Assessment of the current status of Black-legged Kittiwake *Rissa tridactyla* in Wales

NRW Evidence Report No. 558

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Executive Summary

Kittiwakes Rissa tridactyla are red listed by the Birds of Conservation Concern panel for Great Britain and have been classified as being vulnerable, at both the European and global scales, by the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species. Populations of kittiwakes have declined within Wales between 2000 and 2018 by 43%. This decline is a continuation of abundance trends occurring since 1986. Over this period populations of kittiwakes throughout the United Kingdom (UK) and Republic of Ireland (ROI) have declined, however with regionally varying trends.

This report compares regional demographic trends of Kittiwakes within Wales and the UK and ROI by collating existing scientific literature and available survey data of abundance and productivity. Assessment of this knowledge provides a general understanding of the drivers underpinning population trends of Kittiwakes within Wales in the context of other UK populations.

A standardized literature review was performed, focussing on studies carried out within the UK and ROI that investigated demographic parameters of abundance, productivity, and survival. Covariates underlying trends in demographic parameters were identified within each study. The literature review considered 48 studies in total, which related to studies of productivity (n=37), abundance (n=5), and survival (n=4).

Previous literature has indicated that there is a degree of spatial synchrony in demographic trends throughout the Irish and Celtic Sea, largely related to diet and a lack of reliance on sandeels compared to colonies within the North Sea. However, inter-colony variation in demographic trends exists within Wales, potentially linked to habitat heterogeneity, and site-specific impacts such as adverse weather events and predation.

Trends in kittiwake abundance and productivity within the UK and ROI were explored using data obtained from the Seabird Monitoring Programme (SMP) database for the period of 1986-2019. Demographic rates were considered at colony, regional, and Regional Seas scales. Annual trends in productivity and abundance were explored using binomial and negative binomial GLMs, respectively.

Analysis of kittiwake abundance trends within Wales indicates an overall decline between 1986-2019. Larger colonies displayed greatest absolute declines; however, declines were also persistent across smaller colonies. Inter-colony variation in abundance trends was apparent, with some colonies having maintained stable populations. Comparing trends occurring at Welsh colonies to others within the UK and ROI, annual abundance trends broadly reflect the majority of regional trends, however with a bias towards negative annual trends.

Productivity of kittiwake colonies within Wales display varying trends between 1986-2019. Productivity at the largest colony of Skomer has remained relatively stable over the monitoring period. Productivity trends occurring at Welsh colonies are primarily negative, though trends broadly match the distribution of trends occurring within UK and ROI.

Trends in abundance and productivity have been shown here to be in decline, however with some inter-colony variation apparent. While these trends are not unique to Wales, drivers are poorly understood in this region. Improved knowledge of diet, local prey stocks

(such as clupeids and sandeels) and the bottom-up drivers influencing prey could help to better understand the pressures on Welsh kittiwake colonies. Monitoring the impacts of adverse weather and predator presence could potentially inform colony specific demographic trends.

Crynodeb Gweithredol

Mae'r wylan goesddu, Rissa tridactyla, ar restr goch panel Adar o Bryder Cadwraethol Prydain Fawr ac mae wedi cael ei dosbarthu fel rhywogaeth sydd dan fygythiad, ar raddfa Ewrop ac yn fyd-eang, gan Restr Goch yr Undeb Rhyngwladol dros Gadwraeth Natur (IUCN) o Rywogaethau sydd Dan Fygythiad. Mae gostyngiad o 43% wedi bod yn y poblogaethau o wylanod coesddu yng Nghymru rhwng 2000 a 2018. Mae'r dirywiad hwn yn barhad o dueddiadau toreithrwydd ers 1986. Dros y cyfnod hwn mae poblogaethau o wylanod coesddu ledled y Deyrnas Unedig (DU) a Gweriniaeth Iwerddon (GI) wedi dirywio, fodd bynnag gyda thueddiadau amrywiol rhanbarthol.

Mae'r adroddiad hwn yn cymharu tueddiadau demograffig rhanbarthol gwylanod coesddu yng Nghymru a'r DU a GI drwy gasglu llenyddiaeth wyddonol bresennol a data arolygon sydd ar gael o ran toreithrwydd a chynhyrchiant. Mae asesu'r wybodaeth hon yn rhoi dealltwriaeth gyffredinol o'r gyrwyr sy'n sail i dueddiadau poblogaeth gwylanod coesddu yng Nghymru yng nghyd-destun poblogaethau eraill y DU.

Perfformiwyd adolygiad llenyddiaeth safonol, gan ganolbwyntio ar astudiaethau a gynhaliwyd o fewn y DU a GI a ymchwiliodd i baramedrau demograffig o ran toreithrwydd, cynhyrchiant, a goroesiad. Nodwyd cyd-newidynnau oedd yn sail i dueddiadau mewn paramedrau demograffig o fewn pob astudiaeth. Ystyriodd yr adolygiad llenyddiaeth 48 astudiaeth i gyd, a oedd yn ymwneud ag astudiaethau o gynhyrchiant (n=37), toreithrwydd (n=5), a goroesiad (n=4).

Mae llenyddiaeth flaenorol wedi nodi bod rhywfaint o syncroni gofodol mewn tueddiadau demograffig ledled Môr Iwerddon a'r Môr Celtaidd, sy'n gysylltiedig i raddau helaeth â deiet a diffyg dibyniaeth ar lymrïaid o gymharu â chytrefi o fewn Môr y Gogledd. Fodd bynnag, mae amrywiad rhyng-gytrefol mewn tueddiadau demograffig yn bodoli yng Nghymru, a allai fod yn gysylltiedig â heterogenedd cynefinoedd, ac effeithiau safle-benodol megis digwyddiadau tywydd garw ac ysglyfaethu.

Archwiliwyd tueddiadau o ran toreithrwydd a chynhyrchiant gwylanod coesddu yn y DU a GI gan ddefnyddio data a gafwyd o gronfa ddata'r Rhaglen Monitro Adar Môr ar gyfer cyfnod 1986-2019. Ystyriwyd cyfraddau demograffig ar raddfeydd cytrefi, rhanbarthau, a Moroedd Rhanbarthol. Archwiliwyd tueddiadau blynyddol mewn cynhyrchiant a thoreithrwydd gan ddefnyddio GLMau binomaidd a binomaidd negyddol, yn y drefn honno.

Mae dadansoddiad o dueddiadau toreithrwydd gwylanod coesddu yng Nghymru yn dangos gostyngiad cyffredinol rhwng 1986-2019. Roedd cytrefi mwy yn dangos y dirywiad absoliwt mwyaf; fodd bynnag, roedd dirywiad hefyd yn gyson ar draws cytrefi llai. Roedd amrywiad rhyng-gytrefol mewn tueddiadau toreithrwydd yn amlwg, gyda rhai cytrefi wedi cynnal poblogaethau sefydlog. O gymharu tueddiadau yng nghytrefi Cymru i eraill o fewn y DU a GI, mae tueddiadau toreithrwydd blynyddol yn adlewyrchu'n fras y mwyafrif o dueddiadau rhanbarthol, fodd bynnag gyda gogwydd tuag at dueddiadau blynyddol negyddol.

Mae cynhyrchiant cytrefi gwylanod coesddu yng Nghymru yn dangos tueddiadau amrywiol rhwng 1986-2019. Mae cynhyrchiant yn y gytref fwyaf, Sgomer, wedi aros yn gymharol sefydlog dros y cyfnod monitro. Mae tueddiadau cynhyrchiant yng nghytrefi Cymru'n negyddol yn bennaf, er bod tueddiadau'n cyfateb yn fras i ddosbarthiad y tueddiadau sy'n digwydd o fewn y DU a GI.

Dangoswyd yma fod tueddiadau o ran toreithrwydd a chynhyrchiant yn dirywio, fodd bynnag gyda rhywfaint o amrywiad rhyng-gytrefol yn amlwg. Er nad yw'r tueddiadau hyn yn unigryw i Gymru, nid oes dealltwriaeth dda o'r gyrwyr yn y rhanbarth hwn. Gallai gwell gwybodaeth am ddeiet, stociau ysglyfaethau lleol (fel teulu'r Clupeidae a llymrïaid) a'r gyrwyr sylfaenol sy'n dylanwadu ar ysglyfaethau helpu i ddeall yn well y pwysau ar gytrefi gwylanod coesddu yng Nghymru. Gallai monitro effeithiau tywydd garw a phresenoldeb ysglyfaethwyr o bosibl fwrw golau ar dueddiadau demograffig mewn cytrefi penodol.

1. Introduction

Black-legged kittiwakes *Rissa tridactyla* (hereafter referred to as kittiwake) are a gull species distinct in their cliff nesting and exclusively pelagic foraging behaviour (Coulson 2011). Kittiwakes are a relatively long lived (average: 14 years, maximum: 28 years) bird species, reaching breeding age at 4 years old and generally produce a clutch of two eggs but can lay up to three (Robinson 2005). They are the most numerous gull species in the world, with a maximum estimated population of 3,000,000 breeding pairs within the North Atlantic (Mitchell et al. 2004). Despite their apparent global prevalence the species is red listed by the Birds of Conservation Concern panel for Great Britain (Eaton et al. 2015) and has been classified as being vulnerable, at both the European and global scales, by the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species (BirdLife International 2019). Kittiwakes are a protected species within the United Kingdom designated under Section 3 of the EU bird directive and transcribed into UK and its constituent countries laws accordingly.

During Seabird 2000 it was estimated that the Special Protected Area (SPA) network held over 50% of the kittiwakes nesting in the UK (JNCC 2020a). Within Wales, kittiwakes are a feature of just one SPA encompassing the Skomer, Skokholm and the Seas off Pembrokeshire. Kittiwake are also a feature of Aberarth Carreg Wylan SSSI, Pen y Gogarth/ Great Ormes Head SSSI and Skomer SSSI (part of a seabird assemblage SPA). It has been estimated that within Wales 64% of kittiwakes are features of SSSI and or SPAs, whilst 98% of kittiwakes are found within sites where are there are other seabird features (Matthew Murphy pers. comm). The SPA designated island of Skomer, the largest kittiwake colony within Wales, has seen a gradual decline in productivity and abundance over the period 2008-2018 (Stubbings et al. 2018).

Populations of kittiwakes declined within the United Kingdom (UK) and the Republic of Ireland (ROI) between the national censuses of Seabirds Colony Register and Seabird 2000 covering 1985-1988 and 1998-2002 respectively (Mitchell et al. 2004). Decreases have continued according to annual monitoring undertaken at a subset of colonies through the Seabird Monitoring Programme (SMP) (JNCC 2020b). This overall decline is also apparent in Wales, with a 43% decrease in breeding populations at 15 monitored colonies over the 2000-2018 (JNCC 2020a). Whilst a broad population decline across the UK and Wales is apparent, there is also spatial variation in trends with some colonies showing relatively stable numbers or even increases. Many of the declines in breeding abundance have been linked to breeding success which have fallen below a critical level (0.8) required to maintain colony numbers (Coulson 2017).

The relative abundance of the prey species lesser sandeels *Ammodytes marinus* (hereafter referred to as sandeels) have been closely linked to kittiwake productivity and abundance trends in the North Sea, namely at colonies in South East Scotland/North East Scotland and Shetland (Rindorf et al. 2000, Heubeck 2002). This relationship between sandeel availability and breeding kittiwakes populations does not appear to be as prevalent in the Irish and Celtic Seas which are adjacent to the Welsh colonies however (Frederiksen et al. 2007a, Cook et al. 2011). Differing demographic responses of kittiwake populations within the UK and ROI are likely to be due to varying climatic trends and diet compositions associated with their colonies (Lauria et al. 2012, 2013). Drivers of population dynamics within Wales are largely unknown, however prey stocks of 0- and 1 – group herring *Clupea harengus* and

Sprat *Sprattus sprattus* (Chivers et al. 2012b, Lauria et al. 2012) and the availability of fisheries discards (Harris & Wanless 1997, Bicknell et al. 2013) may have had an influence. Adverse weather may be a contributing factor in Wales, with a decline in the number of breeding pairs on Skomer, being attributed to adverse weather conditions stemming from a positive NAO index (Lauria et al. 2012). Top down pressures from avian predators have also been identified within Wales leading to breeding failures (Collins et al. 2014). Therefore, a range of pressures may be acting on Welsh colonies.

This project aimed to investigate the likely causes behind the decline in kittiwake abundance within Wales noting key differences such as prey availability and oceanographic features of other seas around the UK and ROI. This was carried out in two stages, firstly through a review of scientific literature of the drivers influencing kittiwake population's trends within Wales and considered several key demographic parameters including: abundance, productivity, and survival. We also outlined current demographic trends within the UK and ROI as a comparison to those observed in Wales. We then considered how regional kittiwake populations respond to variation in these demographic parameters, and where possible, identify potential extrinsic and intrinsic factors influencing these parameters. Secondly, we examined the SMP database to compare trends in kittiwake abundance and productivity between colonies and regions across the UK, with specific focus on Welsh based colonies.

2. Methods

2.1. Literature Review

The literature review was performed through a standardized internet search, using Google Scholar. Search terms used included relevant names for kittiwakes including: "Rissa tridactyla", "kittiwake", "black-legged kittiwake"; and key words including: "abundance", "population", "productivity", "survival", "breeding", "survey", "monitoring", "count", "diet", and "predation". Potentially relevant studies were identified from their titles and abstracts, explicitly selecting studies conducted within the UK and Republic of Ireland. From each study the following information was extracted: study location, duration, demographic parameter/s investigated (e.g. productivity, abundance, survival), and whether any independent covariates were included (e.g. predation, prey composition). Also recorded was whether a covariate displayed a statistically significant effect.

Literature was summarised for each key demographic parameter (abundance, productivity, and survival). Each summary describes the trends observed within the UK and Republic of Ireland for each parameter. The covariates underlying trends in demographic parameters are summarized in separate section titled “Drivers”, with subheadings demarcating common themes.

2.2. SMP Analysis

2.2.1. SMP Abundance

Trends in kittiwake abundance within the UK and ROI were explored using whole-colony counts obtained from the SMP database (1986-2019). Only colonies monitored for more than 5 consecutive years, and had greater than 10 Apparently Occupied Nests (AONs) were included. Trends in colony abundance were examined in relation to SMP regions (Figure 1.) and Charting Progress 2 (CP2) Regional Seas (Marine Scotland 2013) (Figure 2). Comparative trends in abundance between colonies within Wales, and all other colonies within UK and ROI were explored visually using scatterplots. Additionally, trends in abundance between colonies corresponding to adjoining Regional Seas were displayed visually using scatterplots. The relationship between abundance, year, and colony was investigated using a negative binomial Generalised Linear Model (GLM) using the MASS package within R (Version 4.0.3, R Development Core Team 2020). The correlation coefficient of yearly abundance derived from the GLM was compared to mean abundance of each monitored colony. The relationship between these two covariates in relation to colony was investigated visually using scatterplots and density plots.

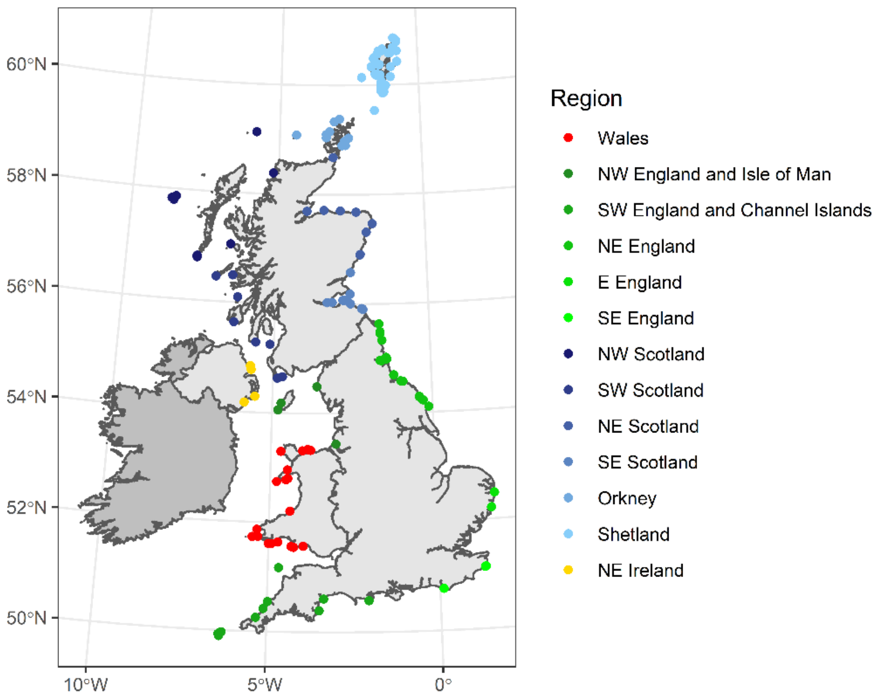

Figure 1. Kittiwake colonies within the UK and ROI where abundance data was contributed by the SMP. Colonies coloured by regions defined by the SMP.

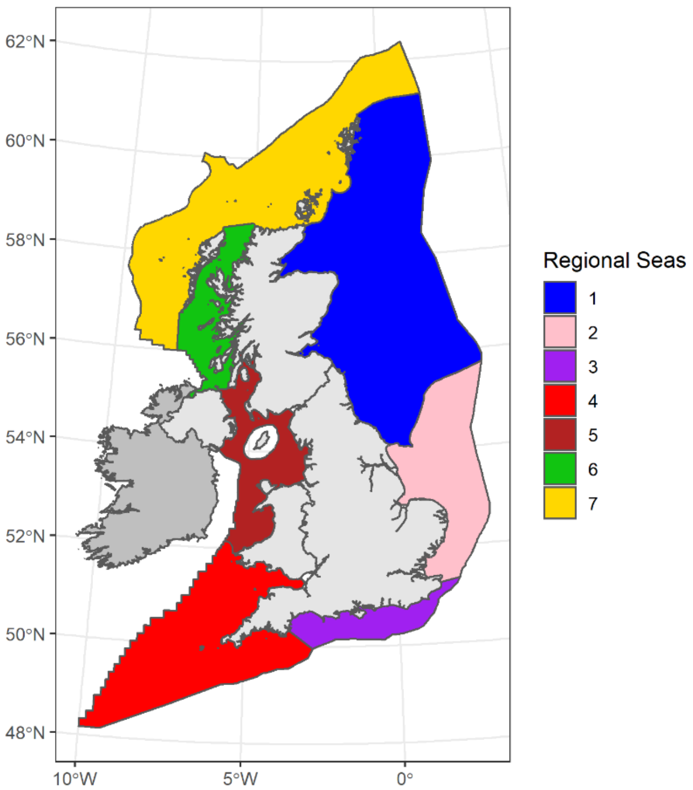

Figure 2. Regional Seas areas around the UK adjoining kittiwake colonies.

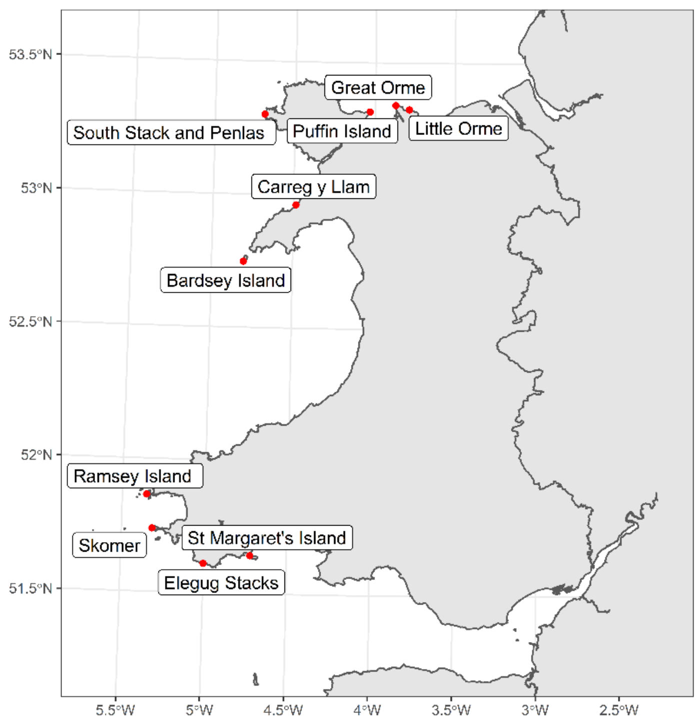

Figure 3. Welsh kittiwake colonies monitored by the SMP.

2.2.2. SMP Productivity

Trends in kittiwake productivity within the UK and ROI were explored using counts of nests/breeding pairs and counts of fledged chicks obtained from the SMP database (1986-2019). Only colonies monitored for more than 5 consecutive years, and which had greater than 10 active AONs were included. Explorations of colony productivity were carried out for two regional grouping including SMP Region and Regional Seas. The relationship between productivity, year, and colony was investigated using a binomial GLM within R (Version 4.0.3, R Development Core Team 2020). The correlation coefficient of yearly productivity derived from the GLM was compared to the mean colony productivity. The relationship between these two covariates in relation to colony was investigated visually using scatterplots.

3. Results

3.1. Literature Review

The literature search resulted in a total of 48 studies. The majority of studies (n=37) considered productivity, while five studies considered abundance and four examined survival.

3.1.1. Abundance

Populations of kittiwakes have declined within the UK and ROI from 505,465 Apparently Occupied Nests (AON) to 379,895 between the national census periods of 1985-1988 and 1998-2002 (Mitchell et al. 2004). These losses have continued according to annual monitoring undertaken at a subset of colonies between 2000 and 2018, with the population reducing by a further 50% (JNCC 2020b). The most notable declines have occurred on Shetland, exemplified by the colonies at Foula and Noss, which fell by 86 and 98% respectively from 2000 (1934 AON, Foula; 2395 AON, Noss) to 2017/2018 (262 AON, Foula; 44 AON, Noss) (Heubeck 2002, JNCC 2020a). Similarly, the colony at Marwick Head on Orkney declined 84% from 1999 (5573 AON) to 2018 (906 AON) (JNCC 2020a). In contrast to declines in the Northern Isles in Scotland, the colony at Flamborough Head and Bempton Cliffs on the English North-East coast experienced a population increase of (7%) between 2000 (42582 AON) and 2017 (45504 AON) (SMP data).

Based on Seabird 2000 counts, Wales (7,293 AON) contains a smaller kittiwake population in comparison to Scotland (282,213 AON), England (77,329 AON), Northern Ireland (13,042 AON), and the Republic of Ireland (36,118 AON). In addition, no Welsh colonies reach the abundance of larger colonies found in Scotland and England. Within Wales the population of kittiwakes underwent a decline of 17% from 8,771 to 7,293 AON between the census periods of 1985-1988 and 1998-2002 (Mitchell et al. 2004). Despite this overall declining trend in abundance, breeding abundance fluctuated between 15 colonies monitored annually within Wales between 1986 and 2018 (Table 1). Skomer the largest colony within Wales experienced the greatest overall decline in recent years (Table 1). Prior to 2018, Skomer sustained a fairly stable population between 1986 (2,148 AON) until 2000 (2,257 AON). Despite interannual fluctuations (JNCC 2020a), the colony on Skomer has since declined to 1,236 AON in 2018 (Table 1). Extensive losses of between 2000 and 2018 were also recorded on Ramsey Island and Carreg y Llam (Table 1) (Brown et al. 2004, McMurdo Hamilton et al. 2016). Increases at St Margaret's Island and St. Tudwal's Island East over the comparative period do not compensate for declines occurring at the majority of colonies within Wales. Currently, populations are 49% below those recorded in 1986 when the annual monitoring started (JNCC 2020a). These contrasting trends exemplify the large amount of spatial variation experienced between regional populations throughout the UK and ROI. Cook et al. (2011) observed similar trends in abundance of kittiwakes within 6 ecologically distinct regions around the UK and ROI. Abundance trends were broadly separated between the East Coast of the UK and the West Coast/Republic of Ireland (Cook et al. 2011). Within Wales, kittiwake populations are divided between two ecologically distinct areas: the Celtic sea and the Irish Sea.

Table 1. Colony abundance within Wales based on whole colony counts of Apparently Occupied Nests (AON) collated by the Seabird Monitoring Program* Date of nearest

available count is noted in brackets within the table. Colour gradient indicates change in abundance between periods - decline (red) or increase (blue) in abundance). Darker colouration indicates a larger degree of change in abundance between periods. CP2 Regional Seas adjoining each colony have been classified.

Regional Seas	Site	1986 **(AON)**	2000 **(AON)**	2018 **(AON)**	Difference 1986-2000	Difference 2000-2018
4	Elegug Stacks	490	148	2	-342	-146
4	St Margaret's Island	379	6	243	-373	237
4	Stackpole Head	98	0	0(2013)	-98	0
4	Worms Head	140	119(2001)	11	-21	-108
5	Bardsey Island	150	278	90	128	-188
5	Carreg y Llam	502	868	317	366	-551
5	Grassholm	67	9	30	-58	21
5	Great Orme	1188	1147	751	-41	-396
5	Little Orme	754	582	225	-172	-357
5	New Quay Head	175(1987)	375	332	200	-43
5	Puffin Island	310	571(2001)	299	261	-272
5	Ramsey Island	306 (1987)	459	83	153	-376
5	Skomer	2148	2257	1236	109	-1021
5	South Stack and Penlas	0	1	7	1	6
5	St Tudwal's Island East	395	282	310(2016)	-113	28

*data provided on request by the Joint Nature Conservation Committee

3.1.2. Breeding Success

Although the productivity of kittiwakes is characteristically highly variable from one year to the next, the average number of chicks fledged per pair has been estimated as 0.63 for the UK over 2014-2018 (JNCC 2020a). Scotland has experienced an overall decline in productivity from 1986 to 2008, with some recovery in breeding success between 2009-2018 (JNCC 2020a). Breeding success has varied to a large extent between regions of Scotland with relatively higher average breeding success at colonies within the Northwest of Scotland and Isle of May than on Shetland (Table 2).

Kittiwake productivity within Wales has similarly fluctuated with no clear trend although there were signs of decline from 2010 onwards. Of the two Welsh colonies continually monitored since 1986, average breeding success declined on Skomer between the SCR Census and Seabird 2000 for the periods of 1986-1999 and 2000-2019, while remaining relatively stable on Bardsey Island (Table 2). Overall Wales maintains comparatively lower productivity to England and Scotland (Table 2).

Table 2. Average productivity (no. of chicks fledged per pair) of kittiwakes during the periods of 1986-1999 and 2000-2019 at continually monitored colonies in the UK and Republic of Ireland collated by the Seabird Monitoring Program*. Colour gradient indicates change in average productivity between periods - decline (red) or increase (blue) in abundance). Darker colouration indicates a larger degree of change in productivity between periods. CP2 Regional Seas adjoining each colony have been classified.

Regional Seas	**Site**	**Region**	**1986-1999 Average**	**1986-1999 Range**	**2000-2019 Average**	**2000-2019 Range**
1	Farne Islands	NE England	0.94	0.32-1.36	0.73	0.1-1.18
1	Flamborough Head and Bempton Cliffs	NE England	1.05	0.42-1.54	0.73	0.08-1.56
1	Isle of May	SE Scotland	0.39	0-1.38	0.64	0-2
5	Bardsey Island	Wales	0.62	0-1.25	0.71	0-1.12
5	Skomer	Wales	0.72	0.44-0.97	0.56	0-1.01
6	Canna and Sanday	NW Scotland	0.67	0.19-1	0.72	0-1.42
6	Handa Island	NW Scotland	1.33	0.69-1.58	0.89	0-1.97
6	Rathlin Island	NE Ireland	0.85	0.21-1.11	0.81	0-1.33
7	Foula	Shetland	0.73	0-1.39	0.23	0-0.83
7	Marwick Head	Orkney	1.14	0.92-1.53	0.61	0-1.55
7	Noss	Shetland	0.29	0-0.66	0.10	0-0.66
NA	Ram Head	SE Ireland	0.56	0.21-0.93	0.23	0-1
NA	Rockabill	SE Ireland	0.99	0.51-1.55	0.96	0.35-1.51

*data provided on request by the Joint Nature Conservation Committee

3.1.3. Survival

Kittiwake survival rates can be highly variable between years (Coulson & Thomas 1985, Sandvik et al. 2005). The estimation of survival rates in adult kittiwakes are likely to be also influenced by mortality, dispersal, or surviving adults avoiding breeding in following years (Oro & Furness 2002). Survival rates are not reported for the whole of the UK (or the constituent countries) as part of the SMP but are given for Skomer and as return rates for the Isle of May. Both of which shown a lack of long-term trend in rates from 1986-2018 (JNCC 2020a).

3.1.4. Diet

Sandeels have been identified as a primary diet component of kittiwakes during the breeding season within the UK. They form a particularly high proportion of kittiwake diet for breeding colonies located within the North Sea and in the Northern Isles of Scotland (Swann et al. 1991, Hamer et al. 1993, Harris & Wanless 1997, Lewis et al. 2001, Bull et al. 2004). In these areas there is strong evidence to suggest population dynamics are related to prey availability within the breeding season, underpinned by a close association between the explicitly surface-feeding kittiwake, and the pelagic phase of sandeels (Burthe et al., 2012; Carroll et al., 2015; Frederiksen et al., 2007; Lauria et al., 2013; Olin et al., 2020). The influence of sandeel abundance is reflected in the distribution and size of kittiwake colonies around the UK, which can reflect local availability of sandeel aggregations (Lewis et al. 2001, Frederiksen et al. 2005). Studies of kittiwake diet from Wales are few, kittiwake populations here are potentially less reliant on sandeels as other regions (Frederiksen et al. 2007a, Lynam et al. 2013, ICES 2021). Therefore, sandeels are supplemented by prey species such as: gadoid spp., in the Sea of the Hebrides (Canna island)(Harris & Wanless 1990, Swann et al. 1991, 2008, 2015); clupeoid spp., within the Irish Sea (Chivers et al. 2012b); and sprat within the Celtic Sea (Lauria et al. 2013) and periodically in the Sea of the Hebrides (Swann et al. 2008). Diet composition also varies within the Celtic/Irish Sea region with some colonies displaying reliance on single species (clupeids on Rathlin) or variety of species being observed at other colonies (clupeids, sandeels and gadoids on Lambay) (Chivers et al. 2012c, Anderson et al. 2014). Within Wales, diet studies suggest there is less reliance on sandeels in this region (Frederiksen et al. 2005, Anderson et al. 2014), and a greater prevalence of clupeids (Chivers et al. 2012b), and gadoids (Harris & Wanless 1990). Wilson et al. (2021), found that the probability of diet to contain sandeels was much higher in the greater North Sea than in the Irish and Celtic seas, this probability was also found to decline with increasing latitude. However, they also found the opposite trend to occur in the probability of diet to contain gadoids. Inter-colony variability in abundance trends observed within Wales may suggest the presence of locally varying diets, which have been identified between marine and inshore colonies within the Firth of Forth (Bull et al. 2004).

The diet of surface feeding species such as Sandwich terns *Thalasseus sandvicensis*, Common Terns *Sterna hirundo* and Arctic Terns *Sterna paradisaea* within the Irish Sea are similar to kittiwakes, and contain sandeels, gadoid spp. and clupeid spp. (Newton & Crowe 2000, Perrow et al. 2010). Some variation in diet composition was noted between colonies and years within the Irish Sea specifically regarding the proportion of sandeels in contrast to clupeids (Newton & Crowe 2000, Perrow et al. 2010, Green 2017). Despite terns foraging closer inshore than kittiwakes, information on local prey availability derived from terns may inform kittiwake diet within the same region, dependent on the distribution prey.

3.1.5. Drivers

3.1.5.1 Prey abundance

Kittiwakes are surface feeders, and therefore may be sensitive to prey availability should conditions alter the location of prey within the water column (Furness & Tasker 2000). Whilst seabirds show some flexibility in foraging behaviour should prey decrease in availability, chick provisioning birds have limited spare time to make such adjustments (Chivers et al. 2012a). Breeding failure therefore tends to occur during the chick rearing stage of the breeding season through starvation of the young (Harris & Wanless 1990, 1997, Hamer et al. 1993, Chivers et al. 2012a).

Sandeel abundance has correlated with productivity of kittiwakes in Shetland, Orkney, and within the North Sea (Hamer et al. 1993, Frederiksen et al. 2005, Furness 2007, Eerkes-Medrano et al. 2017, Carroll et al. 2017). Colonies within the North Sea and North of Scotland displayed spatial synchrony in breeding success driven in part by sandeel dynamics linked to factors such as Sea Surface Temperatures (SST) (Frederiksen et al. 2005, Olin et al. 2020). The lack of alternative preyto sandeels has potentially exacerbated the impacts of years of low sandeel abundance in the North Sea (Harris & Wanless 1997, Frederiksen et al. 2007b), and Shetland (Hamer et al. 1993, Heubeck 2002). Within the North Sea, additional pressure exerted by the sandeel fishery which operated until 2000, was also observed to depress kittiwake breeding success (Frederiksen et al. 2008, Cook et al. 2014). The impact of fisheries on breeding success may be lagged through prey demography, as was reported in Carroll et al. (2017) where reduced sandeel mortality by fisheries 2 years previously, correlated with increased breeding success.
Regional variation in prey ecology has meant that climatic conditions do not effect productivity uniformly within the UK and ROI (Cook et al. 2014, Carroll et al. 2015). Cook et al. (2014) found no relation between sandeel abundance and the productivity of Celtic Sea residing kittiwakes in contrast to colonies within the North Sea. Lauria et al. (2013) similarly found breeding success at colonies within the Celtic Sea have no relationship with bottom up processes of SST, plankton, and fish larvae. This was attributed to herring and sprat being a primary component of kittiwake diet within the Celtic Sea (Chivers et al. 2012b, Lauria et al. 2012). Therefore, landings and Spawning Stock Biomass (SSB) of both sprat and herring, which have varied between 1986-2019 within the Irish Sea, may influence kittiwake productivity within Wales (ICES 2019, 2020). Alternate prey resources are likely to mitigate against breeding failure. Diet composition may have underpinned variable reproductive success Rathlin (2005-2012) which had a more restricted diet, while Lambay displayed consistently high breeding success, and greater variation in diet (Chivers et al. 2012b).

Spatial variation in foraging conditions may also impact breeding success, and have been attributed to local heterogeneity in bathymetry, tidal stratification, SST and oceanic fronts (Trevail et al. 2019a b). Regions where habitats were more heterogeneous, or patchy, correlated with decreased breeding success as a consequence of more distant foraging trips and time spent foraging and increased overlap between individual kittiwakes from the same colony, increasing competition for finite resources. The North-east of Scotland and the north-east coast of England are characterised by a more homogenous habitat whereas the West coast of Scotland, Irish Sea, and South East England are more heterogenous. This divergence in habitat between regions may influence differing rates of kittiwake breeding abundance and productivity (Chivers et al. 2013, Trevail et al. 2019b).

The influence of prey abundance on kittiwake survival, especially for juvenile and immature age classes, remains poorly understood. Carry over effects of foraging conditions during the breeding season are likely to maintain an influence on adult survival (Oro & Furness 2002). During the breeding season adults are buffered to some extent from the primary factors effecting breeding success as they exhibit flexible foraging journey lengths to find prey potentially enabled by low wing loading (Chivers et al. 2012a). During incubation they may exhibit this flexibility, while breeding failure has often been recorded to occur during the hatching period, when foraging becomes more constrained by high feeding rate. Therefore, poor foraging conditions tend to be reflected in failed breeding attempts rather than adult mortality and survival during the breeding season (Aebischer & Coulson 1990), although mortality is likely occurs within the winter when conditions are challenging (Oro & Furness 2002). Greater body mass in adults following the breeding season may lead to higher survival rates in kittiwakes (Oro & Furness 2002).

The influence of prey abundance on breeding success has been argued to be the main pathway in which population abundance may be impacted, as colonies must sustain productivity over a critical level to maintain breeding abundance (Coulson 2017). Breeding failure has been shown to maintain a 2 year lagged effect on population abundance (Cook et al. 2011). The influence of prey abundance on kittiwake breeding success has displayed lagged effects on populations (Wanless et al. 2007, Frederiksen et al. 2013). The lack of evidence of impacts of reduced survival rates on abundance cannot be ruled out however. Population growth, and therefore overall abundance, has been comprehensively shown to be more sensitive to variation in survival than variation in productivity (Sæther & Bakke 2000). There is a need therefore for better information on this demographic parameter.

3.1.5.2. Predators

While the impacts of prey may indirectly affect kittiwake demography, direct impacts may arise from predation. Interactions with predatory species such as great skuas *Stercorarius skua* and peregrine falcons *Falco peregrinus* potentially cause adult desertion due to nest failure (Huebeck et al. 1997, Collins et al. 2014), which can lead to loss of breeding habitat, and nesting birds to shift to more sheltered areas (Heubeck 2002, Votier et al. 2008). Due to this top-down pressure, adult dispersal from a population may occur which means that decreasing populations may show greater dispersal rates than those which are increasing (Oro & Furness 2002). The impacts of avian predation may be two fold due to predators shifting to kittiwake eggs and chicks in response to a lack of marine prey, which is also simultaneously impacting kittiwake chick provisioning (Regehr & Montevecchi 1997, Heubeck 2002, Chivers et al. 2012a, Perkins et al. 2018). Therefore, top-down impacts may also be compounded in years when breeding kittiwakes are experiencing low prey availability though bottom up effects, which may also contribute to declines in breeding success and adult survival (Oro & Furness 2002). Low colony density may also expose nests to higher rates of predation from peregrine falcons, further impacting colonies experiencing low breeding success (Collins et al. 2014). Some predation is also carried out by herring gulls *Larus argentatus*, however this occurred within the nesting territories of gulls and was exhibited by specialist individuals on exposed nests, and therefore was found not to have a significant impact (Galbraith 1983, Harris & Wanless 1997). The impacts of mortality caused by predation on differing age groups are difficult to quantify as investigation of pellets from species such as greats skua’s may contain the remains of adults, chicks, fledglings, and non-breeding birds, which are difficult to differentiate (Phillips et al. 1999).

3.1.5.3. Adverse Weather

Adverse weather may directly impact productivity and adult survival. Heavy rainfall previously significantly reduced breeding success by negatively impacting chick survival (Turner 2010). Isolated catastrophic years of low productivity have been caused by storms washing nests away on Skomer (Brown et al. 2004), and the Isle of May (Newell et al. 2015).

Foraging conditions may be influenced by adverse weather conditions through reduced prey availability, which may have occurred in Northern fulmars *Fulmarus glacialis* (Thompson & Ollason 2001, Lewis et al. 2009), or common guillemots *Uria aalge* (Morley et al. 2016). During the winter, foraging conditions are potentially negatively affected by environmental conditions such as high winter SSTs and positive NAO (Frederiksen et al. 2004, Wanless et al. 2009). These warm and variable conditions have high metabolic cost for sandeels, leading to prolonged periods of burial and reduced body condition, which as a consequence results in reduced prey availability and energy quality (Wanless et al. 2009, Carroll et al. 2015, Wright et al. 2020). Wrecks of immature and adult kittiwakes provide an insight into some of the causes of winter mortality at-sea caused by adverse weather (Mccartan 1958, Craik 1992, Morley et al. 2016). Primarily wrecks have been attributed to starvation arising from adverse weather preventing foraging (Barrett et al. 2004). However, the effects of wrecks on survival rates and abundance are hard to detect (Camphuysen et al. 1999), as they may be spread over several colonies.

3.1.5.4. Emigration/Immigration

To date there is limited information available on the movement of kittiwakes between breeding colonies and there is a lack of data collated at national level. Large scale metapopulation dynamics may influence colony populations not only within Wales, but the UK and bordering European countries. This may occur through emigration of immature kittiwakes to other viable colonies (Coulson & Coulson 2008). Recruits into some colonies within the North Sea were found to be arrivals from other colonies, and natal philopatry to be low (Coulson & Coulson 2008), and to vary with sex (Wooller & Coulson 1977). Attributes of a colony including breeding success, age, and size may influence the number of recruits a colony receives. Prospecting immature individuals may visit colonies during the advanced stages of the breeding season and have been suggested to be attracted to future breeding sites based on the number of young in nests, a potential indictor of prey abundance and low predation (Coulson & Coulson 2008). Contrasting to the potentially high rates of natal dispersal, adults display high breeding philopatry. These factors should be accounted for when considering colony declines as individuals transferring between colonies may underpin perceived population trends, with particular caution required where colonies fall outside continuous monitoring efforts. However, within Wales, population declines on colonies such as Skomer have not been compensated by increases at colonies such as St. Margaret's Island, Ynys Moelfre or St Tudwal's Island (Table 1).

3.1.5.5. Wintering strategies

Breeding success and survival may be mediated through wintering strategies (Bogdanova et al. 2011). Carry-over effects from the breeding season have been observed to have an influence on wintering areas on birds tracked from the Isle of May. Individuals which travelled to the western Atlantic left earlier and also were more likely to have failed in their breeding attempt. The Western Atlantic may be associated with reduced competitive costs in comparison to the Eastern Atlantic (Bogdanova et al. 2011). However, the variation in wintering locations between colonies and successful/unsuccessful birds may vary the harshness of winter conditions experienced with potential implications for survival. Individuals from colonies throughout the North-East Atlantic travelled to both the western Atlantic and eastern Atlantic wintering areas (Bogdanova et al. 2011, Frederiksen et al.

2012). Overlap in wintering at-sea areas may not explain the majority of regionally varying trends in abundance between the Northern Isles and North Sea. However, some colonies did diverge in their winter locations, specifically birds from both Skomer and Rathlin which appeared to remain year-round within the Celtic and Irish Seas respectively (Frederiksen et al. 2012). Birds may return to same areas in successive years (Frederiksen et al. 2012) and the costs and benefits of these differing wintering areas, and the subsequent effect on survival are currently unknown.

3.2. SMP Analysis

3.2.1. Abundance

Trends in kittiwake abundance at Welsh colonies are displayed in Figure 4, trends corresponding to all other regions within the UK and ROI are displayed in Appendix 1. Kittiwake abundance within Wales has undergone an overall decline between 1986-2019 (Figure 4). Larger colonies such as Skomer, Little Orme, and Great Orme have displayed the largest declines, however declines were persistent across smaller colonies such as Elegug Stack and Ramsey Island. Despite interannual fluctuations, some colonies have maintained an overall stable abundance over the monitoring period such as at Carreg y Llam and Puffin island. The majority of colonies in Wales displayed a dip in abundance in 2013 (Figure 4).

Comparative trends in abundance between colonies within Wales, and all other colonies within UK and ROI are displayed within Figure 5. Colonies in Wales tend to be smaller than those located elsewhere, the largest being Skomer (peak 2543 in 1987). Whereas colonies such as Fair Isle in Shetland, Scotland and Flamborough Head/Bempton Cliffs in North East England at their peak have held 19340 (Year=1988) and 45563 (Year=2016) AONs respectively (Appendix Figure A1a, and A1h). Trends in abundance between colonies corresponding to adjoining Regional Seas are displayed in Figure 6. Regional Seas 4 and 5 (encompassing the Celtic Sea and Irish Sea) which adjoin Wales maintain similar colony abundances to Regional Seas 2,3, and 6. Regional Seas 1 and 7 (encompassing the northern North Sea and North-East Atlantic), while also possessing some colonies of similar size held in Wales, also contain colonies with relatively larger populations (Figure 6).

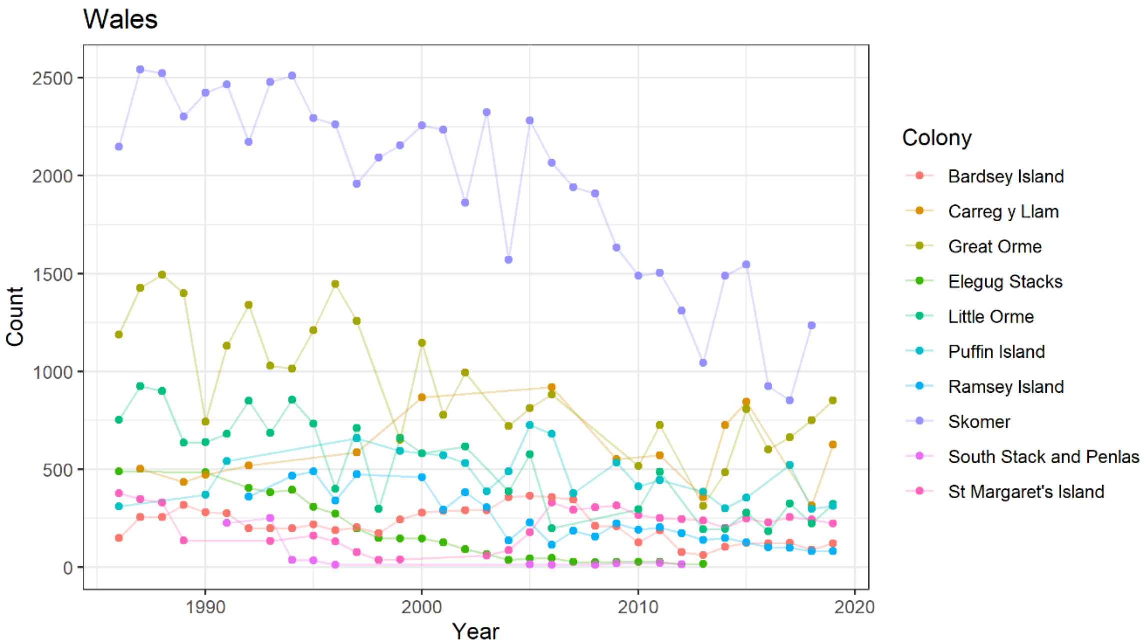

Figure 4. Wales based whole-colony abundance counts 1986-2019. All other SMP regions displayed within Appendix 1.

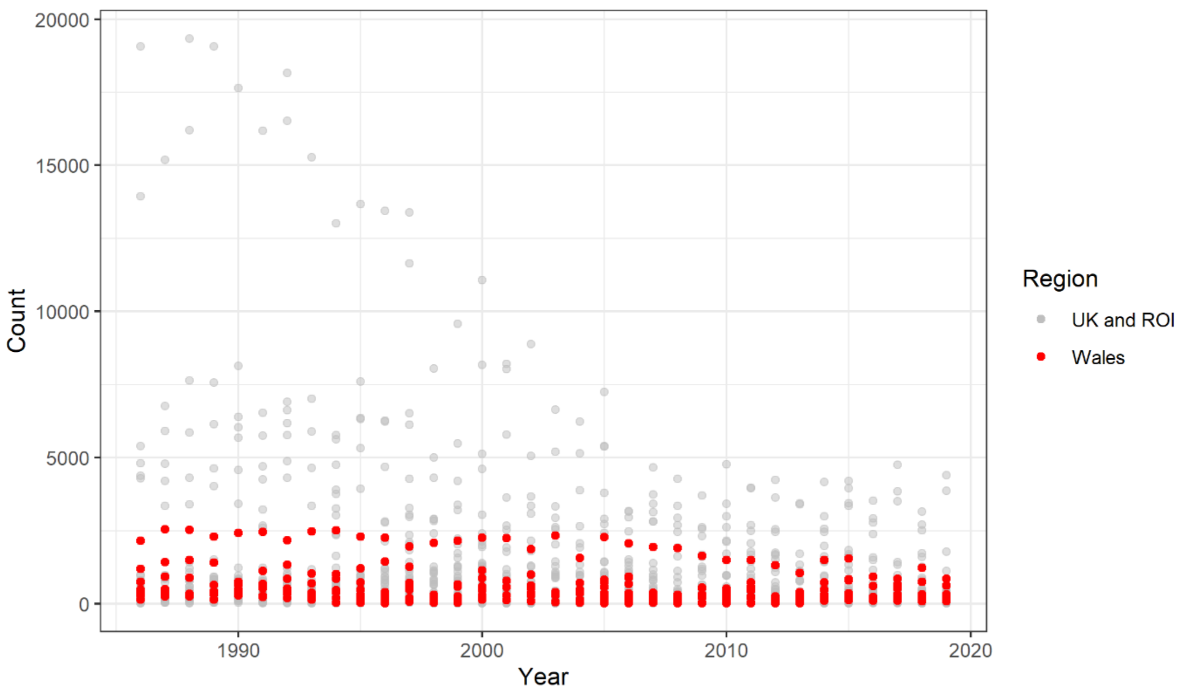

Figure 5. Wales and UK/ROI based whole-colony abundance counts 1986-2019.

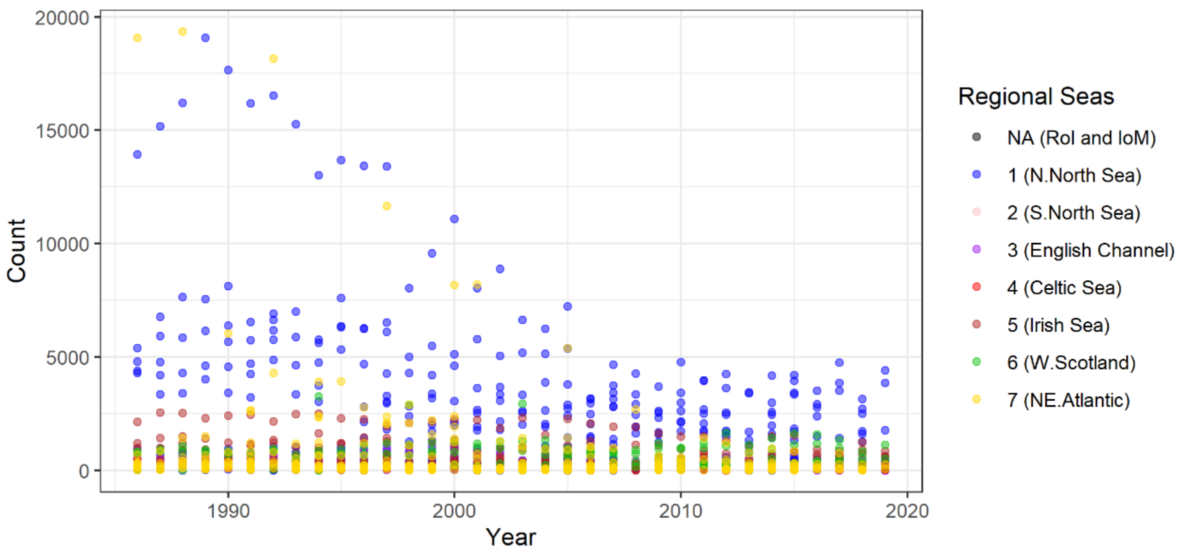

Figure 6. Whole-colony abundance counts 1986-2019, in relation to Regional Seas monitoring regions. Abundance Correlation Coefficient Colony Comparison by SMP Region and Regional Seas. Regional Seas 4 and 5 adjoin the coasts of Wales.

When the correlation coefficient of annual abundance (as derived from negative binomial GLM), was examined in relation to the mean colony abundance, it was apparent the majority of colonies are in decline, with no apparent link between abundance trend and mean colony abundance (Figure 7). Trends in annual abundance at Welsh colonies mirror declines occurring throughout colonies within UK and ROI. However, several colonies within England and some within Scotland display increasing annual abundance. While not displaying strong positive trends in abundance, two Welsh colonies of Carreg y Llam and St. Margaret's Island have remained stable with mild positive trends (Figure 7). Regarding annual abundance trends occurring between Regional Sea 7, which contains Orkney and Shetland, possessed the strongest declines (Figure 8). In general colonies of smaller size (>500 AON) based within Regional Sea 1 and 2 (northern and southern North Sea), displayed increasing trends in abundance. Regional Seas 1 and 2 contain the North Sea and adjoining kittiwake colonies will be situated on to the East coast of Scotland and England. While Regional Seas 4 and 5 (the encompassing Celtic Sea and Irish Sea), which correspond to Welsh colonies, also showed similar trends to those held within Regional Seas 1 (i.e. the northern North Sea), mean colony abundance and annual abundance trend were aligned closest with Regional Sea 6 (West of Scotland) (Figure 8 and 10). Annual abundance trends at Welsh colonies broadly reflect regional trends occurring throughout the UK and ROI, however Wales exhibits a bias towards negative annual trends (Figure 9). When trends in annual abundance are compared between Regional Seas, Region 1 (northern North Sea) maintains the greatest density of positive trends in abundance, while Region 7 (Shetland and Orkney) contains the most colonies with declining abundances. Annual trends in abundance within Regions 4 and 5 (adjoining Wales) are primarily concentrated around slightly negative trends in abundance, or zero.

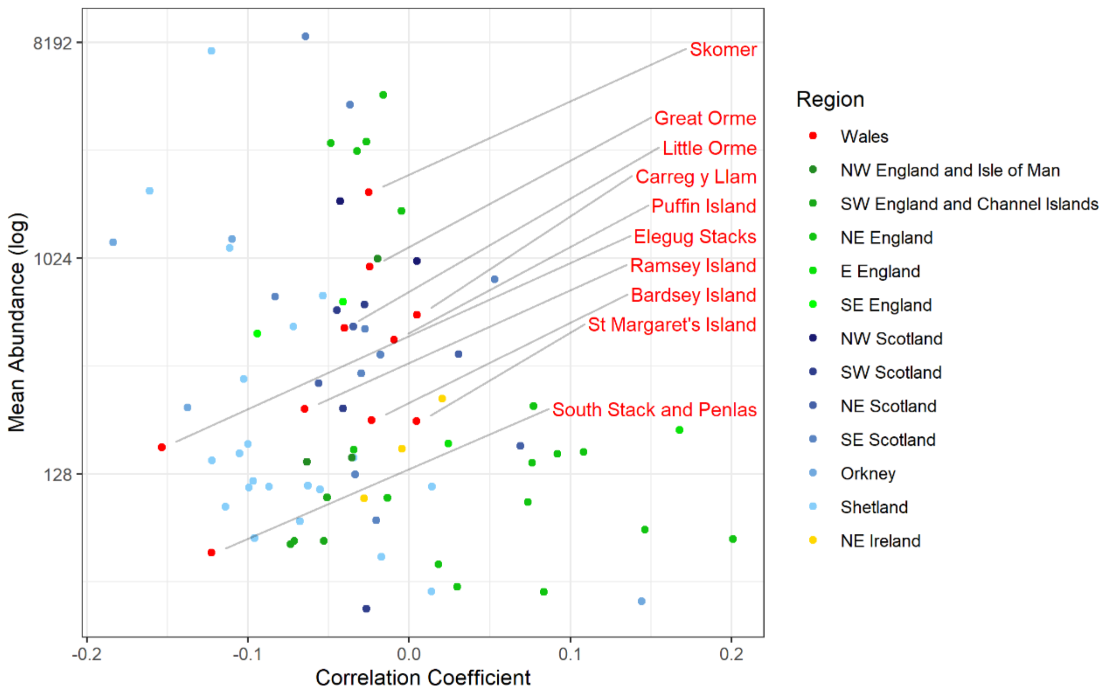

Figure 7. Model coefficient for annual change in abundance from negative binomial GLM of monitored colonies plotted in relation to the mean abundance (log scaled) of each colony. Positive and negative correlation coefficients relate to increasing and declining abundance trends respectively. Each data point represents a separate colony, and they are coloured by the corresponding SMP Region of each colony. Labels in red indicate points attributed to Welsh colonies.

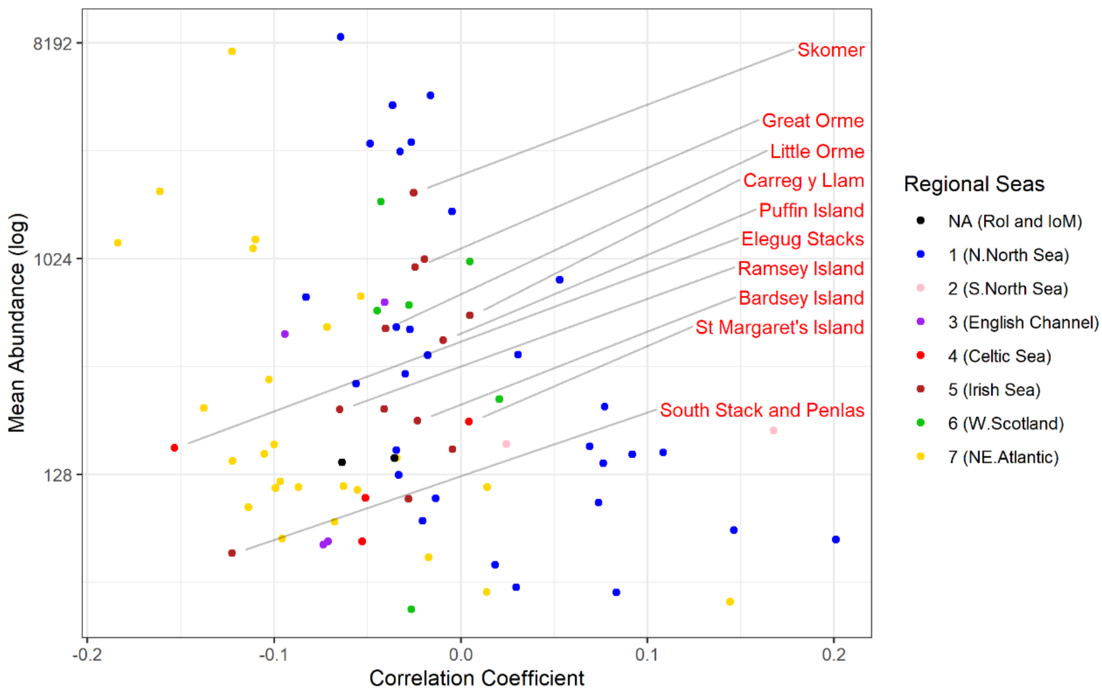

Figure 8. Model coefficient for annual change in abundance from negative binomial GLM of monitored colonies plotted against the mean abundance (log scaled) of each colony. Positive and negative correlation coefficients relate to increasing and declining abundance trends respectively. Each data point represents a separate colony, and they are coloured by

the corresponding Regional Seas designation of each colony. Labels indicate points attributed to Welsh colonies. Regional Seas 4 and 5 adjoin the coasts of Wales.

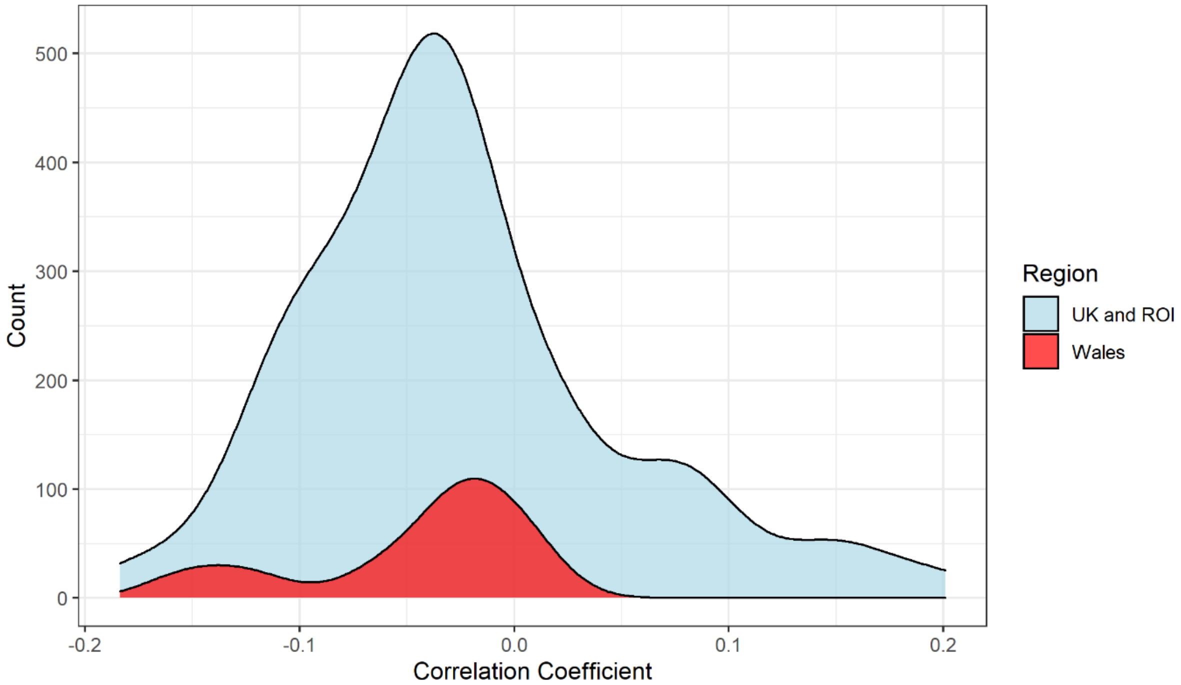

Figure 9. Density of correlation coefficient (negative binomial GLM) of colony level annual change in abundance. Positive and negative correlation coefficients relate to increasing and declining abundance trends respectively. Colonies are grouped by presence within Wales (red), and the rest of the UK and ROI (grey).

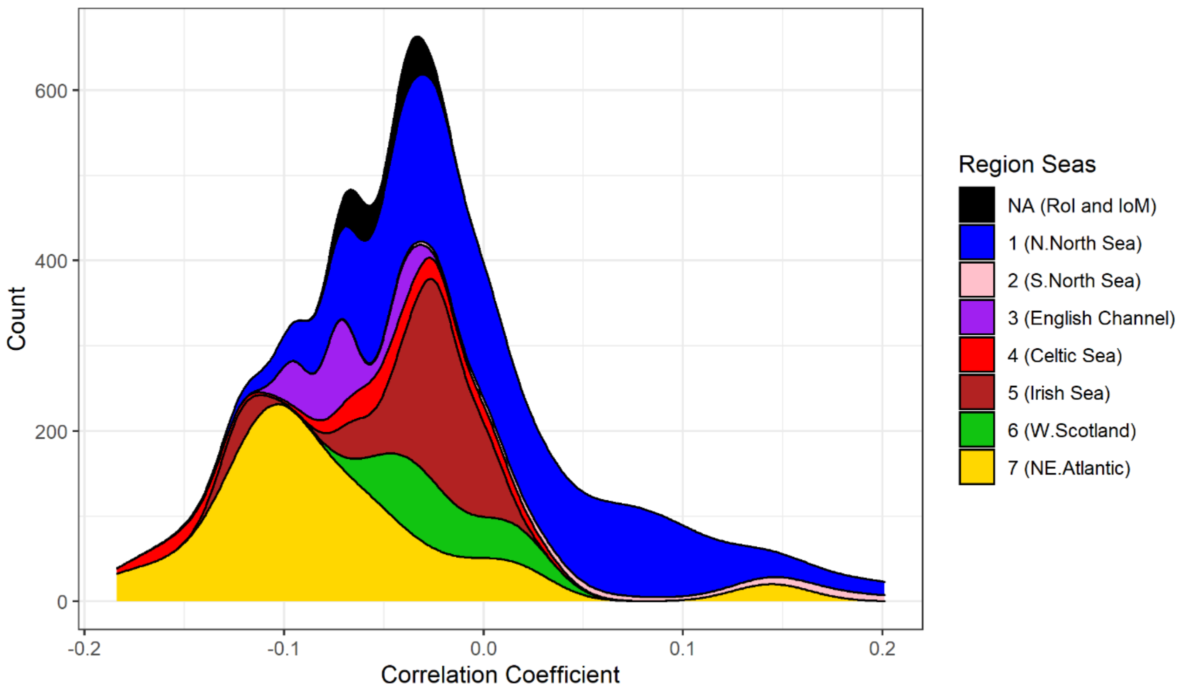

Figure 10. Density of correlation coefficient (negative binomial GLM) of colony level annual change in abundance, in relation to Regional Seas designations. Positive and negative

correlation coefficients relate to increasing and declining abundance trends respectively. Regional Seas 4 and 5 adjoin the coasts of Wales.

3.2.2. Productivity

Trends in productivity within Welsh colonies are displayed in Figure 11, trends corresponding to all other regions within the UK and ROI are displayed in Appendix 2. Productivity at the largest colony of Skomer has remained relatively stable over the monitoring period between 1986-2019 (Figure 11). There is a consistent trend of long-term decline for most other colonies however (despite some increases between 1990-2000 at Bardsey Island, Elegug Stacks and Great Orme).

Correlation coefficients of annual productivity (as derived from binomial GLM) indicate that all colonies in Wales except for Bardsey Island maintain negative productivity trends (Figure 12). In relation to mean colony productivity, annual productivity at Welsh colonies mirror trends occurring at colonies Scotland and Ireland (Figure 12). Overall, declining annual productivities correlate with lower mean productivities (Figure 12, 13). Colonies within England (Figure 12) and Regional Seas 1, adjoining the northern North Sea (Figure 13), have higher mean productivities and increasing annual trends in productivity. Colonies within Wales and Scotland, and the Regional Seas 1, 4, and 5 (northern North Sea, Celtic Sea, and Irish Sea) which adjoining them, maintain the lowest mean productivities and greatest declines in productivity (Figure 12 and 13).

Productivity trend occurring at Welsh colonies are primarily negative, though trends broadly match the distribution of trends occurring within UK and ROI (Figure 14). When trends in yearly productivity are examined in relation to Regional Seas, positive annual productivities are generally concentrated within Region 1 (northern North Sea), and the greatest density of colonies with negative annual productivities are within Region 7 (Shetland and Orkney). Regions 4 and 5 which adjoin Wales maintain a range of trends in annual productivities, with greatest density a zero (no trend) (Figure 15).

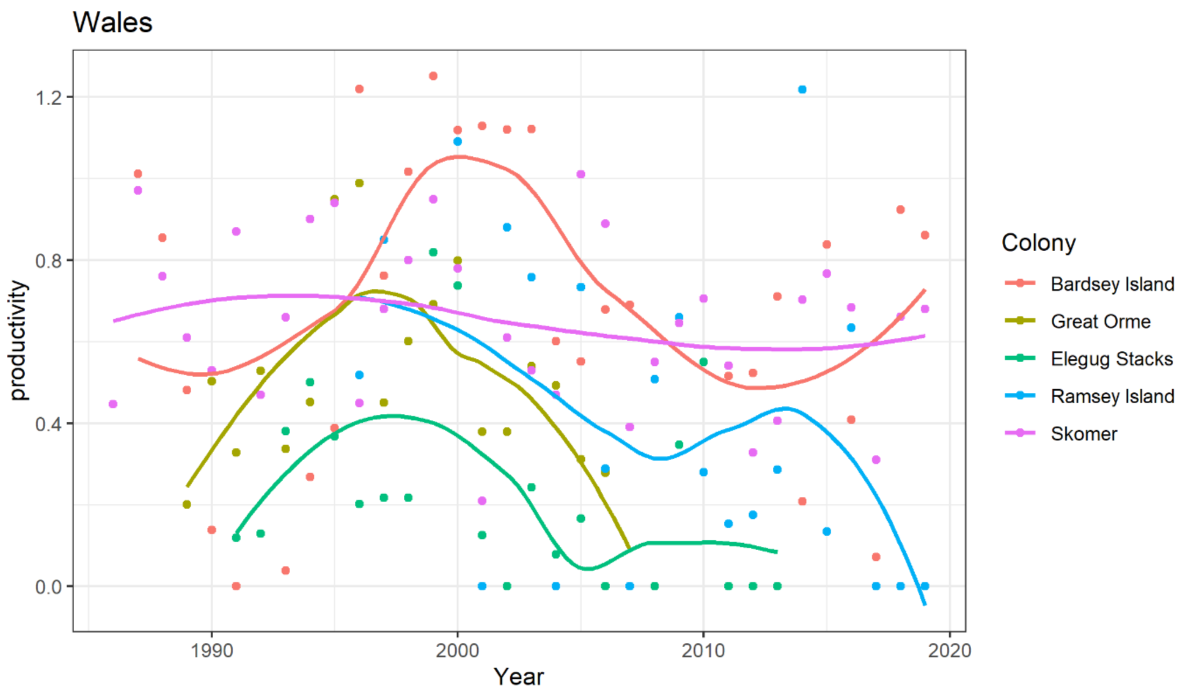

Figure 11. Wales based annual productivity 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony. All other regions of UK and ROI are displayed within Appendix 2.

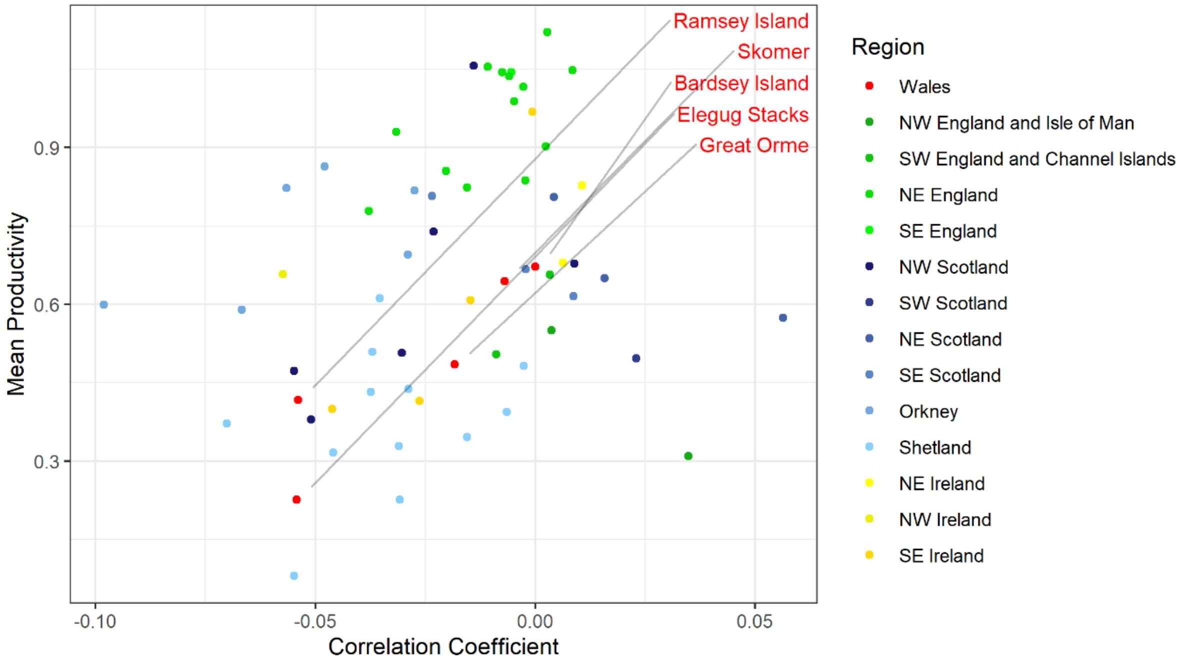

Figure 12. Model coefficient for annual change in productivity derived from binomial GLM of monitored colonies plotted in relation to the mean productivity of each colony. Positive and negative correlation coefficients relate to increasing and declining productivity trends respectively. Each data point represents a separate colony, and they are coloured by the corresponding region of each colony. Labels indicate points attributed to Welsh colonies.

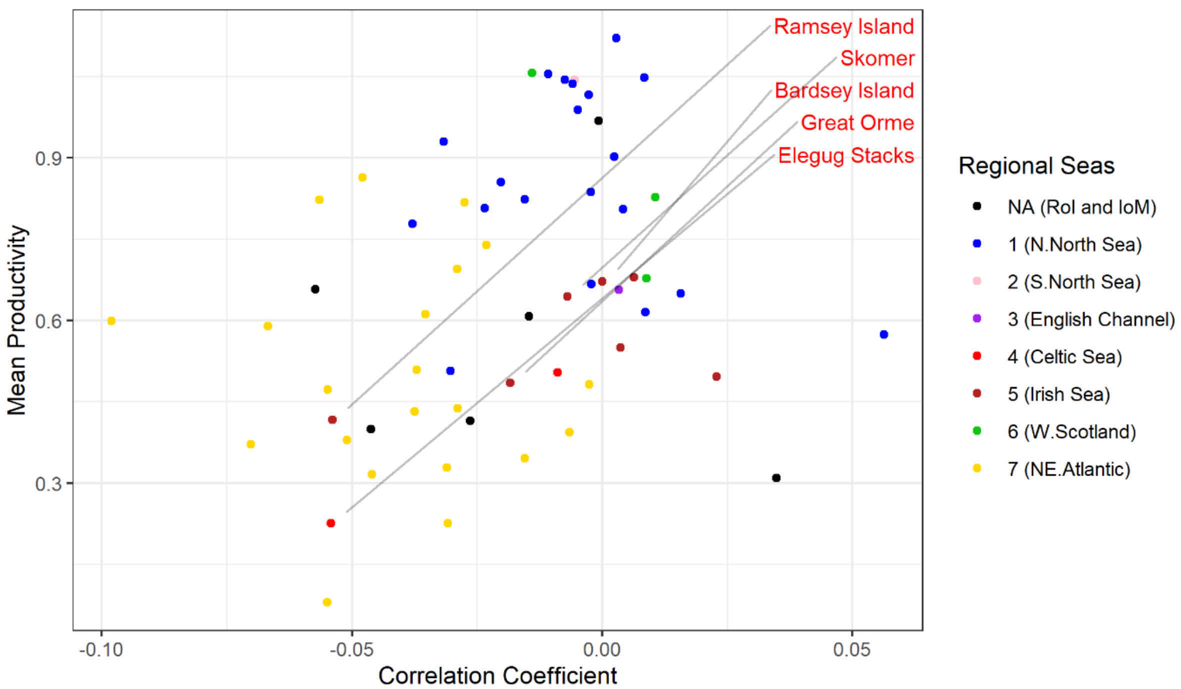

Figure 13. Model coefficient for annual change in productivity derived from binomial GLM of monitored colonies plotted in relation to the mean productivity of each colony. Positive and

negative correlation coefficients relate to increasing and declining productivity trends respectively. Each data point represents a separate colony, and they are coloured by the corresponding Regional Sea designation adjoining each colony. Labels indicate points attributed to Welsh colonies. Regional Seas 4 and 5 adjoin the coasts of Wales.

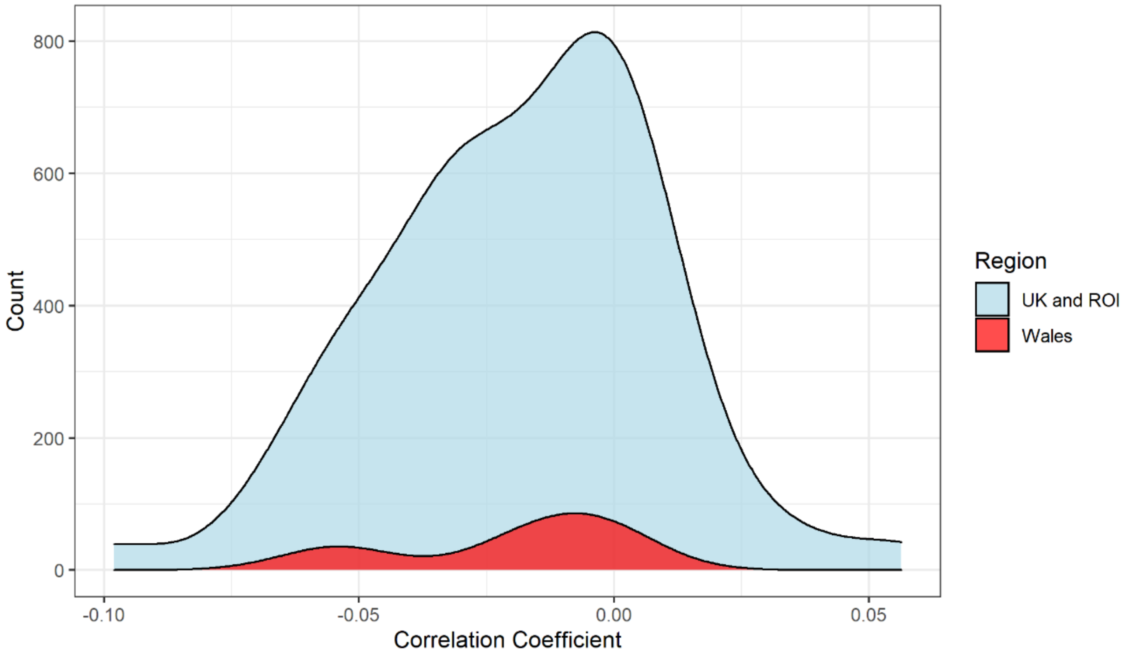

Figure 14. Density of correlation coefficient (binomial GLM) of yearly productivity per to colony. Colonies are grouped by presence within Wales (red), and the rest of the UK and ROI (grey). Positive and negative correlation coefficients relate to increasing and declining productivity trends respectively.

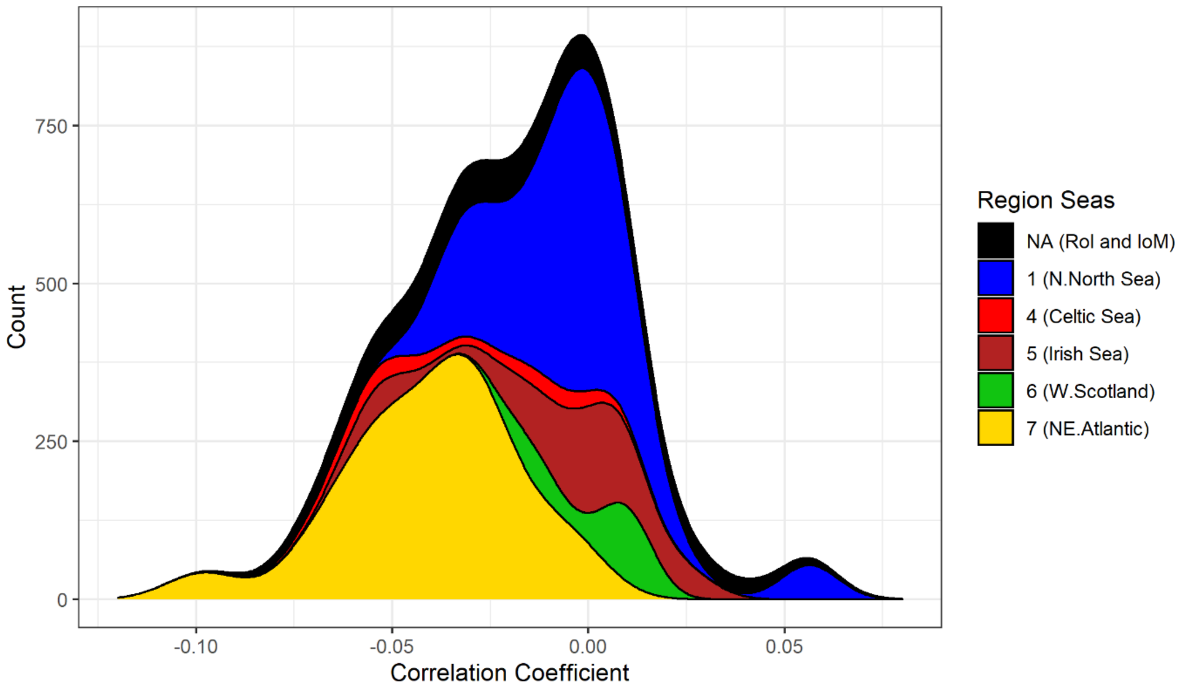

Figure 15. Density of correlation coefficient (binomial GLM) of yearly productivity per to colony, in relation to Regional Sea designations. Positive and negative correlation coefficients relate to increasing and declining productivity trends respectively. Regional Seas 4 and 5 adjoin the coasts of Wales.

4. Discussion

Within the UK and ROI kittiwake abundance and productivity have experienced variable trends between regions and across the period of 1986-2019. Population trends show notable spatial segregation between colonies adjoining Regional Sea 1 (North East Atlantic) and those within Regional Sea 7 (North Atlantic). Within Regional Sea 1 colonies on Orkney and Shetland have declined markedly, contrasting to colonies within the North East of England which have increased both in abundance and productivity. These divergent demographic trends are most likely influenced by differences in oceanographic features and bottom-up changes in prey availability, specifically sandeel abundance (Oro & Furness 2002, Wanless et al. 2018, Perkins et al. 2018). Welsh colonies and those adjoining the Irish Sea are generally of moderate abundance (100-1000 AON), and have displayed similar stable/declining trends in abundance and productivity. Colonies within Wales adjoining differing Regional Sea areas of 4 (Celtic Sea) and 5 (Irish Sea) showed similar trends in abundance and productivity. Therefore, it is likely that oceanographic conditions between the sea regions do not markedly differ. Trends within the Irish and Celtic Seas also aligned with those colonies found on the West of Scotland. Broad regional synchrony in demographic trends previously been identified in kittiwake colonies around the UK and ROI (Frederiksen et al. 2005, Cook et al. 2011), and have largely been attributed to colonies targeting similar prey stocks (Olin et al. 2020). However, ubiquitous drivers of populations around Wales have been difficult to underpin, as previous studies of colonies adjoining the Celtic Sea showed no relationship with SST, plankton, or fish larvae (Lauria et al. 2013), and diet studies within the region are lacking.

Strong links between diet and kittiwake demography within the Irish Sea and Wales have not been established to the same extent as within the North Sea. This may be due to a greater prevalence alternate prey such as of clupeids (Chivers et al. 2012b), and gadoids (Harris & Wanless 1990), and less reliance on sandeels (Frederiksen et al. 2005, Anderson et al. 2014) the influence of which are better understood (Lewis et al. 2001, Burthe et al. 2012, Carroll et al. 2017). However, within the Irish Sea, when clupeids have been shown to be absent and alternate resources unavailable, greater time spent foraging in breeding adults and lower breeding success has been shown (Chivers et al. 2012a). Therefore within the Irish Sea, SSB and productivity of sprat and herring may influence kittiwake demography (ICES 2019, 2020). SSB and productivity of clupeid spp. have fluctuated during the 1986-2019 period (ICES 2019, 2020)., and declines in herring productivity have been suggested to be linked to environmental conditions (Lynam et al. 2011). Wilson et al. (2021), found that fewer sandeels were taken as prey items in the Irish and Celtic seas than in the Greater North Sea, and the prevalence of sandeels found in diet also declined with increasing latitude. However, the converse of this relationship was found for the presence of gadoids. Their research also detected a weak but positive relationship between breeding success and the proportion of diet samples containing sandeels. Scavenging on fisheries discards may provide an alternate resource to kittiwakes within the Irish Sea (Bicknell et al. 2013)and reforms to discard practices as well as a reduction in a trawling fleet may have reduced this resource, with consequences for kittiwake demographic rates (Votier et al. 2004, Sherley et al. 2020).

Within Wales, variable trends in abundance were found between colonies. Bardsey Island was the only colony to maintain a positive annual trend in productivity within Wales. Bardsey Island has been previously identified to diverge from other colonies within the region having been shown to maintain a positive relationship between breeding success and fish larvae, absent at other colonies (Lauria et al. 2013). Tracking studies of colonies within Wales during the breeding season including Bardsey Island, have shown foraging areas to be distinct (RSPB 2011). The cause of varying demographic rates between colonies could be linked to local variations in the physical environment leading to habitat patchiness, or spatial-temporal prey dynamics (Frederiksen et al. 2005, Trevail et al. 2019b). Heterogeneity in local conditions as highlighted by Trevail et al. (2019) may underlie the deviation of kittiwakes from Bardsey Island from regional synchrony in kittiwake productivity, and response to prey abundance (Lauria et al. 2013). Foraging distances from colonies within the Irish and Celtic sea (e.g. Bardsey Island, Skomer, Puffin Island, Lambay Island) are unlikely to overlap (RSPB 2011, Chivers et al. 2012a, Trevail et al. 2019a), enhancing colony specific trends through local differences in diet (Bull et al. 2004). However, colonies which overlap in foraging areas have also displayed different levels of productivity (Redfern & Bevan 2014), therefore additional factors such as predator presence (Collins et al. 2014), or exposure to adverse weather at the colonies (Newell et al. 2015) may contribute to site specific differences. Olin et al. (2020) found weather conditions and skua predation did not drive synchrony and therefore these factors were regarded as largely site specific. Direct impacts of adverse weather or predation may be occurring on colony level scale, and may cause breeding failures leading to adult dispersal. Colonies with low density of nests may be vulnerable to predators accelerating declines in abundance. Kittiwakes have been shown to move to more sheltered breeding sites following predation (Huebeck et al. 1997), and therefore could increased peregrine predation lead to the movement of kittiwakes from cliffs to areas of reduced vulnerability, such as low-lying islands? Failure due to adverse weather may additionally lead to movement to more sheltered areas. However, these local scale impacts are not well studied, and while colony synchrony has been established (Frederiksen et al. 2005, Cook et al. 2011, Olin et al. 2020), drivers local scale variation in abundance and productivity are still relatively unknown. This study investigated colonies with data available for greater than 10 years to provide suitable sample size. More recent or temporary colonisation by kittiwakes outside monitored coastlines were outside the scope of this study, and may indicate the fate of birds from colonies in decline.

5. Summary

Wales holds the smallest proportion of populations of kittiwakes breeding within the UK and Republic of Ireland. This was attributed to coastline length, as the coastline lengths of Scotland and England are 6x and 2x the length of Wales (Austin et al. 2017), and holds relatively fewer islands compared to Scotland. Additionally, colonies in Wales tend to not achieve the abundance of colonies found in the North East Atlantic and North Sea. Lower colony abundance is likely due to relatively lower prey abundance. Sandeels, which kittiwakes rely on elsewhere in the UK (Huebeck et al. 1997, Frederiksen et al. 2004), are potentially not the dominate prey item within the Irish Sea. However, the availability of alternate prey within this region may have mitigated drastic population declines experienced elsewhere within the UK. Overall, the population of kittiwakes is declining within Wales. Rates of decline in abundance and productivity may be linked to climatic effects such as increasing SSTs which negatively affect prey stocks of clupeid spp. These changes could in turn lead to kittiwakes within the Celtic and Irish seas to feed on prey species of lower nutritional quality, such as gadoids, thus leading to a reduction in productivity (Wilson et al, 2021). However, shifts in SST in the Celtic and Irish seas have not occurred to the same extent as the North Sea (Frederiksen et al. 2013). The winter conditions experienced by kittiwakes from Welsh colonies may also differ from kittiwakes which breed elsewhere within the UK and ROI, as they have been shown to overwinter within the Celtic and Irish Sea rather than the North Atlantic (Frederiksen et al. 2012). Future research on the drivers of kittiwake demographic rates within the Irish and Celtic Sea should focus on potential links between bottom-up influence of herring and sprat stocks on kittiwake productivity. Additional impacts on abundance and productivity such as adverse weather and predation may have an observable influence on Welsh colonies due to the relatively smaller colony size. The combined effects of diet composition, adverse weather, and predation may need to be accounted for in future considerations of kittiwake population trends.

Regarding varying inter-colony trends, heterogeneity of habitat within the seas surround Wales may also influence kittiwake productivity (Trevail et al. 2019b), and cause variable trends between colonies. Foraging areas of kittiwakes from Welsh colonies have been identified at a fine scale (RSPB 2011, Trevail et al. 2019a), and this information, combined with improved knowledge of diet, could inform local trends in productivity and abundance. On a colony specific scale, improved knowledge of diet composition, and events of adverse weather and predation, may indicate the underlying drivers of inter-colony variation in productivity and abundance.

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Appendices

Appendix 1 Region Abundance

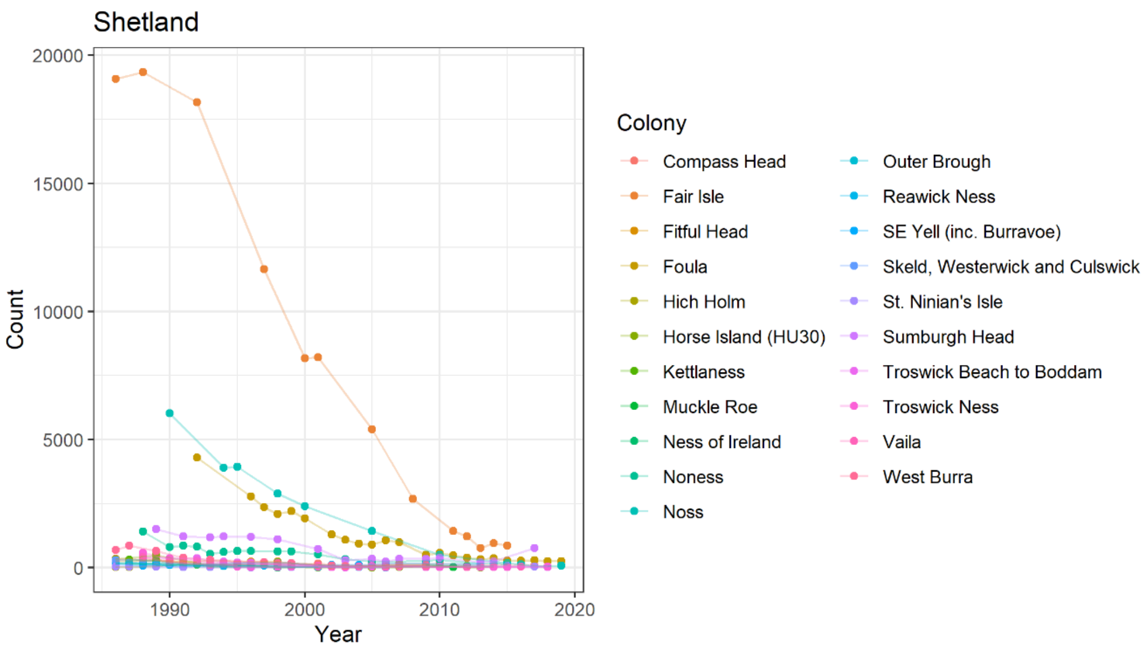

Figure A1a. Shetland based whole-colony abundance counts 1986-2019.

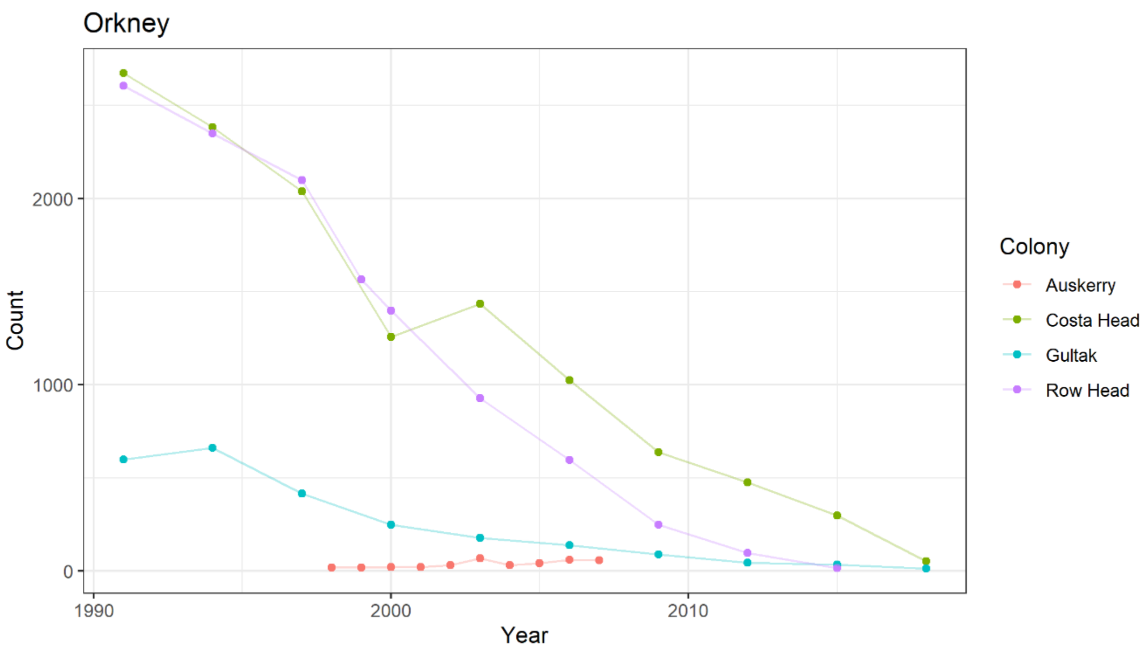

Figure A2b. Orkney based whole-colony kittiwake counts 1986-2019.

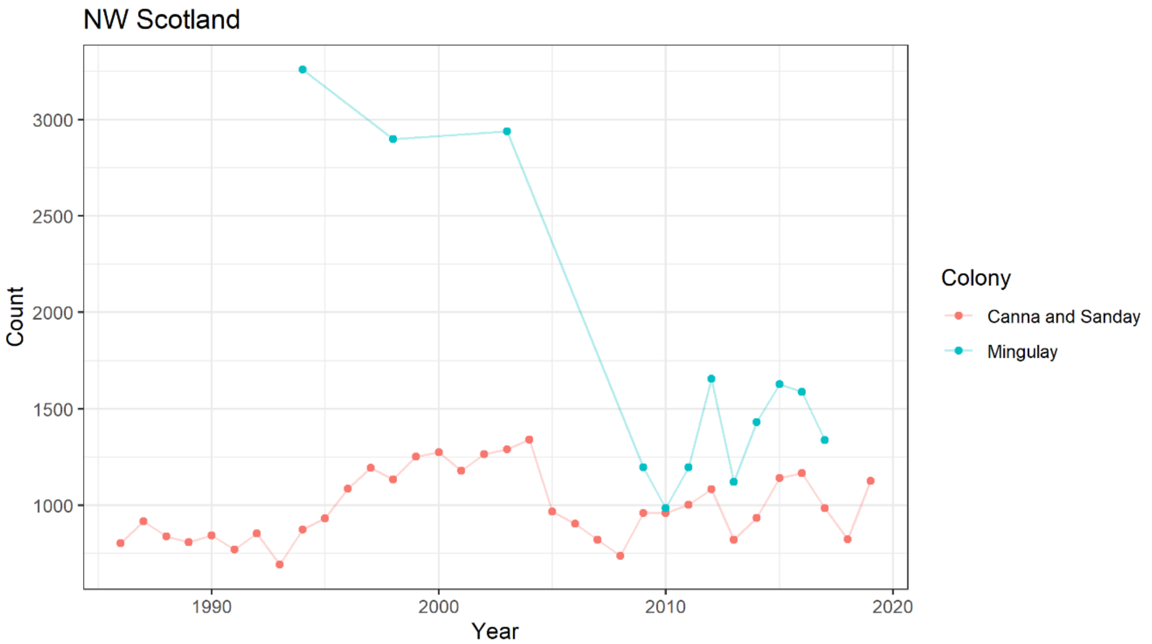

Figure A3c. North-West Scotland whole-colony kittiwake counts 1986-2019.

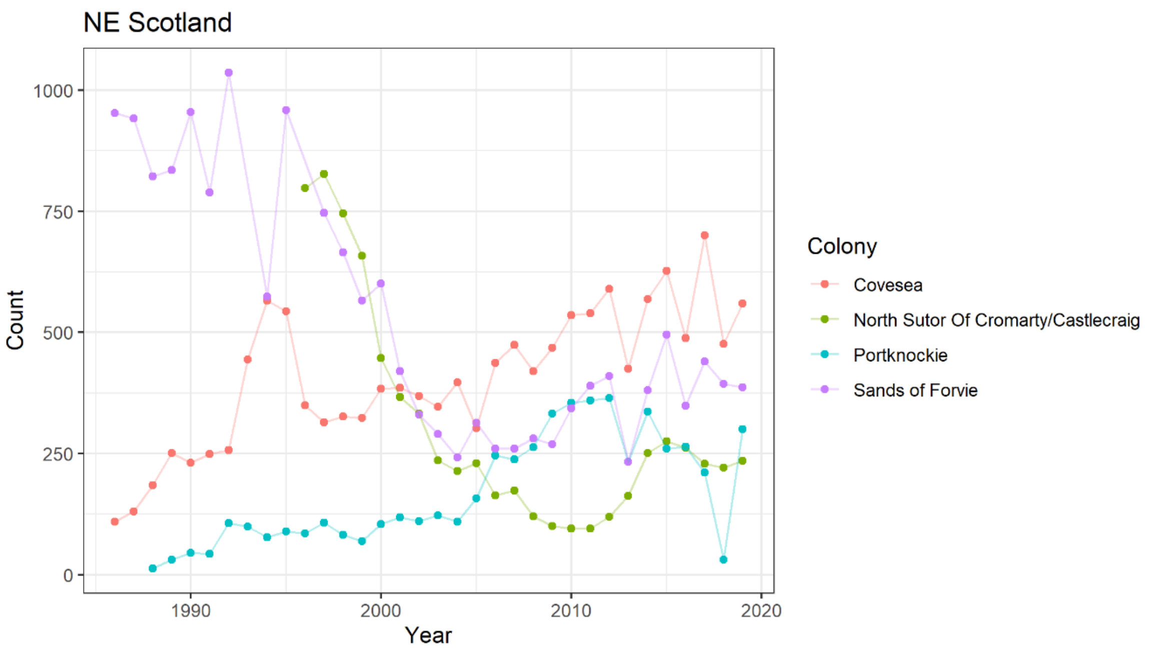

Figure A4d. North-East Scotland whole-colony kittiwake counts 1986-2019.

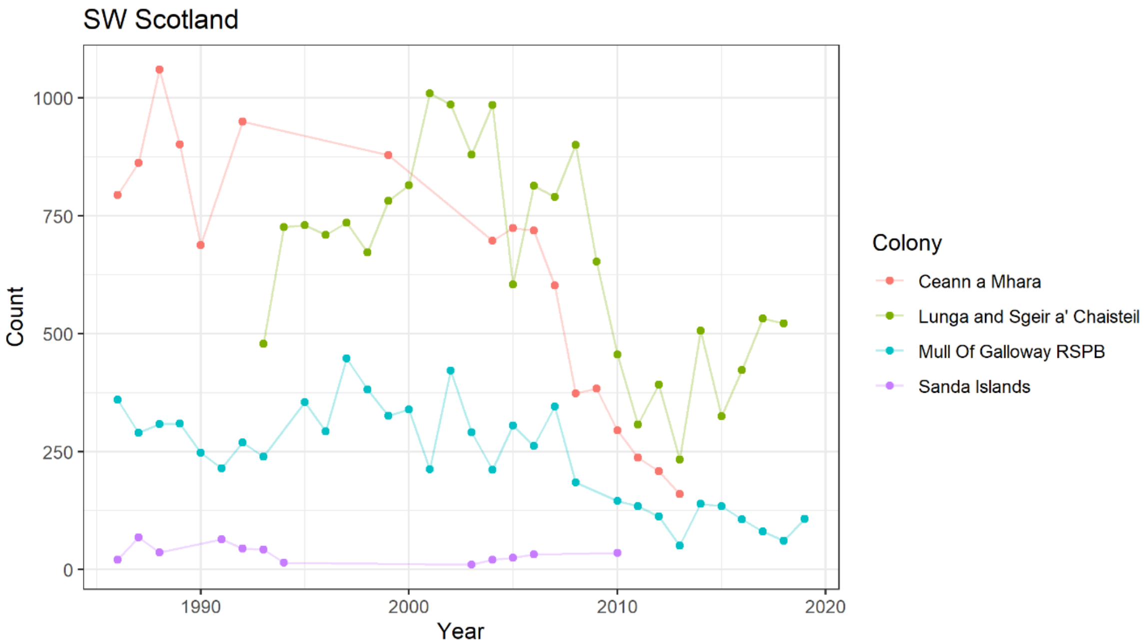

Figure A5e. South-West Scotland whole-colony kittiwake counts 1986-2019.

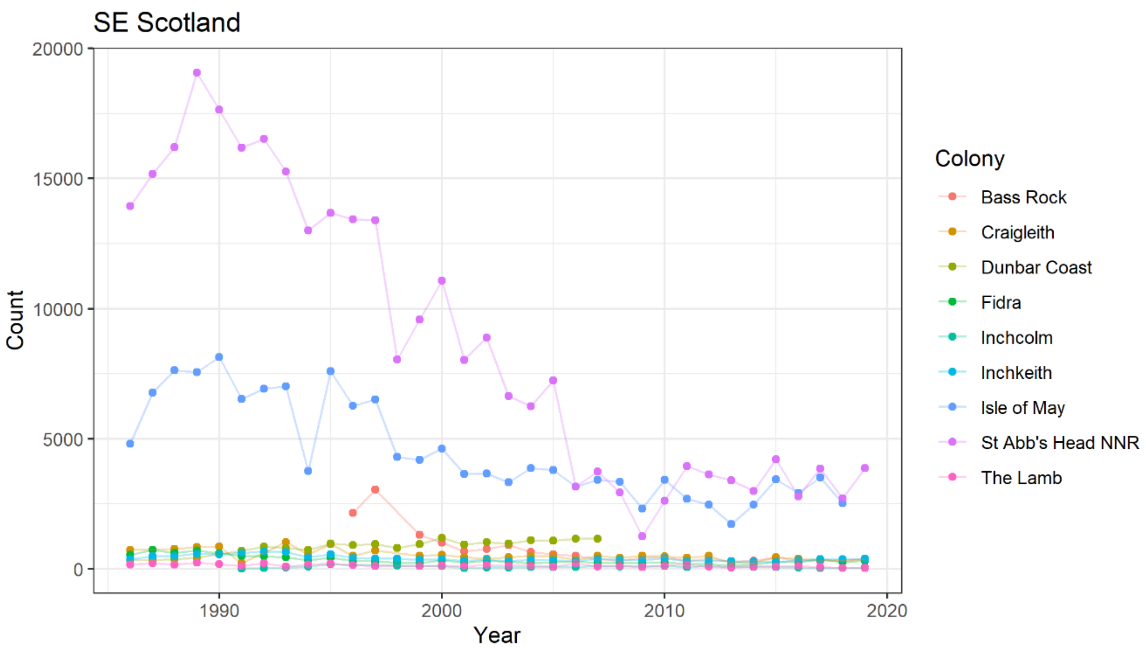

Figure A6f. South-East Scotland whole-colony kittiwake counts 1986-2019.

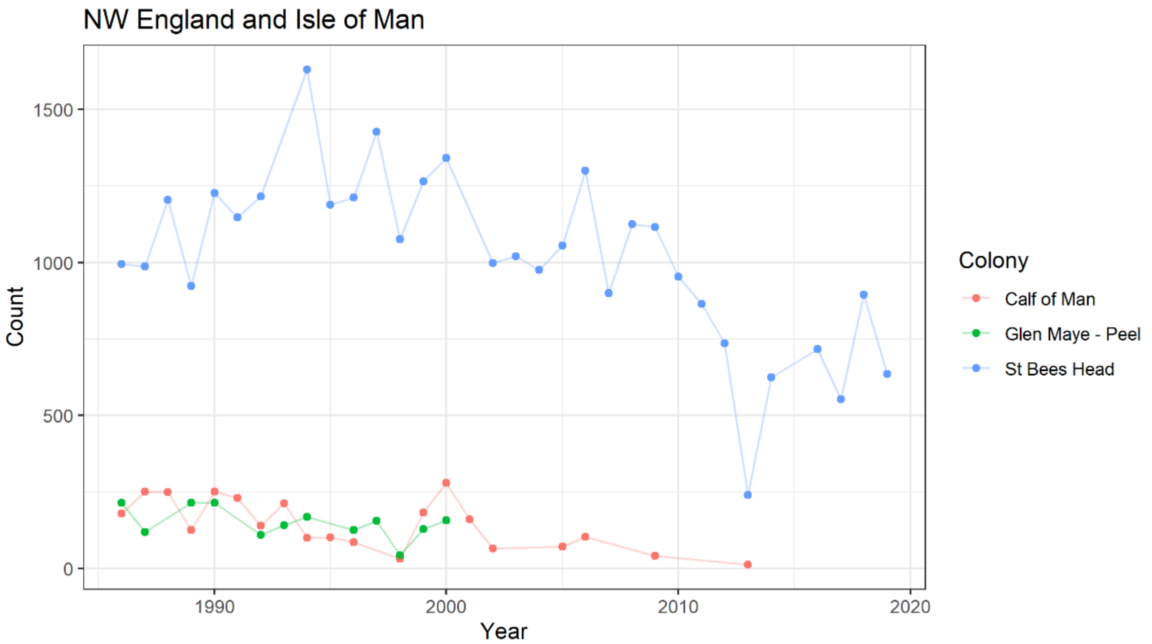

Figure A7g. North-West England and Isle of Man whole-colony kittiwake counts 1986-2019.

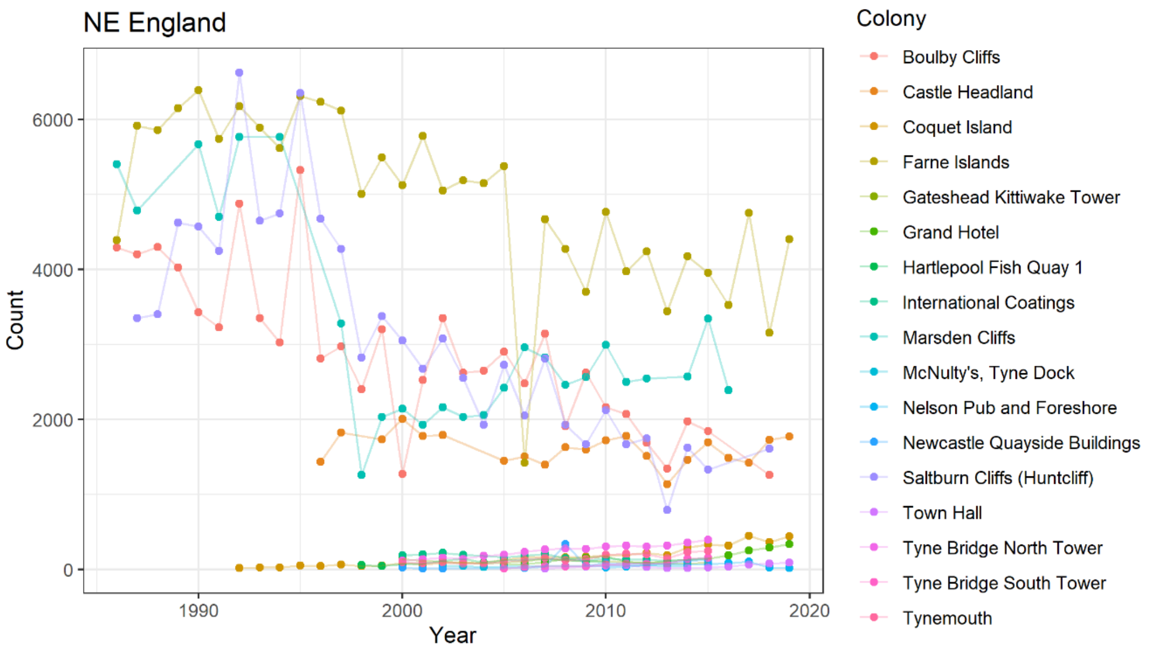

Figure A8h. North-East England whole-colony kittiwake counts 1986-2019.

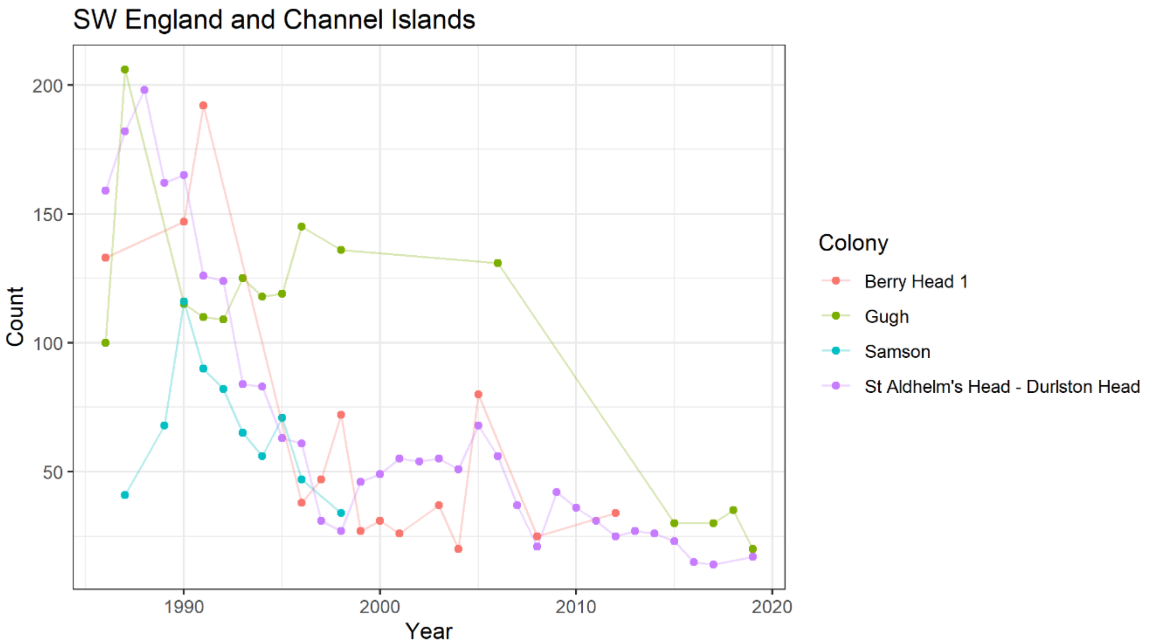

Figure A9i. South-West England and Channel Island whole-colony kittiwake counts 1986-2019.

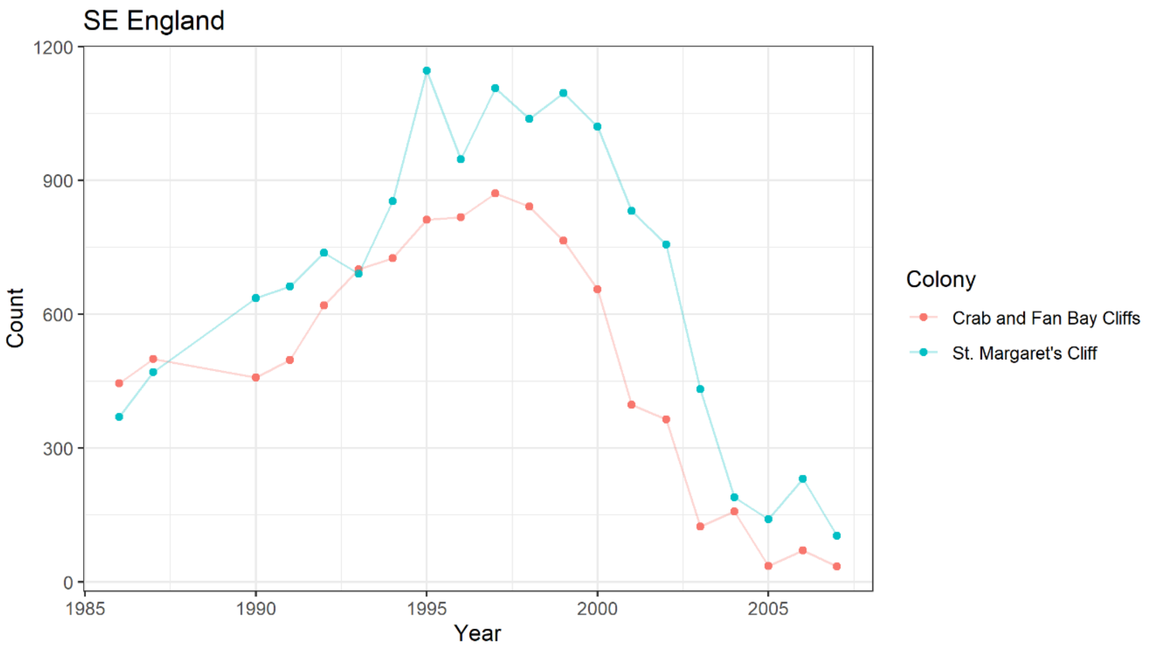

Figure A10j. South-East England whole-colony kittiwake counts 1986-2019.

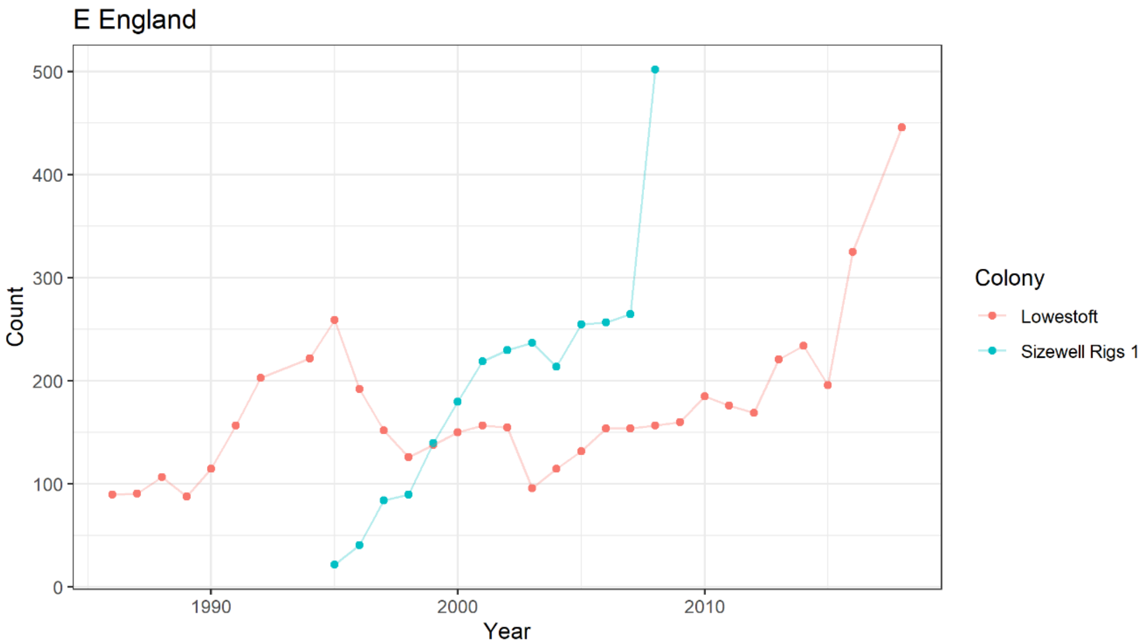

Figure A11k. East England whole-colony kittiwake counts 1986-2019.

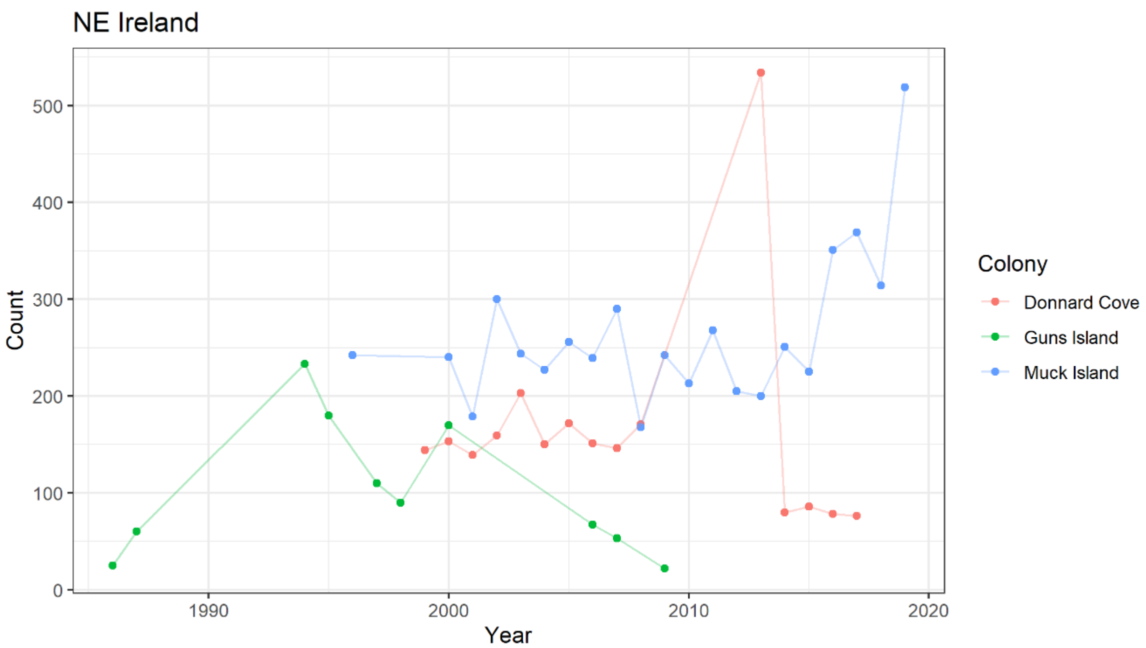

Figure A12l. North-East Ireland whole-colony kittiwake counts 1986-2019.

Appendix 2 Region Productivity

Figure A13a. Annual productivity of colonies based in Shetland 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.

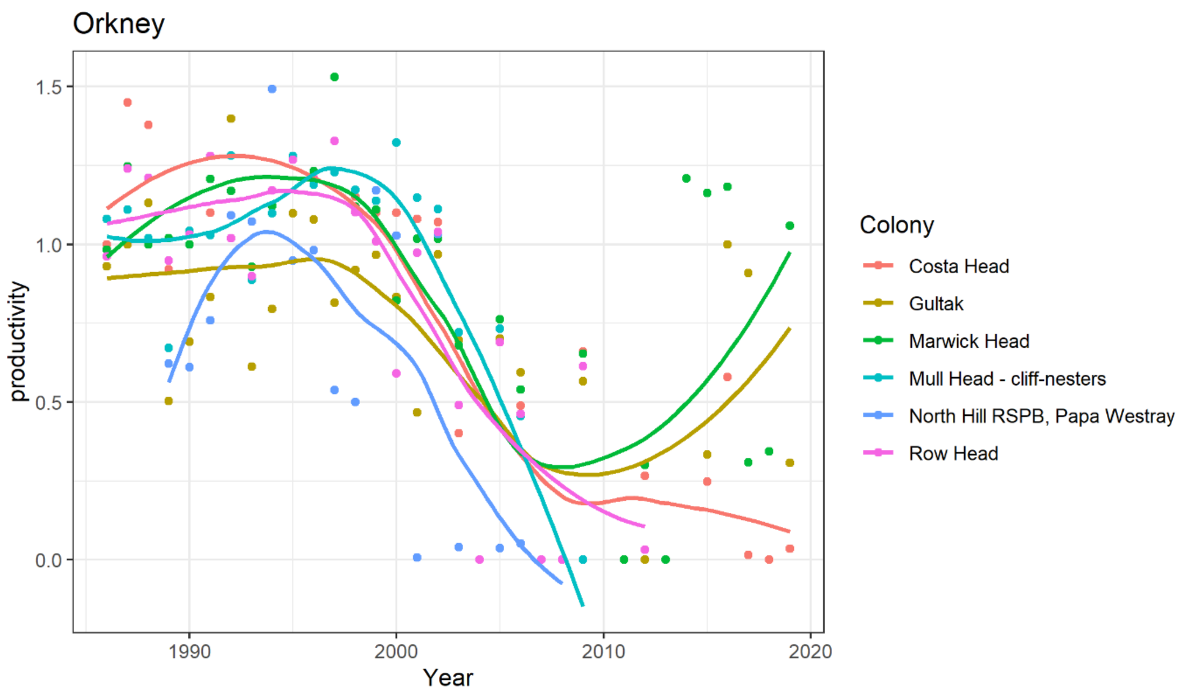

Figure A14b. Annual productivity of colonies based in Orkney 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.

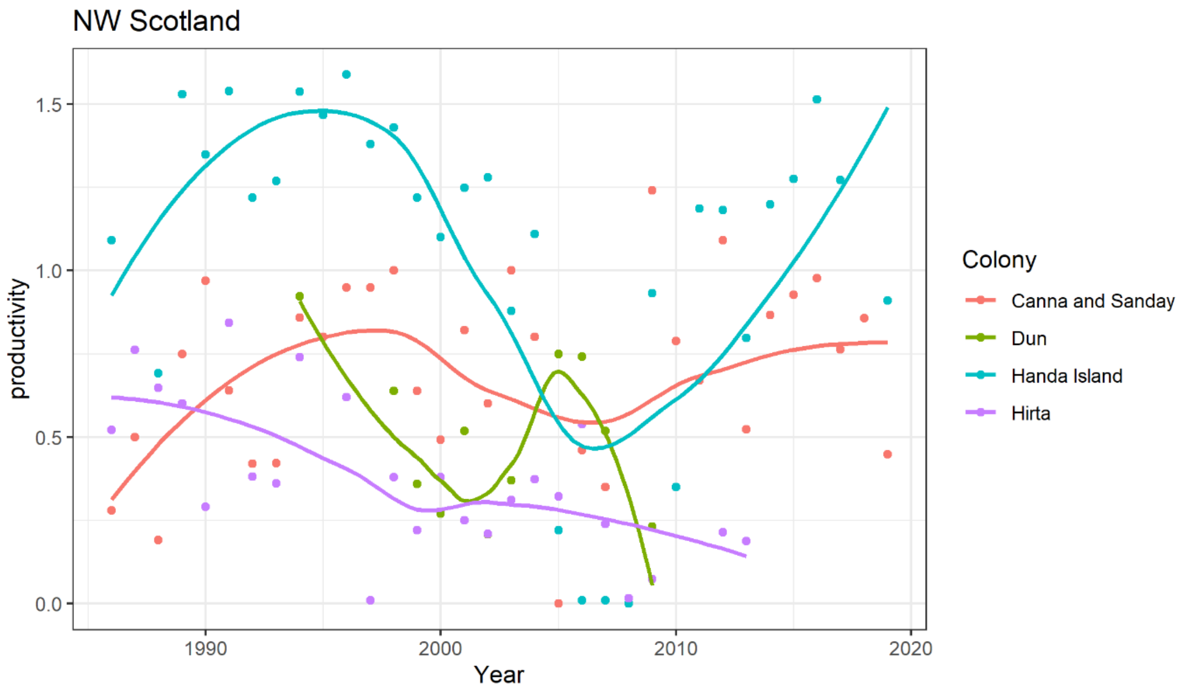

Figure A15c. Annual productivity of colonies based in North-West Scotland 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.

Figure A16d. Annual productivity of colonies based in North-East Scotland 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.

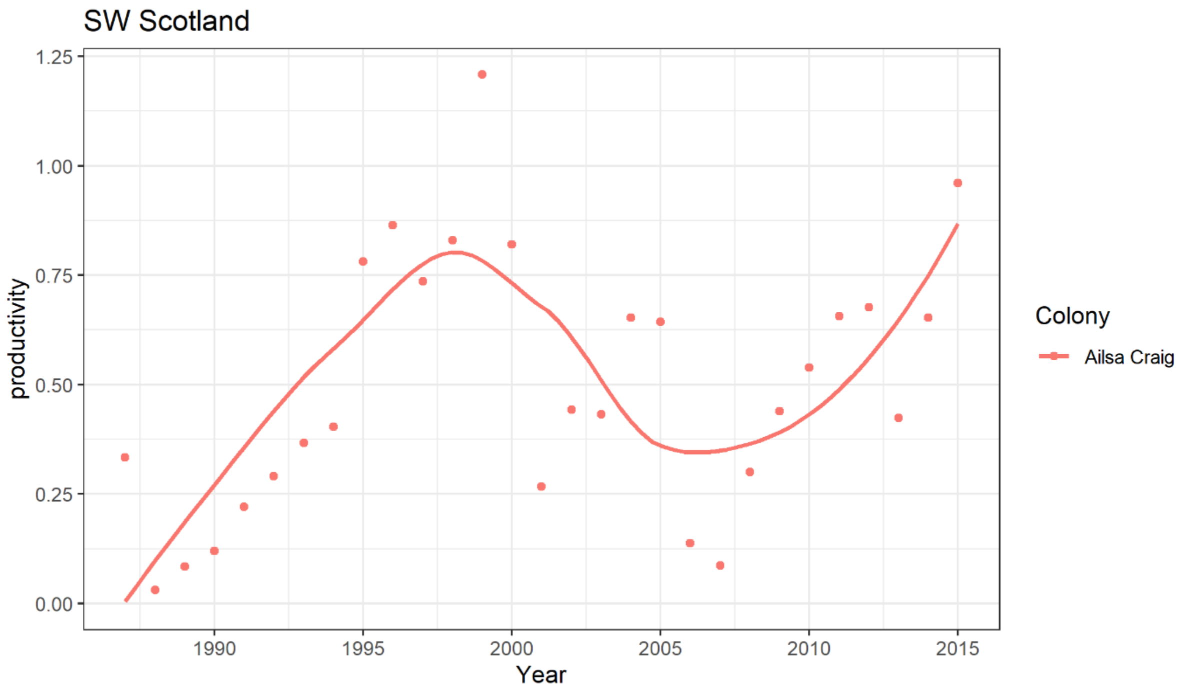

Figure A17e. Annual productivity of colonies based in South-West Scotland 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.

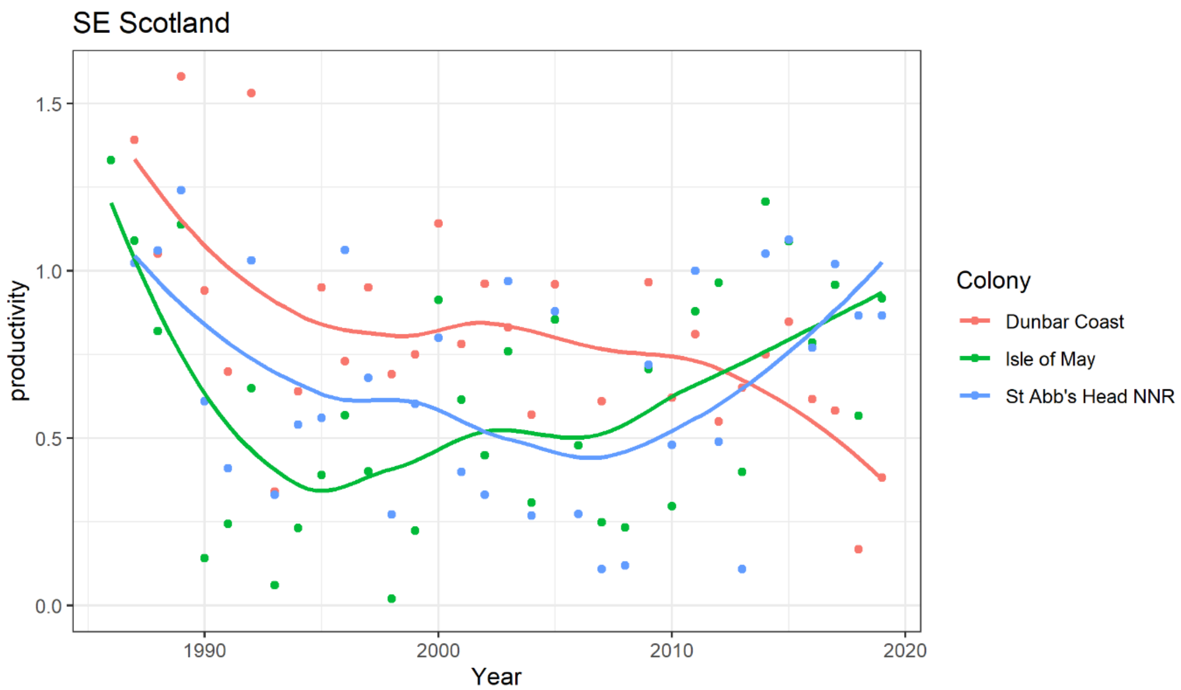

Figure A18f. Annual productivity of colonies based in South-East Scotland 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.

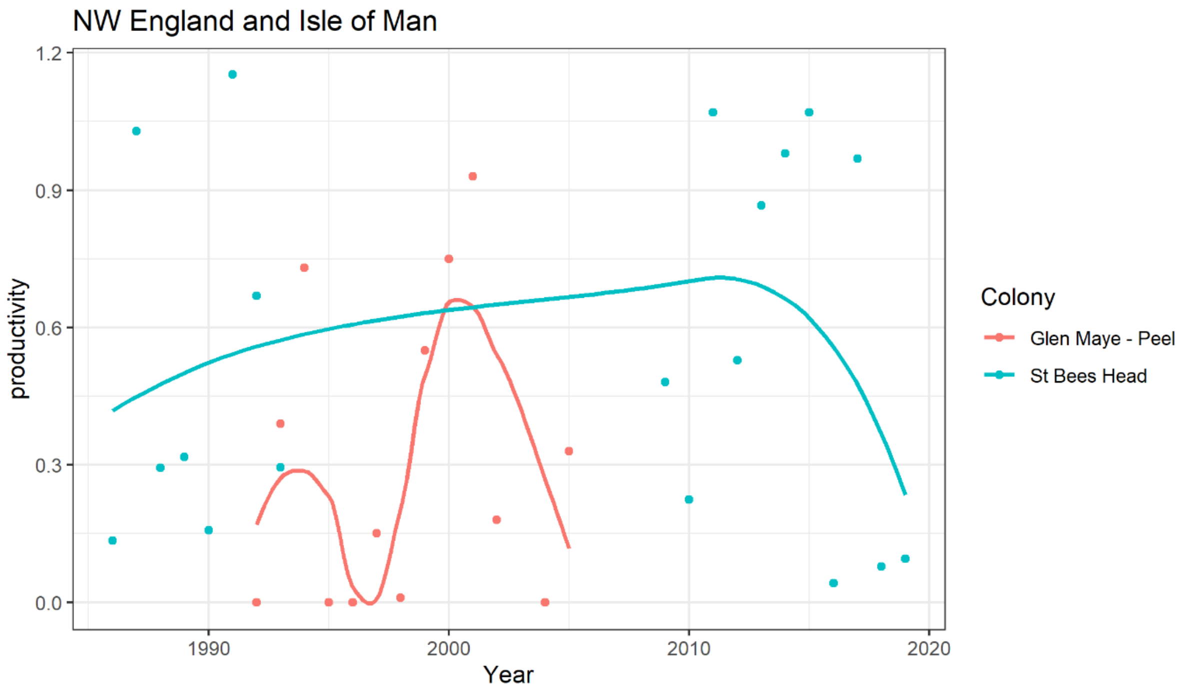

Figure A19g. Annual productivity of colonies based in North-West England and Isle of Man 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.

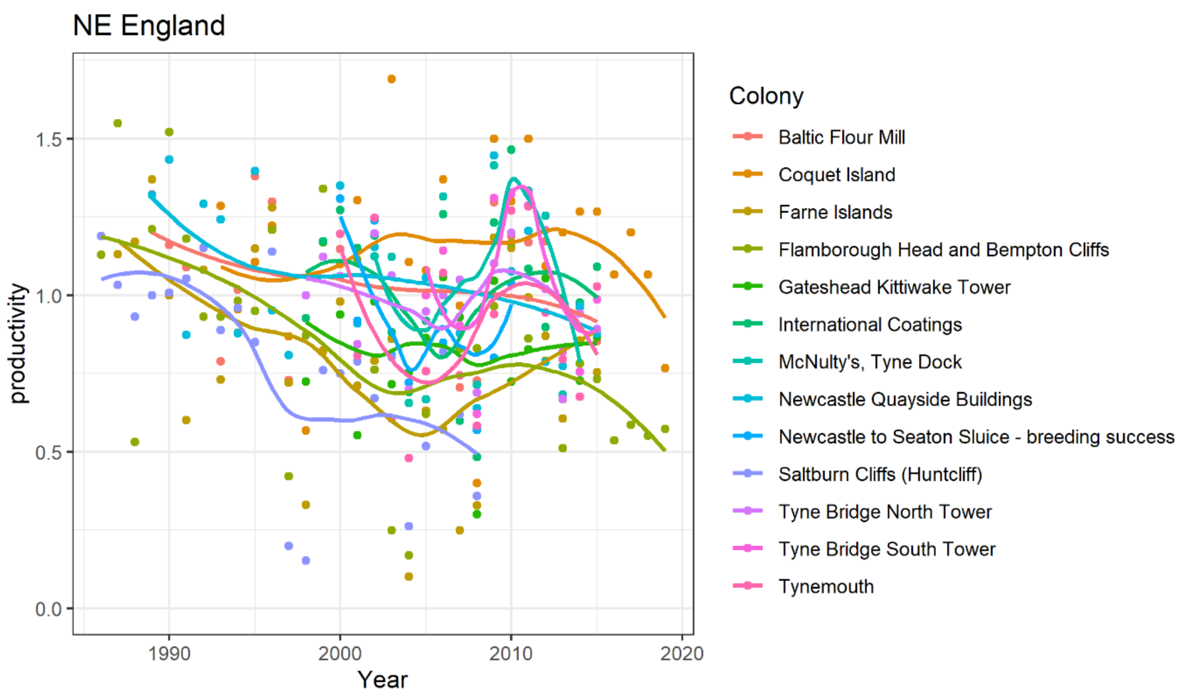

Figure A20h. Annual productivity of colonies based in North-East England 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.

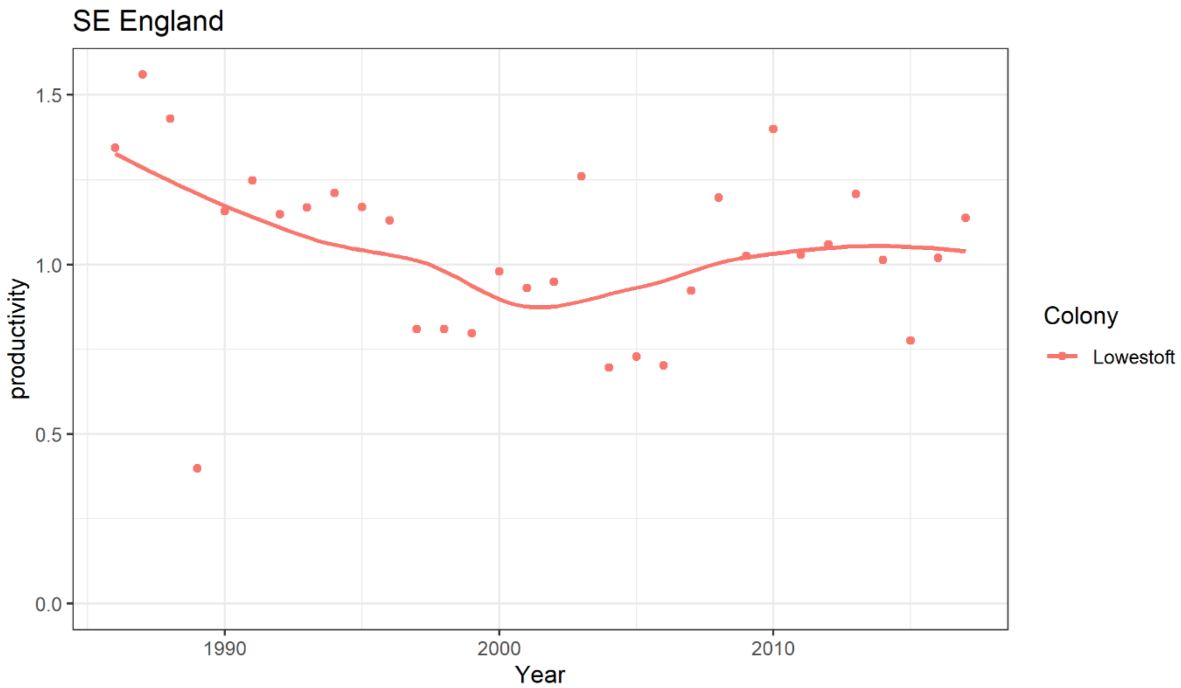

Figure A21i. Annual productivity of colonies based in East England 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.

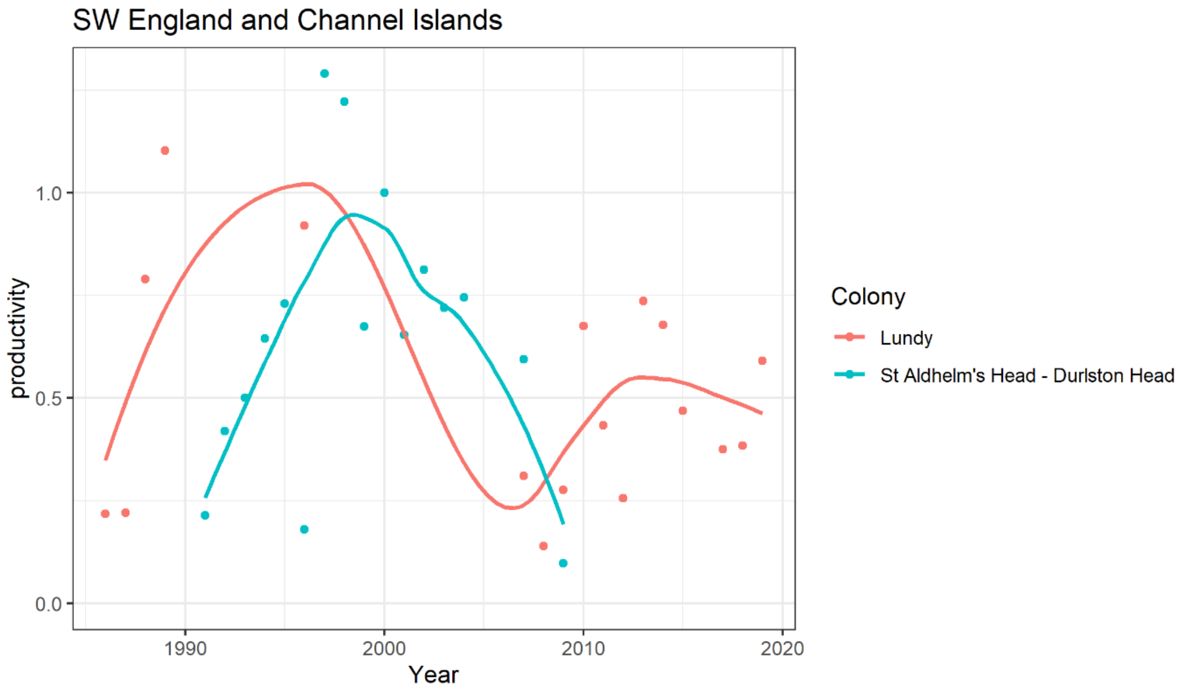

Figure A22j. Annual productivity of colonies based in South-West England and Channel Islands 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.

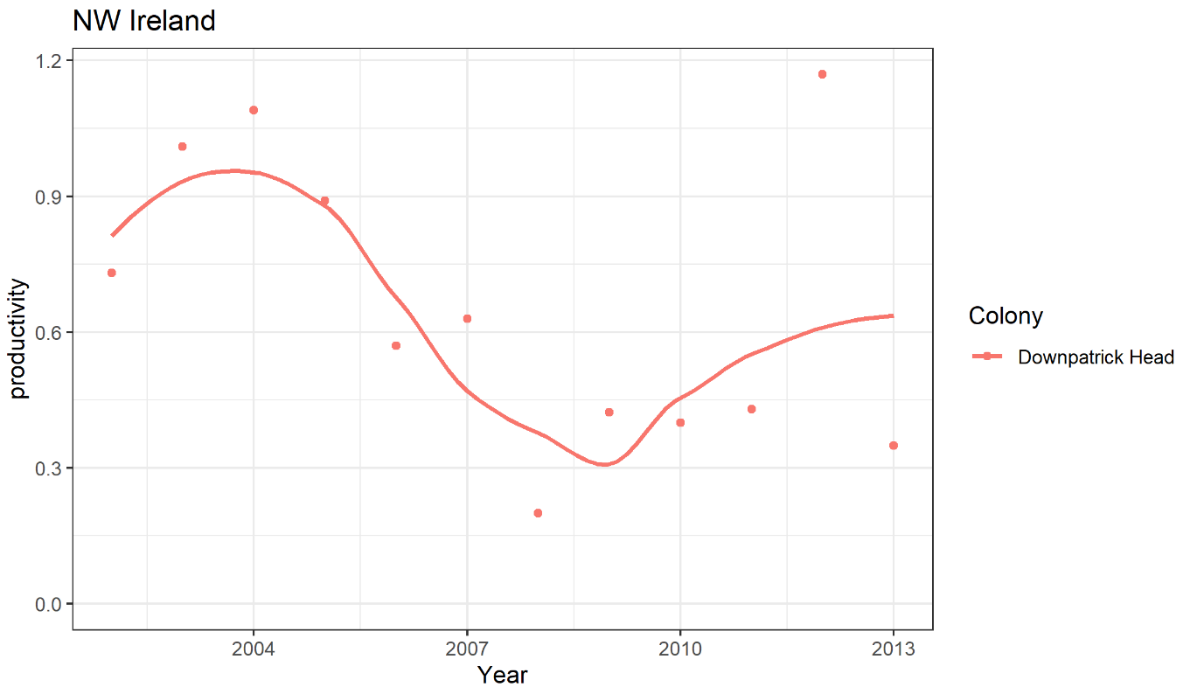

Figure A23k. Annual productivity of colonies based in North-West Ireland 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.

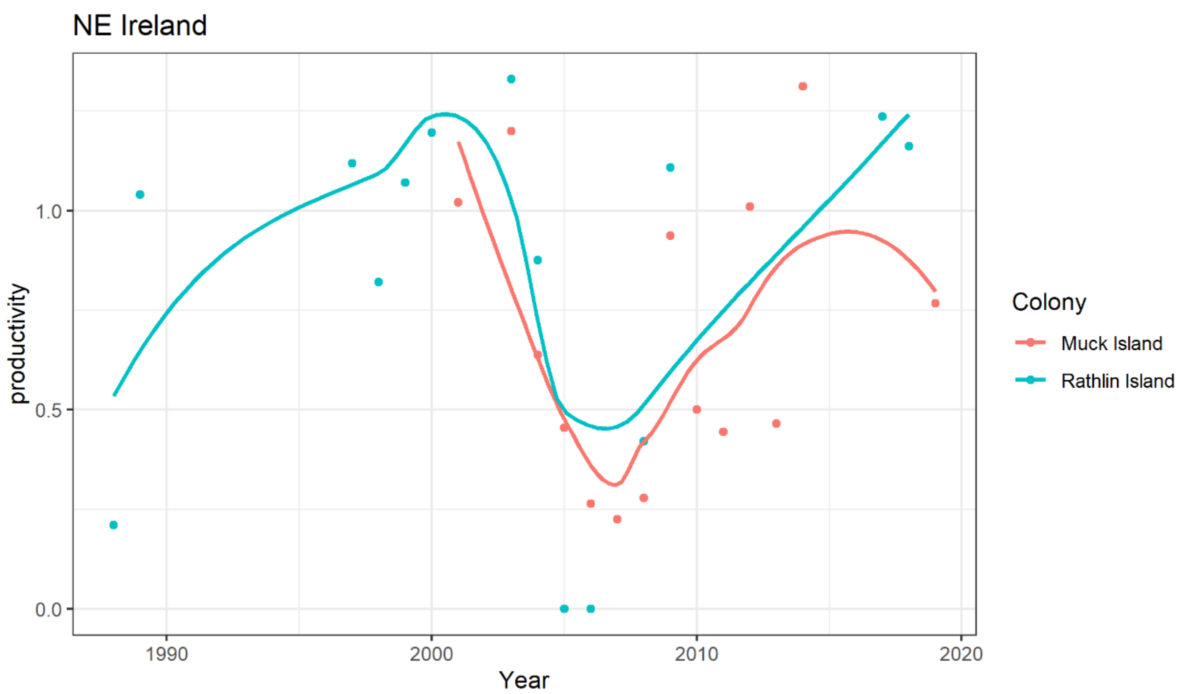

Figure A24l. Annual productivity of colonies based in Northern Ireland 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.

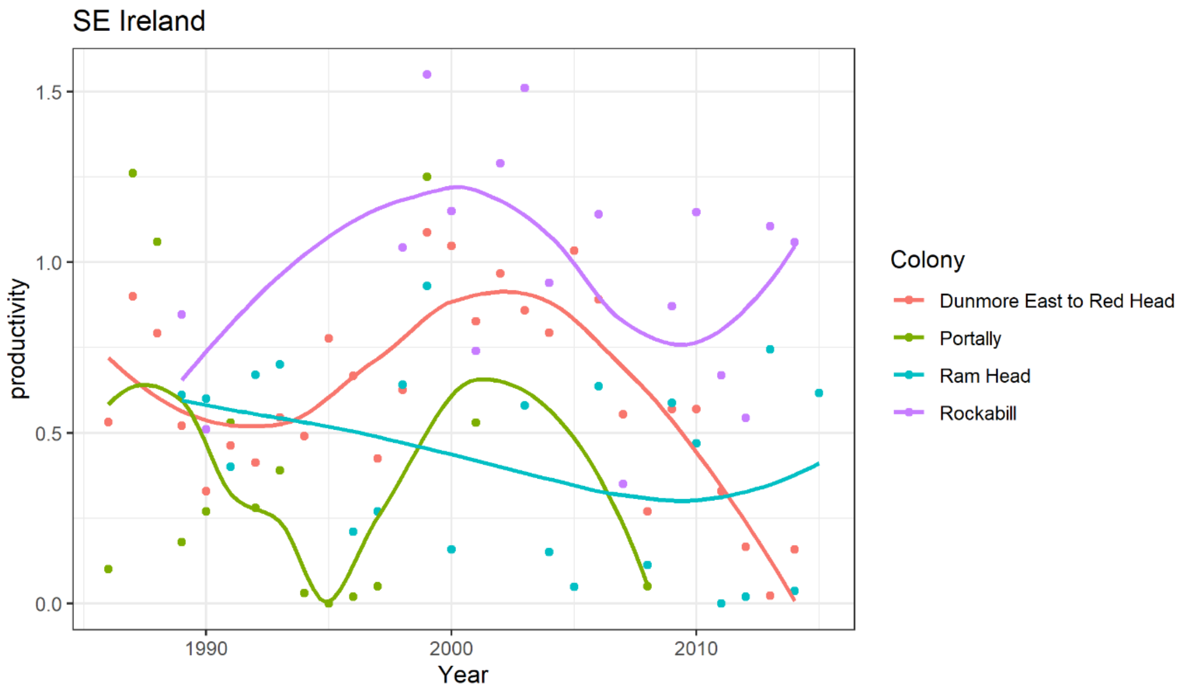

Figure A25m. Annual productivity of colonies based in South-East Ireland 1986-2019. Locally weighted smoothing (LOESS) lines of productivity trend are coloured by colony.