

ECOLOGY OF COMMON GUILLEMOTS ON LUNDY: CHICK PROVISIONING 2008-2019

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ABSTRACT

Provisioning activity of Common Guillemots (*Uria aalge*) was studied at the same ledge on Lundy over ten breeding seasons between 2008 and 2019. Parental attendance decreased and productivity increased over the study period. The increased population of Guillemots on Lundy could be the cause of these changes, but changes in the food-web of the Celtic Sea could also be a factor. Parental attendance was significantly lower in the latter part of the 2012 season associated with the only time that a chick was abandoned.

Keywords: *Lundy, Common Guillemot, parental attendance, productivity, chick provisioning, breeding phenology*

INTRODUCTION

The Common Guillemot (*Uria aalge* Pont) or Common Murre is a large (c.950g), long-lived seabird of the auk family (Gaston & Jones, 1998). They occur in the north of the Pacific and Atlantic Oceans and in the Arctic Ocean. Guillemots breed on sea-cliffs in tightly-packed ledges or in rocky crevices, often in mixed colonies with other seabirds. Breeding adults make no nest but instead their egg or chick is sheltered under the body or wing of one parent. In the southern areas of their range, they return to these breeding colonies from mid-October onwards.

Breeding phenology varies with sea temperature; the start of egg-laying in Arctic colonies can be a month later than those in Britain or California. A single egg is laid and parents take turns in incubating, with one parent present except in times of food shortage. Egg-laying is more synchronised within a ledge than between different ledges of the same colony. Eggs are lost to predators or accidentally knocked from ledges due to high breeding density. A replacement egg (or occasionally second replacement egg) can be laid if the first egg is lost. Only one chick is raised per season, although Harris *et al.* (2000) reported a case where a pair successfully raised an orphan as well as their own chick to fledging age. That pair increased their foraging time at the expense of time spent at the colony.

Hatching is a long process; from the first hole appearing to the final emergence of the chick can take around two days. The chick and its parents learn each other's calls during hatching which allows behavioural separation on the physically crowded ledge. Calls from the chick encourage the brooding adult to roll the egg which allows the chick to extend the hole around the wide end of the egg. Calls from the adults encourage the chick to continue to chip away at the egg (Tschanz, 1968).

Newly hatched chicks are carefully protected by their parents and are difficult to see. The presence of a chick can sometimes be confirmed by changes in the behaviour of its brooding parent. The most obvious change in parental behaviour is returning to the ledge with a fish. This is not always conclusive, as Guillemots will occasionally attempt to feed their egg. Parents take turns in brooding their chick, again with one parent present in all but exceptional times. The off-duty parent will either spend time at the ledge or away from the ledge (flying, washing, and foraging for themselves and for their chick). Guillemots can vary their foraging effort to compensate for variations in food availability, either by switching to alternative prey fish, or by increasing the amount of time spent foraging (Burger & Piatt, 1990). Decreased attendance at times of low food availability has been seen in Norway (Tschanz, 1979), eastern Canada (Birkhead & Hatchwell, 1984, Burger & Piatt, 1990), Scotland (Uttley *et al.*, 1994, Monaghan *et al.* 1994, Wanless *et al.*, 2005, Ashbrook *et al.*, 2008), and Alaska (Zador & Piatt, 1999, Harding *et al.*, 2007). Parental attendance reached a plateau of 12 minutes per hour in Cook Inlet, Alaska, at moderate to high fish abundance (Harding *et al.*, 2007b). The Isle of May recorded mean parental attendance of 16.7% over 17 seasons from 1981.

Pairs that have lost their egg or chick will sometimes brood a neighbouring chick (Tschanz, 1968). This allobrooding can be beneficial to the chick, especially in times of low food availability when chicks may be left unattended while both parents forage (Birkhead & Hatchwell, 1984).

Foraging adults return to their chick with one fish at a time (single-prey loading), usually held lengthways in their bill. The returning adult half-opens its wings to 'tent' its chick whilst the fish is transferred. Older chicks will take the fish directly from their parent. Younger chicks will wait until the fish is dropped and then take it from the ground. Provisioning rates count the number of fish delivered per chick in a given time. Different colonies have different feeding areas, so normal provisioning rates vary from colony to colony. When combined with the size and species of fish, provisioning rates can give an estimate of the total energy intake of a chick. Fish fed to chicks at UK colonies are mainly Sandeels, clupeids (Sprats and Mackerel) or gadioids (Whiting, Cod) (Anderson, 2014).

At times of severe food shortage, adults may abandon their chick to feed themselves. This behaviour allows long-lived seabirds to maximise their breeding success over their life time at the expense of a single chick. Unlike large Gulls, adult Guillemots will only kill neighbouring chicks in times of extreme food stress (Ashbrook *et al.*, 2008). In these cases, it is only birds feeding their own chick that will kill neighbouring chicks; failed breeders still show alloparental behaviour towards unattended chicks.

Guillemot chicks fledge after two to three weeks of being fed on the breeding ledge. At this age they can regulate their own temperature but are unable to fly. They go to sea with the male parent who continues to feed his chick until it is able to feed itself. Captive chicks were able to pick up fish from the bottom of a tank a week after 'fledging'. Fledging can fail through predation, or through communication failure between the chick and adult (Greenwood, 1963 & 1964).

Female Guillemots stay on the breeding ledge after their chick and partner have departed. They may stay for another two weeks in normal conditions, but can leave after a few days in times of low food availability. Their partners may return to the ledge if fledging fails.

STUDY SITE

Lundy is a three-mile long granite island located where the Bristol Channel meets the Atlantic Ocean. It is the largest seabird colony in south-west England. Guillemot numbers increased from 3,302 birds on breeding ledges in 2008 to 6,198 birds in 2017 (Booker *et al.*, 2018). This increase was after the RSPB-led Seabird Recovery Project. The count of 4,114 birds in 2013 (Price *et al.*, 2014) was the then highest number recorded on Lundy since the Second World War when seabird numbers in the Bristol Channel were decimated due to increased oil pollution from shipping losses (Birkhead, 2016). The previous highest post-war count was 3,910 in 1956 when Barbara Snow was the LFS warden (Davis & Jones, 2007).

The first major study of Guillemots on Lundy was by Richard Perry in 1939 (Perry, 1940). Perry made detailed descriptions of the breeding behaviour of Guillemots as well as Razorbills, Puffins and Kittiwakes. He estimated that the population of Guillemots was 19,000. Since then Guillemot research has concentrated on ringing (LFS 1940s-1960s), first-flighting (Greenwood, 1963), breeding success (Taylor, 1970s), population (David Price, RSPB, 1980s-present), comparative feeding ecology (Birkhead *et al.*, 1986, Hatchwell *et al.*, 1992) and productivity (various wardens, 2007-present e.g. Dalrymple, 2008, Wheatley & Saunders, 2010, 2011).

The feeding ecology of Guillemot chicks on Lundy (specifically chick diet, provisioning rates and feeding trip duration) was compared with nearby islands in the mid-1980s. In 1985, Lundy was compared with Skomer and Great Saltee (Birkhead *et al.* 1986). In a continuation of that study in 1986, Lundy was compared with Skomer (Hatchwell *et al.*, 1992). These studies showed Guillemots from the Lundy and Skomer colonies had different feeding areas: feeding-trip durations were too short for birds from each colony to fly to the same feeding area. Relative proportions of Sprats and Sandeels in the diet of chicks were also different in each colony.

Although feeding areas are different, there is movement of non-breeding birds between these three islands. An immature Guillemot ringed on Skomer was later seen on Great Saltee (Birkhead & Hudson, 1977). Birds ringed as chicks on Skomer have been recorded on Lundy (Taylor, 2015), and one of these was re-sighted on Skomer five days after being seen on Lundy (Tim Birkhead, pers. comm.). One of the adult birds for this study was ringed as a nestling on Great Saltee in 2000.

METHODS

Provisioning data were collected on Lundy over ten breeding seasons from 2008 to 2019, using a video recorder. Data were not collected in 2009 and 2017 due to injuries. Data collected for this study were from a site that has been recorded since 23 June 2008 near St Philip's Stone on the west coast of Lundy (SS130462). This ledge is part of colony F4 on the Lundy Seabird Colony Register and was viewed from location Fe (SS1318046354, Price *et al.*, 2008) and from a location near Ff in 2018 and 2019. Up to 19 pairs of adults have been recorded on this ledge in any one year with a maximum of 15 chicks seen in any one year. The ledge was mostly observed in the morning, but afternoon and evening sessions were also recorded. Only morning sessions were used for this study as provisioning rates can vary with the time of day and there were insufficient afternoon or evening sessions to give significant comparisons. Lower air temperature in morning sessions also leads to stable air and less air turbulence which gives better recordings at high magnification.

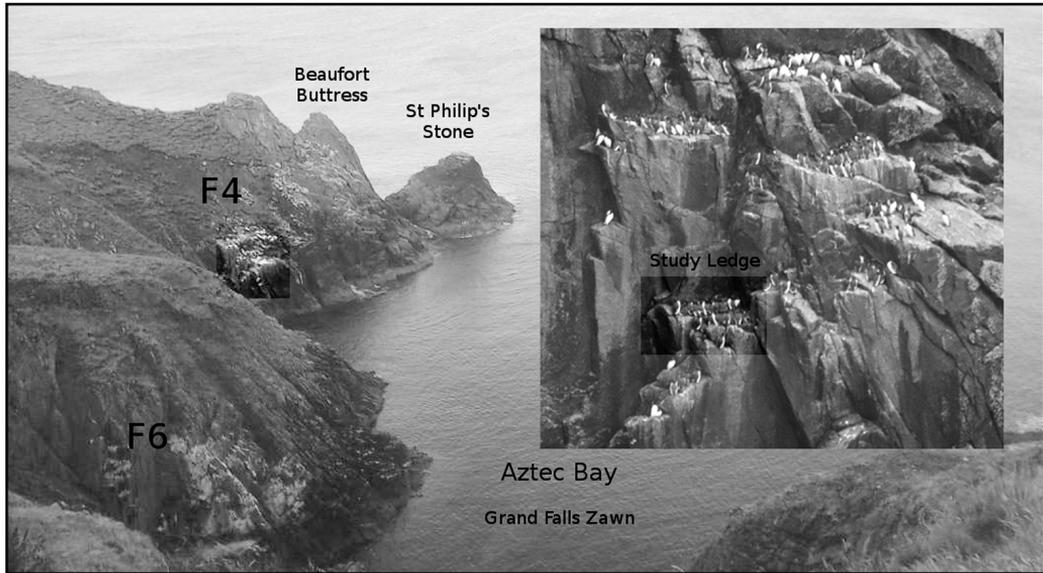


Plate 1: Position of the survey ledge on the west coast of Lundy. Different people have named features on Lundy. St Philip's Stone is attributed to Barbara Snow, Aztec Bay is in Williams (2001). Beaufort Buttress and Grand Falls Zawn have been named by the climbing community (Harrison, 2007). The most consistent method of labelling seabird sites is to use the Seabird Colony Register. This survey ledge is in F4 highlighted with increased contrast. The inset photograph shows the position of the survey ledge within F4

The camera was a Canon XL2 video camera which allows Canon SLR lenses to be used with an effective increase in focal length of around 7×. The site was first recorded with a Sigma 70-300mm APO lens, and later with a Canon 100mm-400mm L lens. In 2015, a 1300mm focal length telescope was attached to the video camera which allowed one of the birds to be identified from its metal leg ring. The camera records Standard Definition 25p PAL video on to 60-minute miniDV tapes; in practice these tapes produce just over 62 minutes of usable video. The tapes were captured onto computer using Sony Video Capture 6.0e and edited using Sony Vegas Pro 8.0c. Corrupt video at the beginning or end of a recording was deleted. Only the first 60 minutes of video was used to calculate provisioning rates and parental attendance. In 2018 a Canon 1100D DSLR camera was used to record 720p HDV on to an SD card in 15-minute segments. In 2019 a Canon 200D DSLR camera was used to record 1080p HDV on to an SD card in 29m 59s segments.

Focal sites were identified by the presence of an incubating or brooding adult, or by the presence of a pair of birds. Pairs were identified by mutual interactions, particularly by mutual preening, although adults also preen neighbouring birds (Lewis *et al.*, 2007). Adults returning to the ledge engage in greeting behaviour with their partner. Both birds stand and stretch their bills skywards and give a call. Their bill will be open if they are not carrying a fish. This greeting will sometimes elicit the same behaviour in neighbouring pairs.

Table 1: Number and length of observing sessions per year

Year	Length of observing session							
	31m	60m	53m+60m	2×60m	8×15m	4×29m59s	3×60m	4×60m
2008				34				14
2010		7		34				
2011	13		13	20				
Early 2012 (<23 Jun)				47				
Late 2012 (>23 Jun)				52			7	
Total 2012				99			7	
Early 2013 (<29 Jun)				57				
Late 2013 (>29 Jun)				67				
Total 2013				124				
Early 2014 (<1 Jul)				51				
Late 2014 (>30 Jun)				65				
Total 2014				116				
Early 2015 (<24 Jun)				60				
Late 2015 (>24 Jun)				50				
Total 2015				110				
Early 2016 (<25 Jun)				43				
Late 2016 (>25 Jun)				63				
Total 2016				106				
Early 2018 (<27 Jun)					42			
Late 2018 (>27 Jun)					52			
Total 2018					94			
Early 2019 (<15 Jun)						52		
Late 2019 (>15 Jun)						84		
Total 2019						136		
Totals	13	7	13	643	94	136	7	14
Grand total of all observing sessions 2008-2019=927								



Plate 2: Positions of all the focal sites within the survey ledge. Most focal sites were occupied ever year from 2008 to 2019. The site H was vacant in 2014 after the storms of the previous winter. The pair at site J tried to push in between pairs E and F in 2015 and 2016 but did not manage to produce a chick. By 2018, the pairs at F and G had moved right to fill the gap left at site H. Site U was only occupied in 2013 and 2015

Recording sessions

Data for each session was collected in two, one-hour tapes in the morning. Three types of data were transcribed from the tapes: arrival time, departure time, and whether an arriving adult was carrying a fish. Data was only recorded for adults known to have chicks. Provisioning Rate was recorded using the method outlined by Wanless & Lewis (2006). Productivity was recorded using the method outlined by Walsh *et al.* (1995). The most difficult observation was the presence or absence of young chicks. Small signs of their presence became easier to detect as the study progressed. Chicks are brooded underneath or against the side of the adult's body. The chick's head is sometimes underneath the adult's wing. The chick's bill can sometimes be seen directly, or sometimes be assumed by the movement of the adult's secondary feathers. Video from earlier years was re-transcribed to check for young chicks. A small number of chicks were not detected on occasional days but were present in the observing sessions before and after. Longer observing sessions would make it easier to detect all of the chicks that are present on any one day.

Parental Attendance

Parental attendance has been measured in different ways at different colonies. The Isle of May records percentage of non-brooding parents present at noon. Cook Inlet, Alaska, recorded total time in minutes that either parent was present over an hour. This was measured either by direct observation or by time-lapse camera.

In this study, parental attendance for each chick was recorded as the percentage of time to the nearest second that its non-brooding adult was present at the ledge during each 2h (2008-2018) or 1h59m56s (2019) session. Attendance could vary between 0% if

only one parent was present to 100% if both parents were present for the whole session. On some occasions in 2012, both parents of the chicks on sites F and N were away from the ledge at the same time. Chick F 'Foxtrot' was allobrooded by the chickless pair from site G. Chick N 'November' was left alone on the ledge without protection. This lack of attendance could have been recorded as a negative percentage. The abandonment of 'Foxtrot' and 'November' represent two different decisions for their parents, so any attendance less than 0% was treated as 0% on these occasions (Tony Taylor, pers. comm.).

Analysis

Each measurement (parental attendance, provisioning rate and productivity) had a distribution of values for each year. Parental attendance and provisioning rates did not have normal distribution and were skewed towards zero. Means of each year were calculated and trends were found using the linear model function in R. Each year's distribution is a sample of the whole distribution for each year as not every day is recorded and only 2 hours are recorded. The variation between the distributions for each year was analysed in two ways. In the first method, the Kolmogorov-Smirnov test was used to compare distributions pairwise year-against-year. This method assumes that the recorded distribution for each year is representative of the whole season. In the second method, the yearly distributions were combined to produce an all year distribution. This all year distribution was then compared against each year using the Kolmogorov-Smirnov test. This second method assumes that every year is part of the same distribution and therefore any tested year has to be more extreme to show a significant difference.

RESULTS

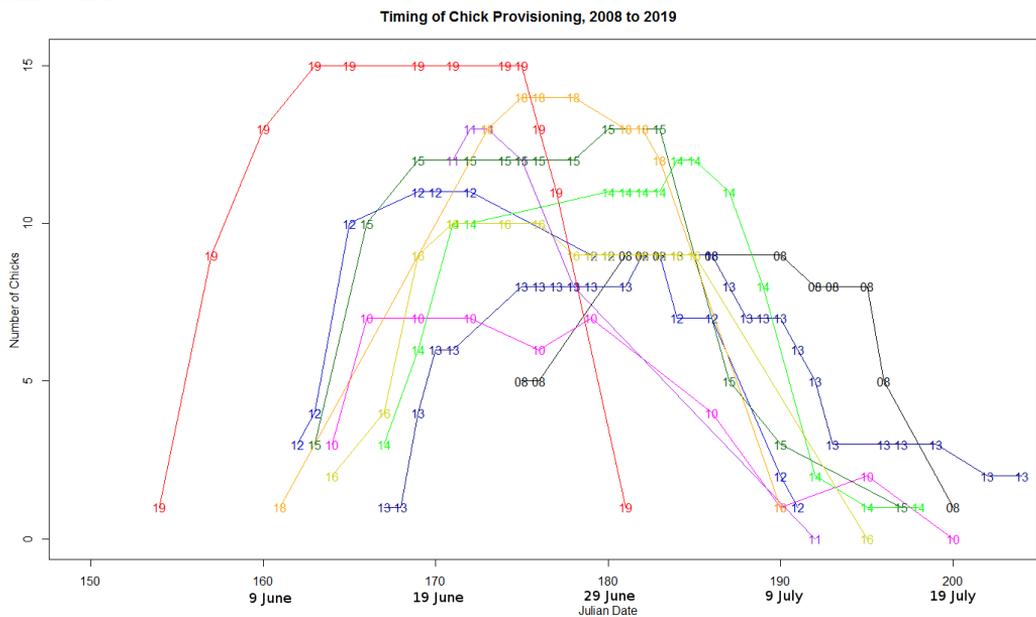


Figure 1: Numbers of chicks observed on the survey ledge during the ten seasons of observation. Each year is colour-coded and labelled as a two-digit year (e.g. the 2008 season is labelled 08). The Julian date is the day of the year taking 1 January as 1. Calendar dates are for non-leap years

Timing of Chick Provisioning

The number of chicks present each year peaked within a three-week window. The timing of that window varied from year to year. 2008 was the latest date that chicks were present (peak 23 June-14 July). 2019 was the earliest date that chicks were present (peak 6 June-26 June). Hatching was early in 2011; observations were not started until most chicks had hatched. The date at which half the chicks had left the ledge in 2011 was similar to 2019 (27 June).

Parental Attendance

Parental Attendance showed a slight decrease over the study period (-0.44% per year, t-statistic $p=0.06$). Mean parental attendance for the whole study period was 14.6%

Taking each breeding season as a whole, parental attendance was significantly lower in 2012 (9.5%) and 2018 (9.3%) (Komogorov-Smirnoff test, year vs all years, $p=0.0712$ and $p=0.0189$ respectively) and significantly higher in 2014 (20.3%, $p=0.0094$).

The seven observed breeding seasons between 2012 to 2019 were split into early and late observations. For the early part of each season, parental attendance was lowest in 2018 but this was not very significant (K-S test, early year vs all early years, $p=0.149$). For the late part of each season, parental attendance was significantly lower in 2012 (5.8%, $p=0.0055$, K-S test late year vs all late years) and significantly higher in 2014 (20.1%, $p=0.0257$).

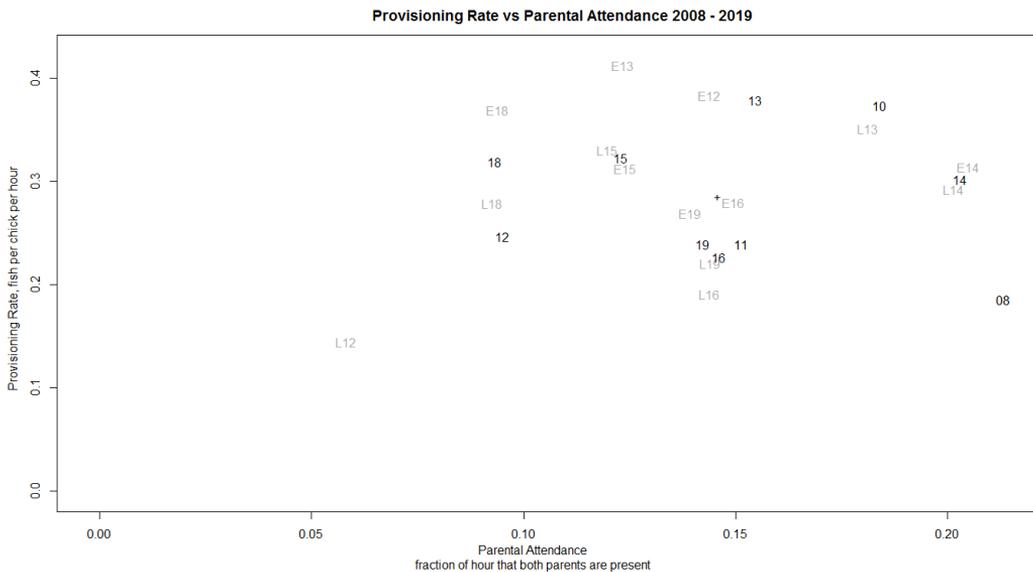


Figure 2: Provisioning rates plotted against parental attendance for the ten seasons. Bold labels as Figure 1. Grey labels for the seven seasons that were also split into early and late sections (e.g. L12 is the late part of the 2012 season)

Provisioning Rates

Mean provisioning rate for the study period was 0.285 feeds/chick/hour. There was no significant trend over the ten seasons. Provisioning rates varied from 0.185 feeds/chick/hour in 2008 to 0.379 feeds/chick/hour in 2013. Rates were significantly higher

in 2013 compared to 2011, 2012 and 2016 ($p=0.0259$, $p=0.0872$ and $p=0.0604$ respectively, K-S test, pair-wise year vs year). Rates were also significantly higher in 2018 compared to 2011 ($p=0.0827$).

When split into early and late observations, provisioning rates in late 2013 were significantly higher than in late 2012 ($p=0.0407$, K-S test, pair-wise late year vs late year).

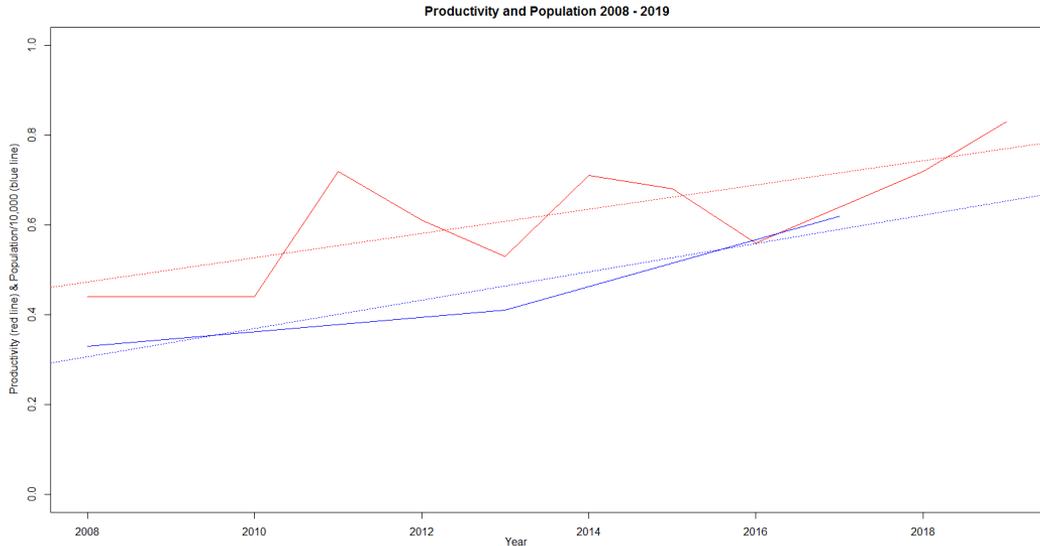


Figure 3: Productivity (red line using maximum value in 2011) from this study and population (blue line, in 10,000s) from Booker (2018) plotted over the survey. Dotted lines are linear models using R

Productivity

There were 181 active or regular sites over the ten breeding seasons of the study. These sites hatched 121 chicks of which 107 chicks were observed until at least 15 days old. This gives a mean productivity of 0.59 chicks per site. Productivity increased over the study. 2011 was difficult to assess due to early hatching and might range from 0.39 to 0.72 chicks fledged per site. Assuming an average productivity in 2011 of 0.55 then productivity increased significantly over the study period (3.1% per year, $p=0.0037$). Assuming the highest productivity in 2011 showed a reduced but still significant increase (2.7% per year, $p=0.012$). More eggs hatched in 2011 (15 eggs hatched) than in 2010 (9) and 2012 (11). More eggs failed to hatch in 2016 (5 eggs failed) than in 2015 (3) and 2018 (none).

DISCUSSION

Comparisons of data between Guillemots at different colonies should be made with care. Birds from relatively close colonies can feed in different areas (Birkhead *et al.*, 1986, Hatchwell *et al.*, 1992). The physical characteristics of a particular ledge limit the number of birds present, and departing and returning birds can knock neighbours from the ledge. Comparisons of a particular sub-colony over a number of breeding seasons allow us to put unusual events into context. The late 2012 event on Lundy showed lower than average parental attendance and provisioning rates as well as the only cases of intentional chick abandonment during the survey period.

Parental Attendance

Parental attendance declined slightly over the study period. A top-down explanation could be that there is Storer-Ashmole Halo (cf. Elliot *et al.*, 2009) effect taking place: that the increased population of seabirds on Lundy is reducing the populations of sprats and sandeels around Lundy. The reduced populations of prey species would increase the amount of time that adult Guillemots spend away from the ledge. The largest historical count of Guillemots on Lundy was approximately 19,000 pairs in 1939. We have no quantitative information on parental attendance in Perry's survey. If we make the conservative assumption that these 19,000 pairs are the most that the seas around Lundy can support, then the current population of 6,198 birds is still far from, but heading towards, that total. Parental attendance returned to 20% in 2014; a top-down interpretation could relate this to the large number of seabird deaths in the storms of 2013-14 (Lock, 2014).

A bottom-up explanation for the slight decline in parental attendance could be changes in the Celtic Sea food-web have decreased stocks of Sprats and Sandeels around Lundy. These changes are difficult to apply to Lundy because we have no long-term data set on parental attendance to compare with changes in sea temperature or indices such as the North Atlantic Oscillation. Instead, we must use variations in our ten breeding-season data set and compare these to annual or seasonal variations in local sea conditions.

Parental attendance in late 2012 was significantly lower, suggesting low food availability. Henderson & Henderson (2017) showed that adult sprats caught in the water intake at Hinkley Point were underweight in December 2011 but had recovered in December 2014. Sprats and Sandeels were shown to be the main forage fish on Lundy in 1985-6 (Hatchwell *et al.*, 1992). Underweight sprats in December 2011 could have the same cause as low Guillemot attendance in late June and early July of 2012. By 2014, Guillemot attendance had risen to 20% and sprat condition was back to normal. Riordan & Birkhead (2018) showed that there was a shift in prey availability for foraging Guillemots at Skomer after 2010.

Sprats and Sandeels feed on zooplankton, primarily copepods. The dominant copepod in the Celtic Sea is *Calanus helgolandicus* which is omnivorous and feeds on smaller zooplankton and phytoplankton. Primary production in the Celtic Sea is seasonal. In April, primary production is concentrated on the surface. The Celtic Sea becomes stratified during the peak of seabird breeding activity in June and July and primary production is concentrated below the surface. The Celtic Sea Front is formed where the stratified Celtic Sea meets the tidally mixed waters of the Bristol and St George's Channels. The Celtic Sea Front is another area of high primary production.

Surface concentrations of phytoplankton can be seen in Continuous Plankton Recorder surveys and by satellites that are sensitive to chlorophyll such as the MODIS instrument on the AQUA satellite. April concentrations of phytoplankton near the surface show well in these instruments (Figure 4.A). Low surface chlorophyll in June and July suggests that there is a sub-surface chlorophyll maximum (Figure 4.B). Dedicated ship-based surveys are needed to show concentrations of phytoplankton below 20m (e.g. Hickman, 2012).

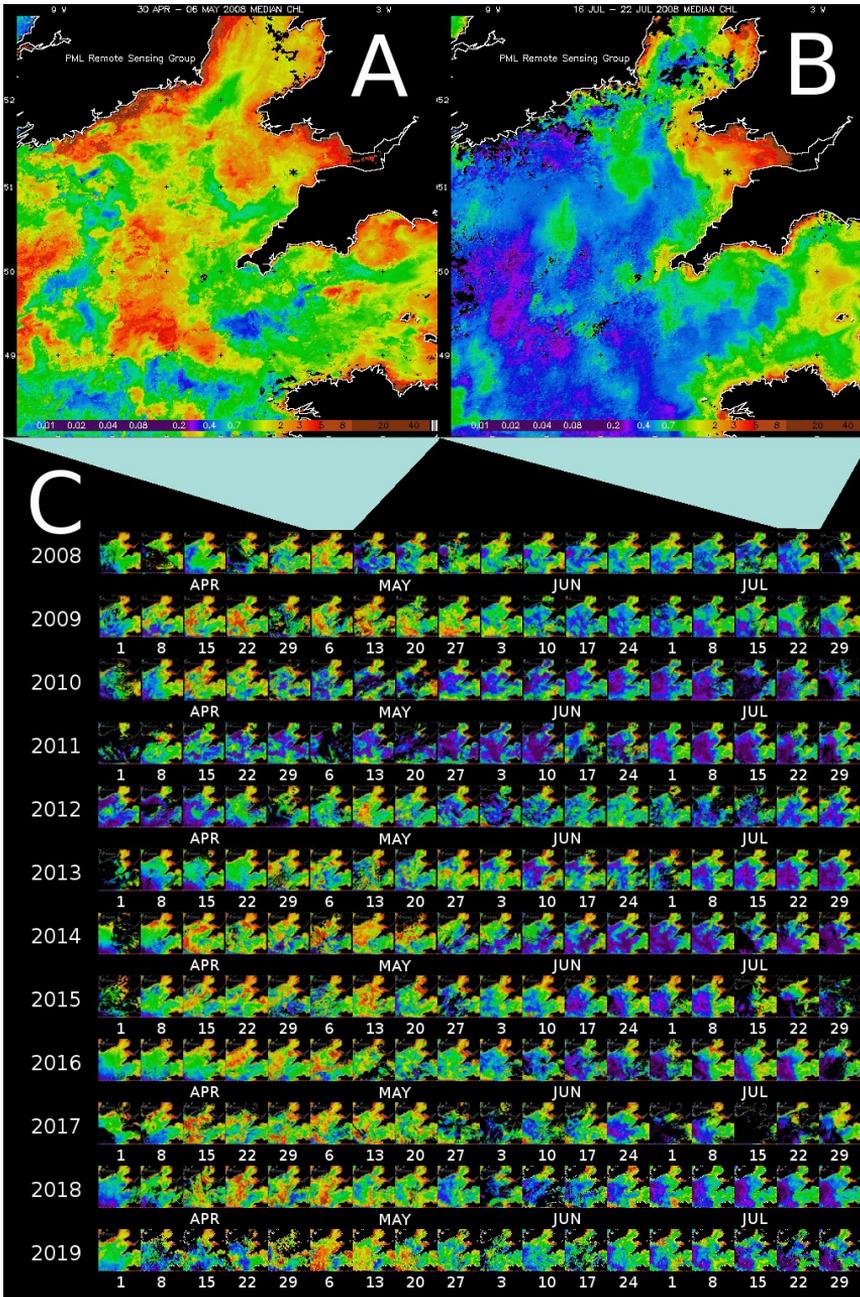


Figure 4: Composite images of surface chlorophyll (OC3M) for the Plymouth area from the MODIS instrument on the AQUA satellite. Composite images of median value of OC3M over seven days. (A) Composite of 30 April to 6 May. Red areas over the Celtic Sea show high surface chlorophyll and therefore high surface phytoplankton abundance during the spring bloom. Position of Lundy shown by black asterisk. (B) Composite of 16 to 22 July. Purple areas other than the Celtic Sea show low surface chlorophyll and therefore imply the presence of a sub-surface chlorophyll maximum. (C) Weekly composite images covering April to July for the survey period. Blue areas in April of 2011 and 2012 imply a weaker spring phytoplankton bloom in these years

Satellite images from the MODIS AQUA instrument suggest that April surface chlorophyll in the Celtic Sea was lower in 2011 and 2012 than other years (Figure 4.C). Low phytoplankton numbers could have led to low or malnourished copepods which in turn could have led to the underweight Sprats observed by Henderson in December 2011 and low parental attendance on Lundy in late 2012.

Satellite images are now used to identify the strength of the Celtic Sea Front and identify smaller short-lived fronts. Relating these fronts to fish and seabird concentrations is an active area of research. Preliminary steps have been made to compare data from this study to front strength and location.

Studies of food availability in the Cook Inlet, Alaska, showed that parental attendance was a better indicator of food availability than provisioning rates or productivity (Harding *et al.*, 2007a, 2007b, Piatt *et al.*, 2007). They looked at three separate colonies: Chisik Island, Gull Island and the Barren Islands. Chisik Island always had the lowest food availability and parental attendance. The Gull Island and Barren Island colonies were always better than Chisik Island and showed greater variation. The Cook Inlet study showed that there was a non-linear dependence of parental attendance on food availability: 'colony attendance by [Guillemots] at colonies in lower Cook Inlet, Alaska, increased rapidly over a limited range of poor-to-moderate prey densities, and then levelled off to become independent of food at high prey densities.' (Harding *et al.*, 2007b).

If we assume that large colonies of Guillemots occur near areas of greater food availability (ignoring the effects of predation or the availability of potential breeding islands near oceanic hot-spots) then parental attendance at the highly-studied colonies such as Skomer and the Isle of May could be less sensitive to small variations in sea conditions. It could be beneficial to start long-term studies at smaller, less optimal, colonies. Studies of parental attendance can be less time consuming than the full-scale studies at Skomer but would compliment them by giving wider geographic scope and may be more sensitive to variations in food availability.

Provisioning Rates and Chick Diet

Provisioning rates are difficult to assess without also knowing the species, size and condition of the forage fish. High provisioning rates in 1986 were associated with smaller fish than in 1985 when provisioning rates were lower (Hatchwell *et al.* 1992). It is hoped that video from this study will yield species and size identification. Video from early seasons was used for species identification in Anderson *et al.*, (2014).

Condition of the fish is also difficult to assess. Researchers at Skomer regularly collect stomach samples from adult Guillemots and collect discarded fish to measure the condition of prey species. This work is invaluable but does not need to be replicated on Lundy. Stomach sample collection is invasive, time-consuming, and requires a high level of training. Collecting discarded fish is easier to achieve, especially as we have large numbers of rock-climbers that visit Lundy immediately after the seabird breeding-season. Many of these climbers have visited Lundy for many years and have contributed to conservation efforts by reporting sites where breeding is late, taking photographs of predated seabird carcasses, and returning leg rings from otherwise inaccessible cliffs. Climbers could be asked to collect any discarded fish for identification (but see Barrett *et al.*, 2007 for limitations of this method).

Productivity

The productivity of the study ledge increased as the whole island Guillemot population increased. There are signs of decline in numbers of gulls on Lundy. A stable or declining gull population would reduce the predation pressure on an increased Guillemot population. Wide flat ledges are known to be more susceptible to predation than the narrow ledges, observed for this study. Comparisons between individual sites on this ledge and between other study ledges on Lundy may show specific reasons for the increased productivity on this ledge. Sutton (2016) showed that Lundy's Peregrine Falcons were taking an unexpectedly large number of immature larids. A study of the feeding ecology of corvids and *Larus* gulls throughout the year might show reasons why predation pressure on this ledge has decreased (e.g. decrease in rat and rabbit numbers reduce the numbers of predators that could be supported outside of the breeding-season).

CONCLUSIONS

This study only recorded two-hour sessions so it was not able to produce detailed information about feeding-trip duration or the variation of provisioning rates over a whole day that are obtained by studies at Skomer and the Isle of May. The strengths of this study were that it produced useful data on parental attendance with less effort. It also produced video that can be used for other studies of behaviour. Monitoring the health of our highly-productive shelf seas is increasing important in times of climate change. Studies at smaller colonies such as Lundy increase our ability to see the effects of climate change on marine food webs.

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REFERENCES

- Anderson, H.B., Evans, P.G.H., Potts, J.M., Harris, M.P. & Wanless, S. 2014. The diet of Common Guillemot *Uria aalge* chicks provides evidence of changing prey communities in the North Sea. *Ibis* 156: 23-34
- Ashbrook, K., Wanless, S., Harris, M.P. & Hamer, K.C. 2008. Hitting the buffers: conspecific aggression undermines benefits of colonial breeding under adverse conditions. *Biol. Lett.* 4(6): 630-633
- Barrett, R.T., Camphuysen, C.J., Anker-Nilssen, T., Chardine, J.W., Furness, R.W., Garthe, S., Hüppop, O., Leopold, M.F., Montevecchi, W.A. & Veit, R.R. 2007. Diet studies of seabirds: a review and recommendations. *ICES Journal of Marine Science*, 64: 1675-1691
- Birkhead, T.R. 2016. Changes in the numbers of common guillemots on Skomer since the 1930s. *British Birds* 109(11): 651-659

- Birkhead, T.R., Goodburn, S.F. & Hatchwell, B.J. 1986. Feeding Ecology of Common Guillemot Chicks on Lundy. *Annual Report of the Lundy Field Society* 1985 36: 25-26
- Birkhead, T.R. & Hudson, P.J. 1977. *Population parameters for the Common Guillemot Uria aalge*. *Ornis Scan.* 8: 145-154
- Birkhead, T.R. & Nettleship, D.N. 1984. Alloparental care in the common murre (*Uria aalge*). *Can. J. Zool.* 62(11): 2121-2124
- Booker, H., Slader, P., Price, D., Bellamy, A.J. & Frayling, T. 2018. Cliff nesting sea birds on Lundy: Population trends from 1981 to 2017. *Journal of the Lundy Field Society*, 6, 65-76
- Burger, A.E. & Piatt, J.F. 1990. Flexible time budgets in breeding common murres: buffers against variable prey abundance. *Studies in Avian Biology* 14: 71-83
- Cairns, D.K. 1988. Seabirds as monitors of marine food supplies. *Biological Oceanography* 5(4): 261-271
- Dalrymple, S. 2008. Cliff nesting sea bird productivity on Lundy 2007. *Journal of the Lundy Field Society* 1: 41-46
- Davies, M. 1982. Lundy seabird monitoring sites. *Annual Report of the Lundy Field Society* 1981. 32: 21-27
- Davies, M. & Price, D. 1986 Lundy census of breeding seabirds (1981, 1982 & 1986) Site Register. *Unpublished Report*
- Davis, T. & Jones, T. 2007. *The Birds of Lundy*. Harpers Mill, Berrynarbor
- Elliott, K.H., Woo, K.J., Gaston, A.J., Benvenuti, S., Dall'Antonia, L. & Davoren, G.K. 2009. *Central-Place Foraging in an Arctic Seabird Provides Evidence for Storer-Ashmole's Halo*. *The Auk* 126(3): 613-625
- Gaston, A. & Jones, I. 1998 *The Auks*. Oxford University Press
- Greenwood, J.J.D. 1964. The fledging of the Guillemot *Uria aalge* with notes on the Razorbill *Alca torda*. *Ibis* 106: 469-481
- Greenwood, J.J.D. 1963. First-fighting in Auks. *Annual Report of the Lundy Field Society* 1962. 15,18
- Harding, A.M.A., Piatt, J.F. & Schmutz, J.A. 2007a. Seabird behavior as an indicator of food supplies: sensitivity across the breeding season. *Marine Ecology Progress Series* 352: 269-274
- Harding, A.M.A., Piatt, J.F., Schmutz, J.A., Shultz, M., Van Pelt, T.I., Kettle, A.B., & Speckman, S.G. 2007b. Prey density and the behavioural flexibility of a marine predator: the common guillemot (*Uria aalge*). *Ecology* 88(8): 2024-2033
- Harris, M.P., Bull, J. & Wanless, S. 2000. Common Guillemots *Uria aalge* successfully feed two chicks. *Atlantic Seabirds* 2(2): 92-94
- Hatchwell, B.J., Birkhead, T.R., Goodburn, S.F., Perrins, J.M. & Jones, S.E. 1992. Chick diets and food intake of nestling Common Guillemots *Uria aalge*: an inter-colony comparison. *Seabird* 14: 15-20
- Henderson, P.A. & Henderson, R.C. 2017. *Population regulation in a changing environment: Long-term changes in growth, condition and survival of sprat, *Sprattus sprattus* L. in the Bristol Channel, UK*. *Journal of Sea Research* 120: 24-34
- Lewis, S., Roberts, G., Harris, M.P., Prigmore, C. & Wanless, S. 2007. *Fitness increases with partner and neighbour allopreening*. *Biol. Lett.* 3: 386-389

- Lock, M. 2014. It's happened before... *Devon Birds* 67(2): 42
- Miller, P.I. & Christodoulou, S. 2014. Frequent locations of ocean fronts as an indicator of pelagic diversity: application to marine protected areas and renewables. *Marine Policy* 45: 318-329
- Monaghan, P., Walton, P., Wanless, S., Uttley, J.D. & Burns, M.D. 1994. Effects of prey abundance on the foraging behavior, diving efficiency and time allocation of breeding guillemots (*Uria aalge*). *Ibis* 136: 214-222
- Perry, R. 1940. *Lundy, Isle of Puffins*. Lindsay Drummond, London
- Piatt, J.F., Harding, A.M.A., Shultz, M., Speckman, S.G., van Pelt, T.I., Drew, G.S., & Kettle, A.B. 2007. Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series* 352: 221-234
- Price, D. & Booker H. 2008. *Lundy Census of breeding seabirds: 2008*. Unpublished survey results to RSPB, JNCC and Lundy Field Society
- Price, D., Slader, P. & Booker, H. 2014. Survey of cliff nesting seabirds 2013. *Annual Report of the Lundy Field Society* 2013, 63, 85-89
- R Core Team. 2017. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Riordan, J. & Birkhead, T.R. 2018. Changes in the diet composition of Common Guillemot *Uria aalge* chicks on Skomer Island, Wales, between 1973 and 2017 *Ibis* 160(2): 470-474
- Speckman, S.G. 2004. *Characterizing fish schools in relation to the marine environment and their use by seabirds in lower Cook Inlet, Alaska*. Ph.D dissertation, University of Washington
- Speckman, S.G., Piatt, J.F., Minte-Vera, C.V. & Parrish, J.K. 2005. Parallel structure amongst environmental gradients and three trophic levels in a subarctic estuary. *Progress in Oceanography* 66: 25-65
- Sutton, L.J. 2016. Status of the Peregrine Falcon *Falco peregrinus* on Lundy: Breeding Ecology and Prey Spectrum. *Journal of the Lundy Field Society* 5: 75-88
- Taylor, A.M. 2015 Bird Ringing in 2014. *LFS Annual Report 2014*
- Tschanz, B. 1968. Trottellummen. *Zeitschrift für Tierpsychologie*, Suppl. vol. 4: 1-103
- Tschanz, B. 1979. Helfer-Beziehungen bei Trottellummen. *Zeitschrift für Tierpsychologie* 49(1): 10-34
- Uttley, J.D., Walton, P., Monaghan, P. & Austin, G. 1994. The effects of food abundance on breeding performance and adult time budgets of Guillemots (*Uria aalge*). *Ibis* 136: 205-213
- Walsh, P.M., Halley, D.J., Harris, M.P., del Nevo, A., Sim, I.M.W. & Tasker, M.L. 1995. Seabird monitoring handbook for Britain and Ireland. Published by JNCC/RSPB/ITE/Seabird Group, Peterborough
- Wanless, S., Harris, M.P., Redman, P. & Speakman, J.R. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294: 1-8
- Wanless, S. & Lewis, S. 2006. Instructions for collecting data on Guillemot diet and provisioning rate

- Wheatley, S. & Saunders, N. 2011. Cliff nesting Seabird Productivity on Lundy 2010. *Annual Report of the Lundy Field Society 2010*, 60: 67-74
- Wheatley, S. & Saunders, N. 2010. Cliff nesting sea bird productivity on Lundy 2008. *Journal of the Lundy Field Society 2*, 85-90
- Willcox, N.A. 1988. Seabird studies on Lundy. *Annual Report of the Lundy Field Society 1987* 38: 24-32
- Zador, S.G. & Piatt, J.F. 1999. Time-budgets of common murrelets at a declining and increasing colony in Alaska. *Condor* 101(1): 149-152