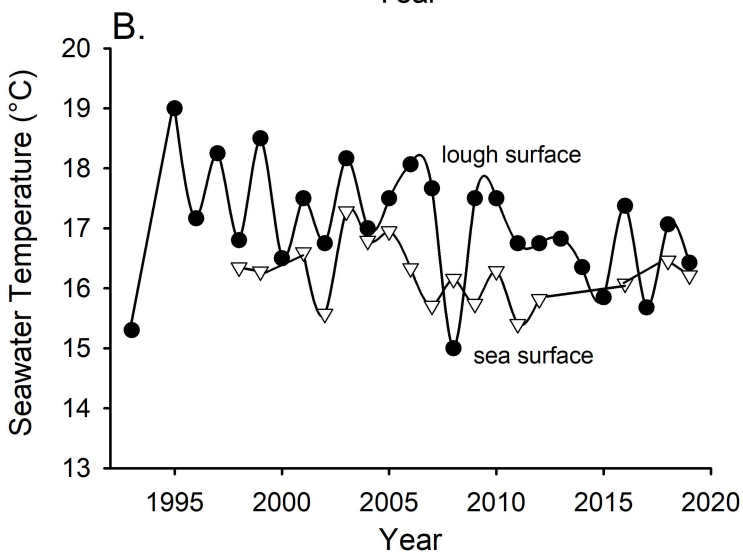
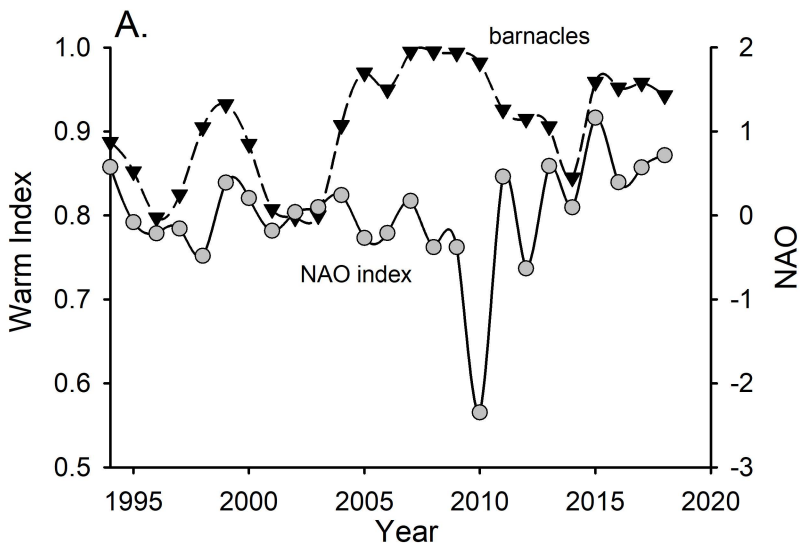
Supplemental Fig. 3. Temporal cycles of *Semibalanus balanoides* in Lough Hyne Marine Reserve, SW Ireland. Error bars denote ± 1 SE.

Supplemental Fig. 4. Temporal cycles of *Chthamalus stellatus* in Lough Hyne Marine Reserve, SW Ireland. Error bars denote ± 1 SE.

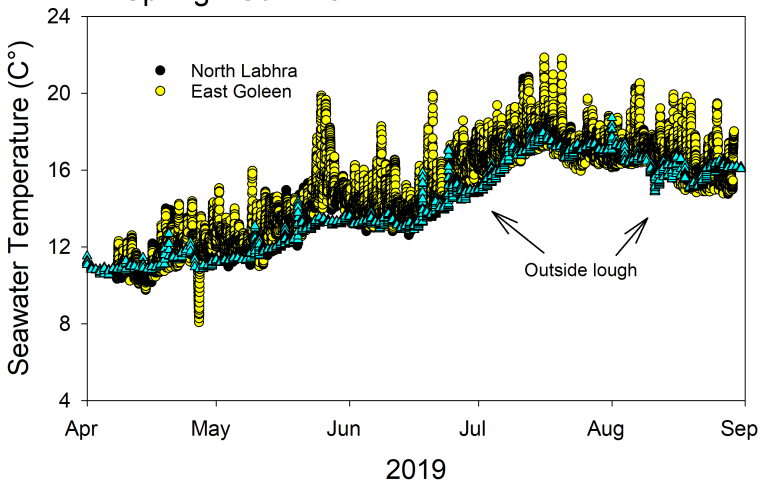
Supplemental Fig. 5. Temporal cycles of *Chthamalus montagui* in Lough Hyne Marine Reserve, SW Ireland. Error bars denote ± 1 SE.

A**B****C**

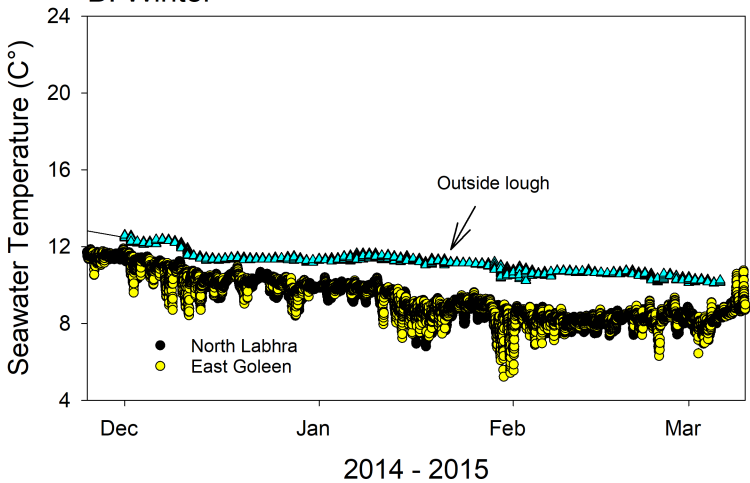


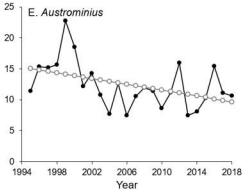
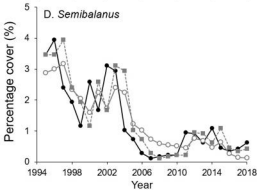
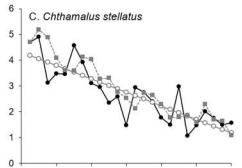
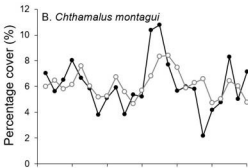
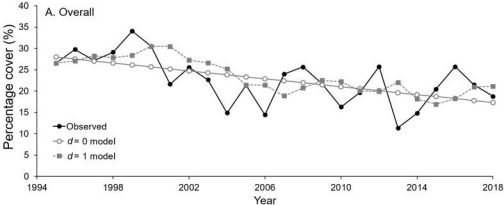


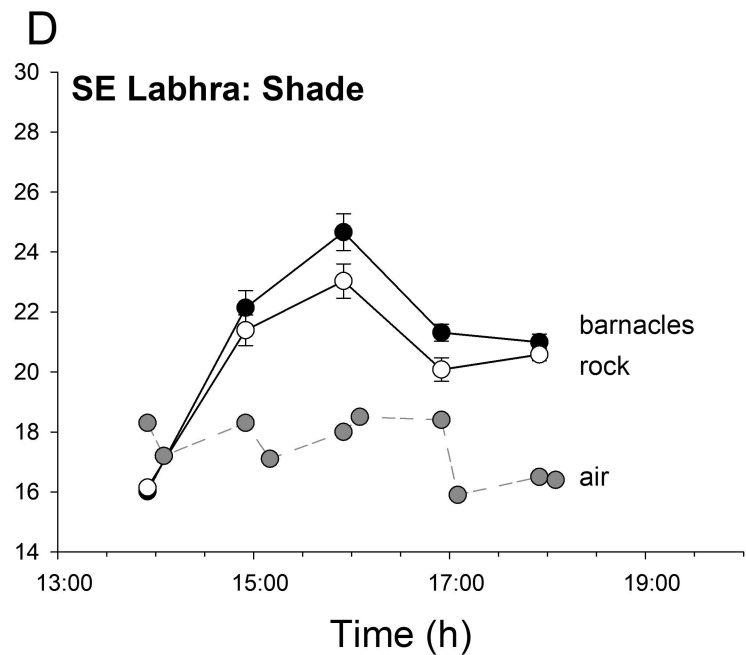
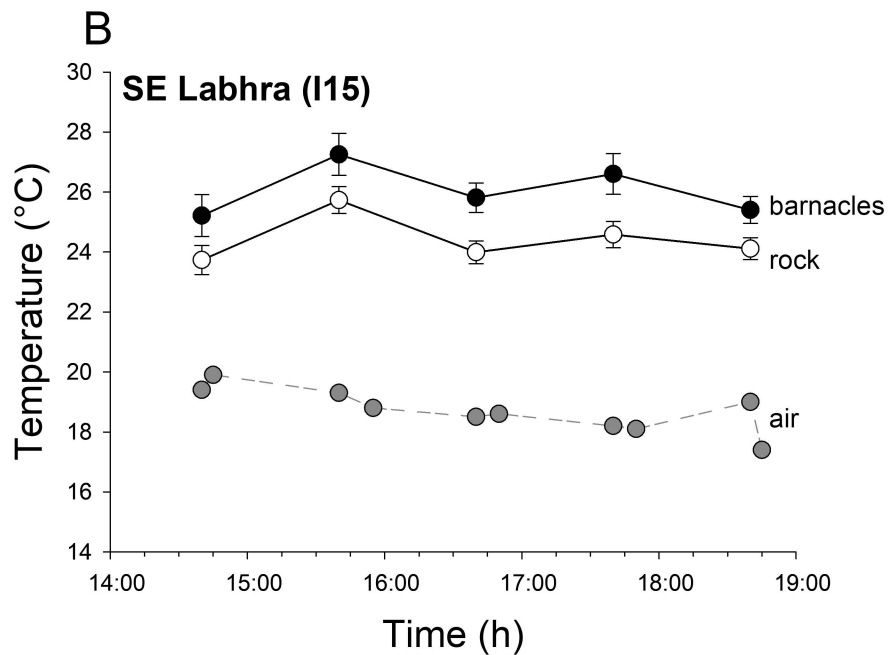
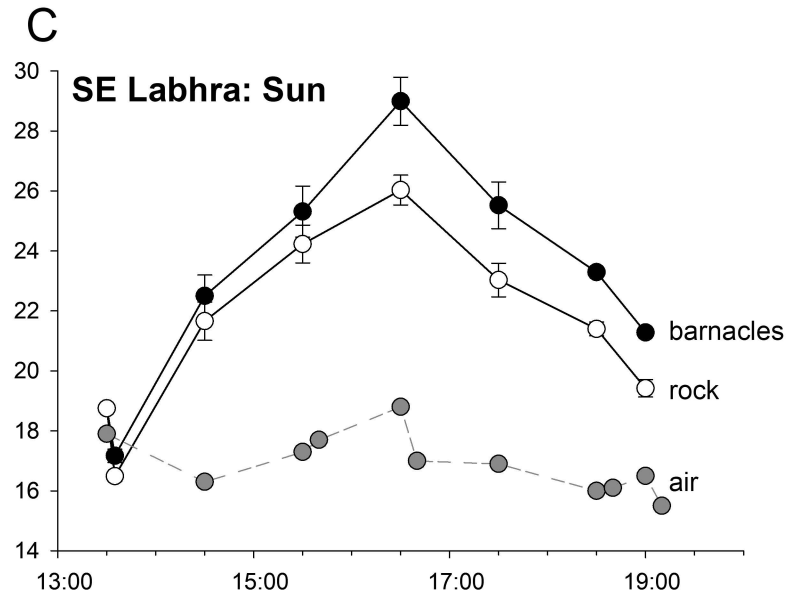
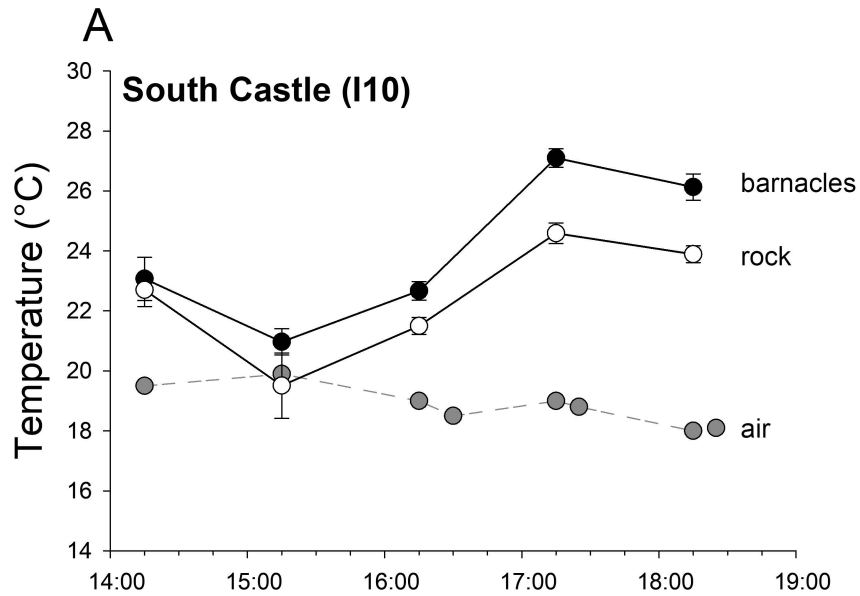
A. Spring - Summer



B. Winter





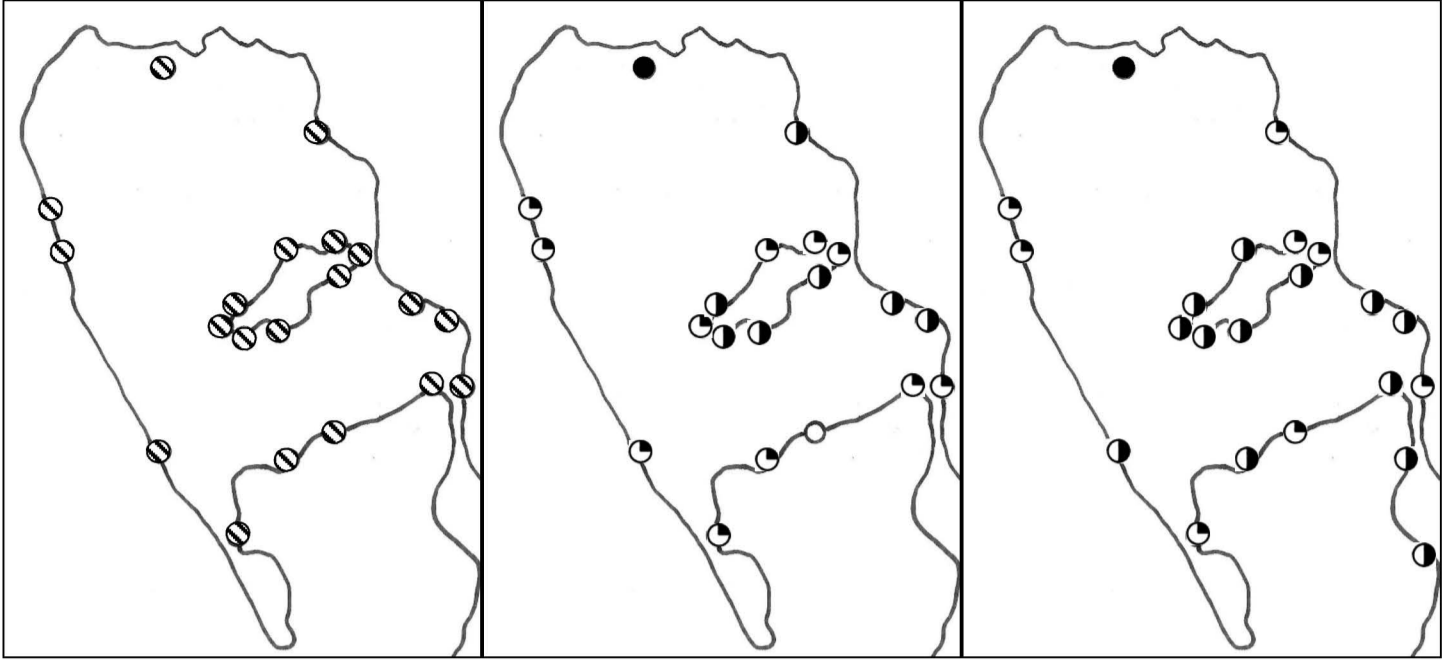


1955

1990

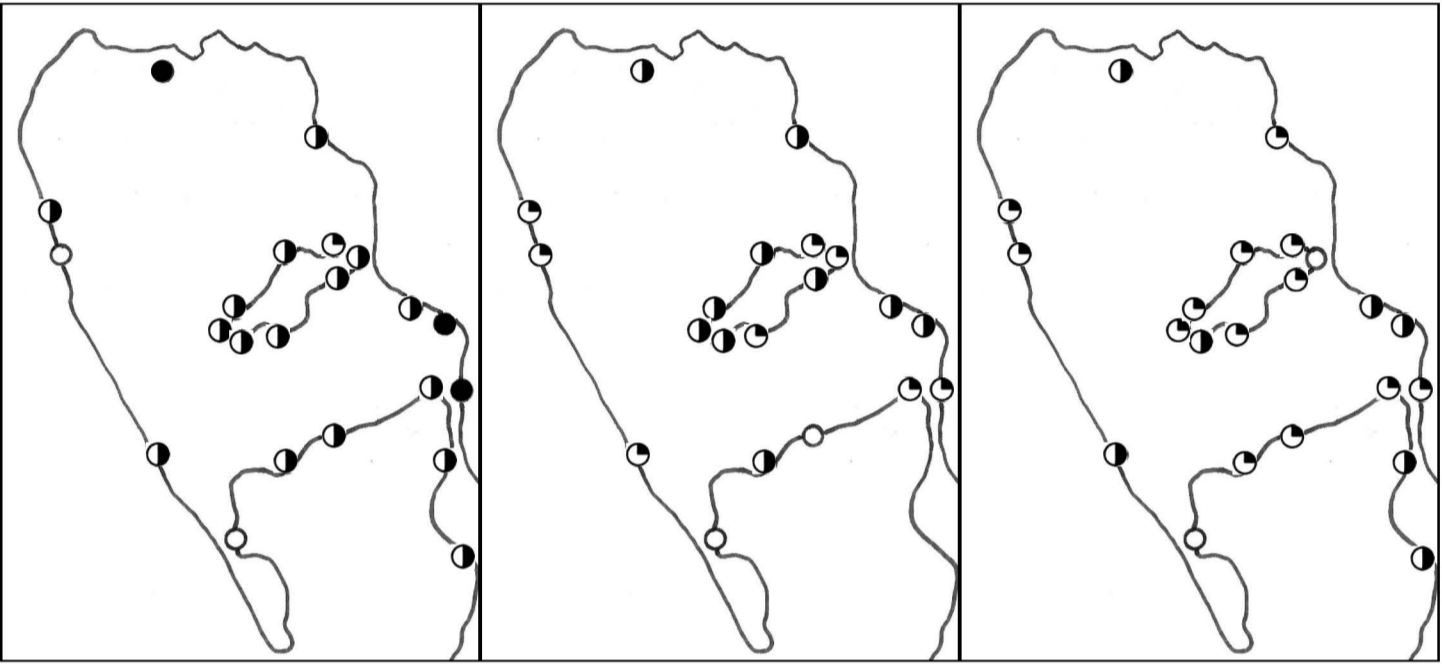
2018

C. montagui

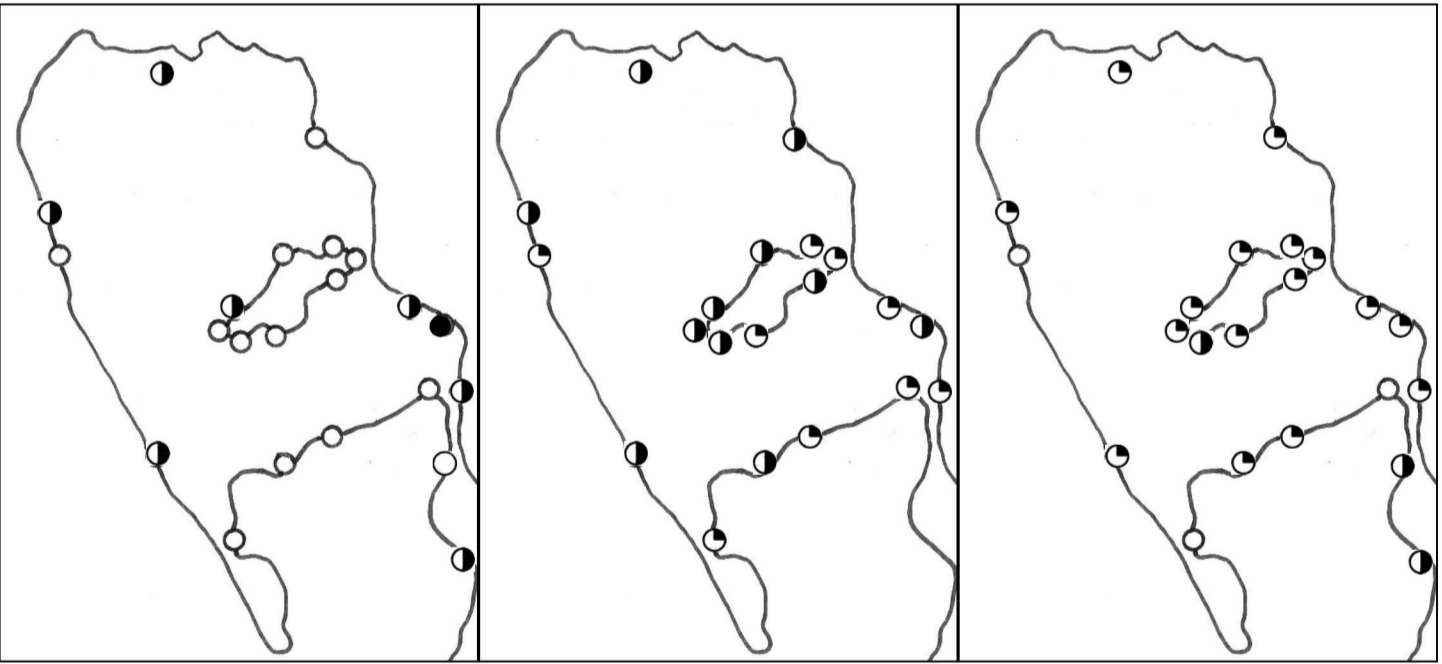


- ⊘ No data
- Absent
- ≤ 10
- 11-500
- > 500

C. stellatus



S. balanoides

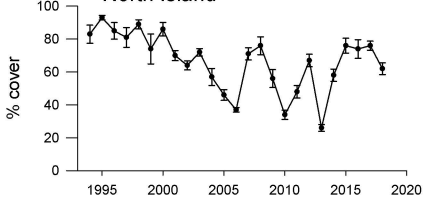


A. modestus

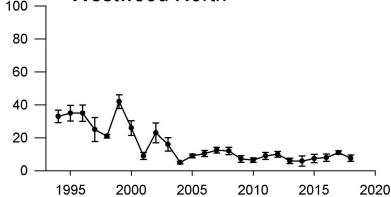


Acorn barnacles (overall)

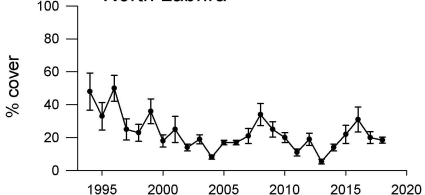
North Island



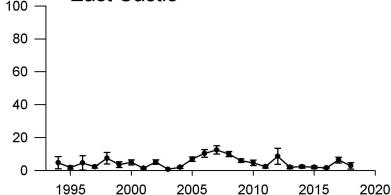
Westwood North



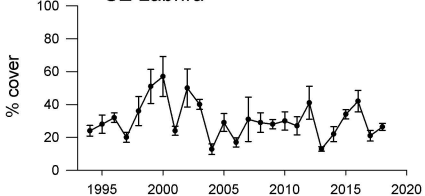
North Labhra



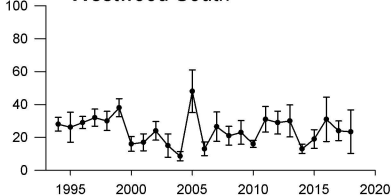
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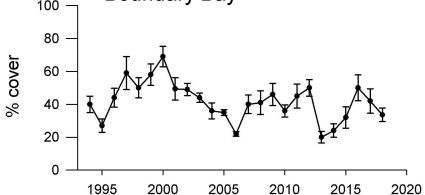
SE Labhra



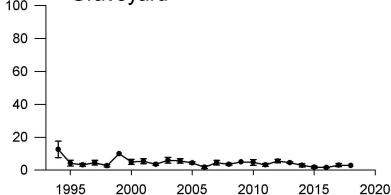
Westwood South



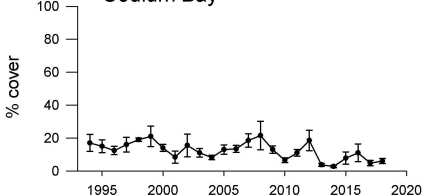
Boundary Bay



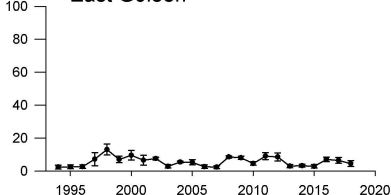
Graveyard



Codium Bay



East Goleen

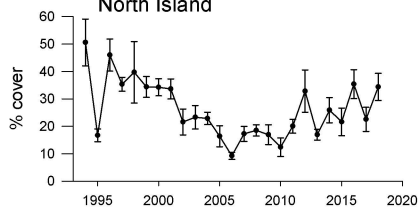


Year

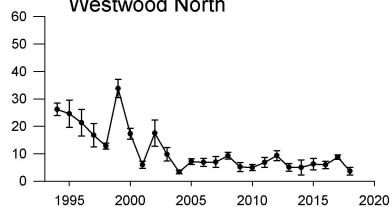
Year

Austrominius modestus

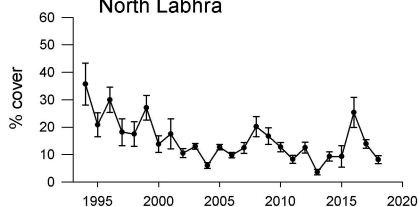
North Island



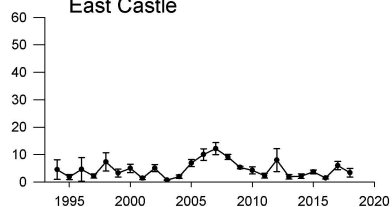
Westwood North



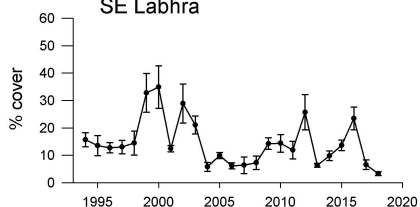
North Labhra



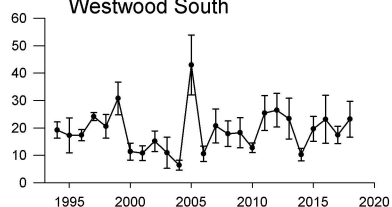
East Castle



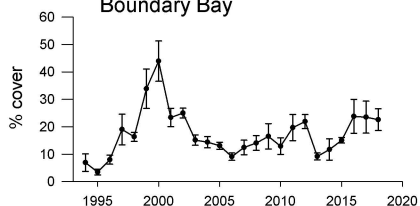
SE Labhra



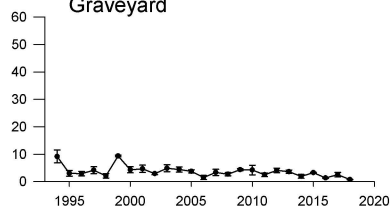
Westwood South



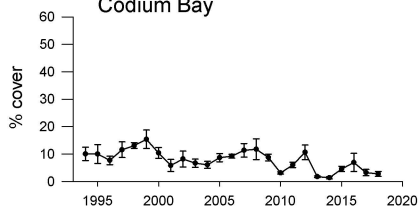
Boundary Bay



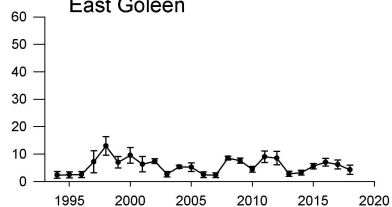
Graveyard



Codium Bay



East Goleen

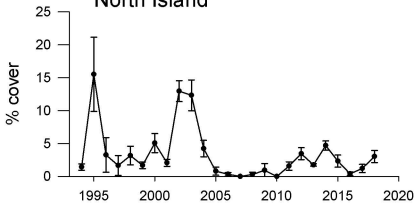


Year

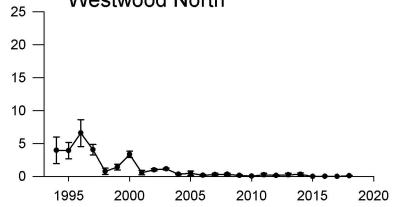
Year

Semibalanus balanoides

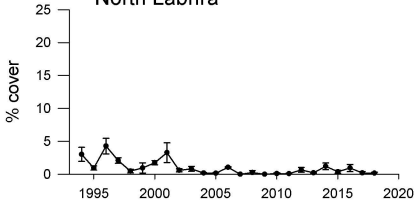
North Island



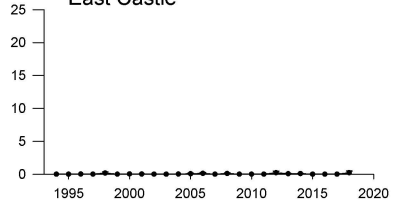
Westwood North



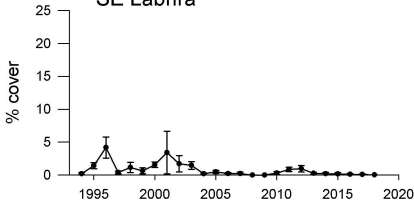
North Labhra



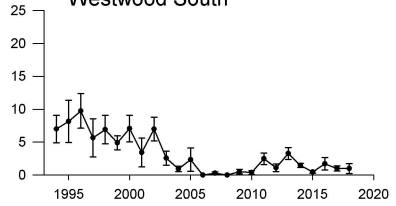
East Castle



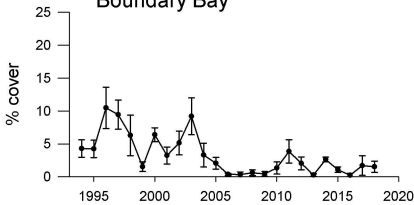
SE Labhra



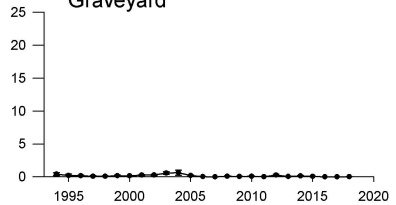
Westwood South



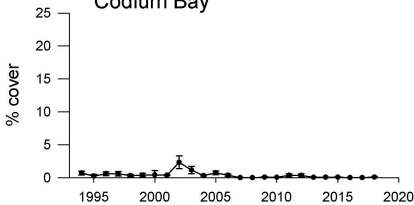
Boundary Bay



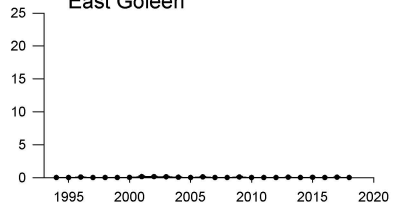
Graveyard



Codium Bay

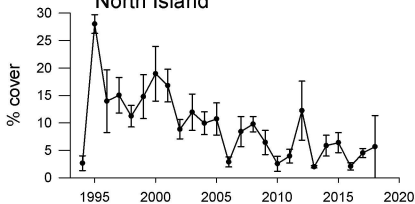


East Goleen

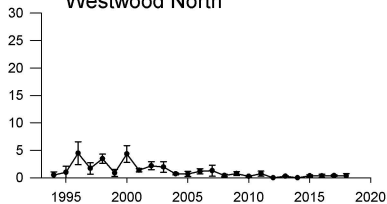


Chthamalus stellatus

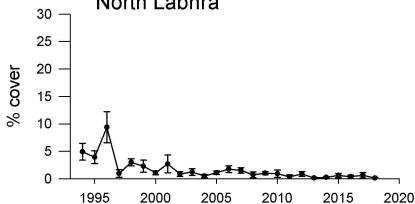
North Island



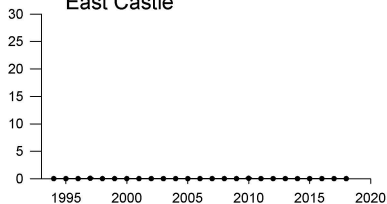
Westwood North



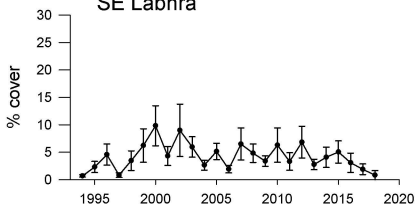
North Labhra



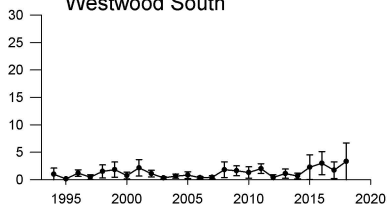
East Castle



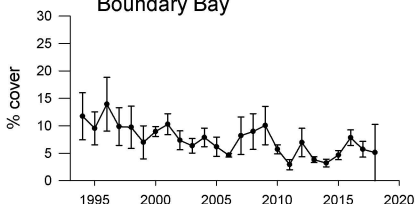
SE Labhra



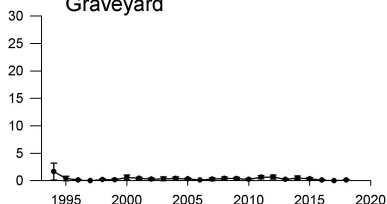
Westwood South



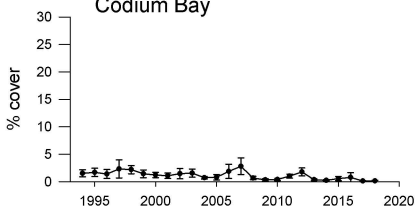
Boundary Bay



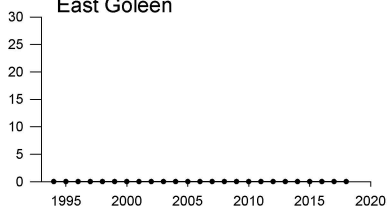
Graveyard



Codium Bay



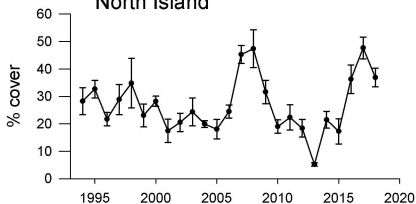
East Goleen



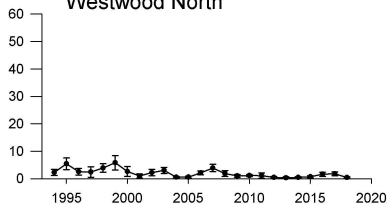
Year

Chthamalus montagui

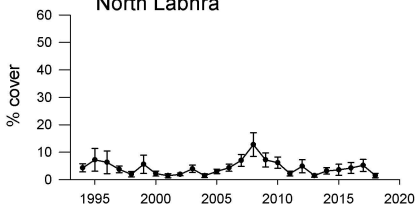
North Island



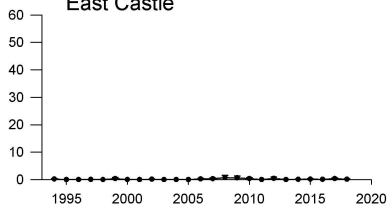
Westwood North



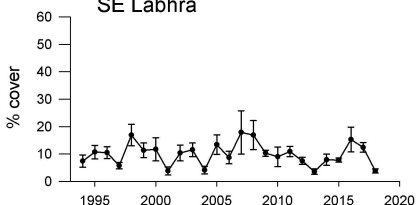
North Labhra



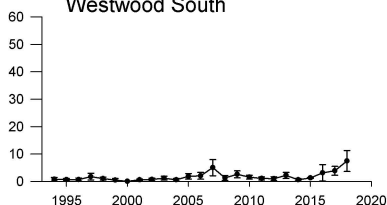
East Castle



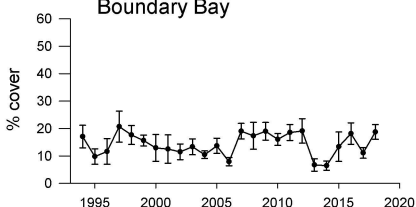
SE Labhra



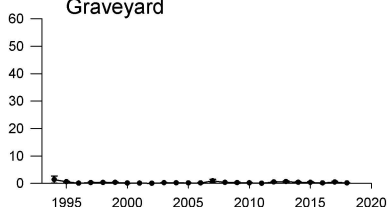
Westwood South



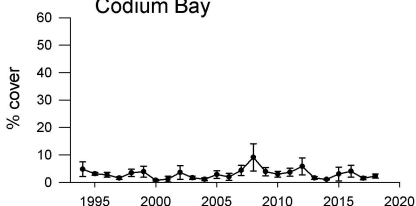
Boundary Bay



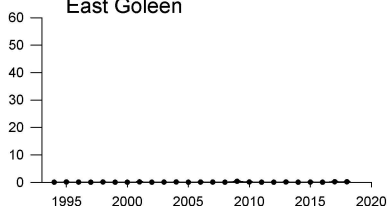
Graveyard



Codium Bay



East Goleen



Year

Year