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RESEARCH ARTICLE

Small-scale natural landscape features and seabird nesting sites: the importance of geodiversity for conservation

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Abstract
Context Landscape geodiversity, and in particular small natural features (SNF), are crucial components of habitat suitability for many threatened species. Rocky cliffs at the sea-continent interface present complex small-scale geomorphologies which are exploited by nesting seabirds.
Objectives Elucidation of the relation between nest-site geomorphology and species preference in cliff-nesting seabirds. Evaluation of the potential of cliff-face SNF as seabird conservation tools.
Methods Nest site geomorphological characteristics of four Atlantic (Brittany, France) cliff-dwelling seabirds (Razorbill, Guillemot, Fulmar, and Kittiwake) were categorized, and scored for degree of enclosure.
Results Of the 1048 nest sites examined, the greatest species overlap in location was the mid-region of the cliff face: Fulmar was concentrated in the upper half of the cliff, while Kittiwake showed the most extended vertical distribution. A distinct trend was evident with respect to ceiling presence and size: Razorbill + Kittiwake > Guillemot > Fulmar. Clear trends were also evident in ceiling inclination, ledge size, and side wall presence and inclination. A distinct 'degree of enclosure' hierarchy was documented, consolidated with the addition of sympatric species known for their extreme preferences: Atlantic Gannets and Guillemots at the extreme 'open' end, and Puffins and Storm Petrels at the extreme 'closed' end. Some plasticity in site choice was observed, probably corresponding to sub-optimal default choices.
Conclusions Despite some plasticity, both vertical level and enclosure characteristics are associated with particular seabird species. Given the importance of nesting sites to seabird reproduction, the identification and conservation of these SNF constitute crucial conservation objectives.

Keywords Geomorphology · Small natural features · Nesting site · Seabird · Conservation

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Introduction

The ocean-land interface is a relatively neglected dimension of landscape ecology (Hinchey et al. 2008; Jelinski 2015), perhaps because the concept of 'landscape' is semantically incongruous in the marine environment, and also because the equivalent term 'seascape' has only slowly begun to be adopted in the marine vocabulary (e.g. Hinchey et al. 2008; Hovel and Regan 2008; Curd and Pibot 2014; Jelinski 2015 vs. Caldwell and Gergel 2013; Carroll and Peterson 2013; Musard et al. 2014; van Lier et al. 2018). Regardless of the term used to designate the marine or continental landscapes, their interface is somewhat of a semantic orphan, and this may explain why it is largely absent from the landscape literature. This state of affairs only underscores the need to fill this void.

Cliff-nesting seabirds use an ocean-land interface characterized by small-scale topographic complexity. Spatial scale is one of the most important parameters in landscape ecology (https://www.nature.com/scitable/knowledge/library/principles-of-landscape-ecology-13260702), especially for seabirds, which utilize a wide range of scales (Russell et al. 1992; Huettmann and Diamond 2006). However, seabirds are seldom considered from the standpoint of landscape. Indeed, a search of the *Landscape Ecology* database reveals only two publications dealing with seabirds and landscape, since the journal's inception in 1987.

The importance of relatively large-scale habitats to animal, and, in particular, bird conservation, has long been recognized (see Martin et al. 2007; Game et al. 2009; Yorio 2009; Allen and Singh 2016; McGowan et al. 2017; Oppel et al. 2018). From the study of habitat has emerged the importance of geodiversity and, most recently, of small natural features (SNF)—small-scale landscape characteristics which are essential to exploitation by organisms. Due to the disproportionately large ecosystem services they provide, small natural features (SNF) have been compared to keystone species in ecology (Hjort et al. 2015; Hunter et al. 2017; Malcolm and Hunter 2017). Small natural features have been studied (whether they have been identified as such or not) in both landscapes and seascapes (Diaz et al. 2003; Berkström et al. 2012; Calhoun et al. 2014; Hjort et al. 2015; Pfeiffer et al. 2016; Davis et al. 2017; Fitzsimons and Michael 2017; Lindenmayer 2017; Poschlod and Braun-Reichert 2017), yet the interface between these two systems obviously also contains SNF. One such overlooked candidate may be the geomorphological features of seabird cliff-nesting sites.

Early studies of nest site physical characteristics distinguished between open-nest and closed-nest sites, and the impact of this distinction on seabird reproductive success and conservation (Hudson 1982; Ewins 1989; Rowe and Jones 2000; Smith et al. 2011; Hasebe et al. 2012). Other studies have mentioned the importance of the ledge and wall (Birkhead et al. 1985; Harris and Wanless 1988; Olsthoorn and Nelson 1990; Gilchrist and Gaston 1997; Harris et al. 1997; Gilchrist et al. 1998; Mallory and Forbes 2011). The comprehensive geomorphology of nest sites and its relation to seabird reproductive success is a relatively recent concept (Mallory and Forbes 2011; Eveillard-Buchoux 2018).

Whether from the standpoint of predator avoidance (Cullen 1957; Gilchrist and Gaston 1997; Gilchrist et al. 1998; Webb et al. 2012), physical disturbance (wind, waves—Newell et al. 2015; Millones and Frere 2017), or egg loss through falling, the geomorphological characteristics of cliff features may be expected to play a role, and hence be involved in the selection process of nest sites (Chalfoun and Martin 2007; Chalfoun and Schmidt 2012; Webb et al. 2012). As is the case for habitat selection in general (Devries et al. 2018), understanding the processes affecting nest site selection is one of the critically-important research goals in seabird conservation. Although there is much qualitative evidence of nest-site preferences in different cliff-nesting seabird species (Hudson 1982; Olsthoorn and Nelson 1990; Ferns 1992; Harris et al. 1997; Kokko et al. 2004; Mallory and Forbes 2011), and even for continental cliff-nesting species (Anushiravani et al. 2016; Lambertucci and Ruggiero 2016; Pfeiffer et al. 2016), quantitative studies are lacking to date.

The present study explores the relation of small-scale geomorphological landscape features to the nesting site choice of European Atlantic cliff-nesting seabirds, through the detailed analysis of nest-sites in Brittany, France.

Materials and methods

Study sites

Four study sites were chosen on the basis of their large areas and number of individuals: the continental colonies of Cap Fréhel and Cap Sizun, and the island colonies of the Sept-Îles archipelago and Ouessant (Fig. 1). These sites present steep rocky coasts, rising 35–80 m above sea level. The rocky escarpments are composed of either sandstone (Cap Fréhel) or granitoid (remaining sites) (Fig. 1). Although sandstone cliffs are generally steeper than granitoid cliffs, the latter were very steep in some narrow coves. Sandstone cliff micro-topography is mainly the result of differential erosion of the various sedimentary layers, producing pronounced ledges and recesses, while that of the granitoid cliffs is the result of diaclasis, resulting in a much more irregular topography with a less pronounced horizontal component; these micro-forms are exploited by seabirds for their nest sites (Fig. 1).

After initial approach, access to the study sites was accomplished on foot for Cap Fréhel, Cap Sizun, and Ouessant Island. Observations were carried out using binoculars and long-range photography from shipboard at the Sept-Îles site, where disembarkation is not authorized.

Species studied

Steep rocky cliff-face 'seabirds' were defined as those which are truly pelagic, having a wholly marine diet (thus excluding shags, cormorants, gulls, terns, herons, etc.), and nesting on steeply-inclined rocky substrates (Nelson 1980; Cadiou et al. 2004). The presence of three burrowing species was recorded (Atlantic Puffin *Fratercula arctica*, European Storm Petrel *Hydrobates pelagicus*, Manx Shearwater *Puffinus puffinus*), but due to the difficulty of observation inside the burrows, these species were not included in the present study. Similarly, at the other extreme, the presence of the Atlantic Gannet *Morus bassanus* was recorded, but due to the completely open nesting sites, geomorphological study was obviated. The remaining ledge-nesting seabirds comprised four species: Common Guillemot *Uria aalge*, Razorbill *Alca torda*, Northern Fulmar *Fulmarus glacialis* and Kittiwake *Rissa tridactyla*.

Of the four chosen species, none are agile on land. All normally lay only one egg per season, except kittiwakes which can lay up to three. Guillemot and Razorbill exploited both ledges (90% for Guillemots, 50% for Razorbills) and cavities; only the nests on ledges were included in the present geomorphological analysis. Guillemots are large seabirds (approx. 1 kg, 38–45 cm in length, 60–74 cm wingspan, which lay eggs directly on the supporting surface. Razorbills are

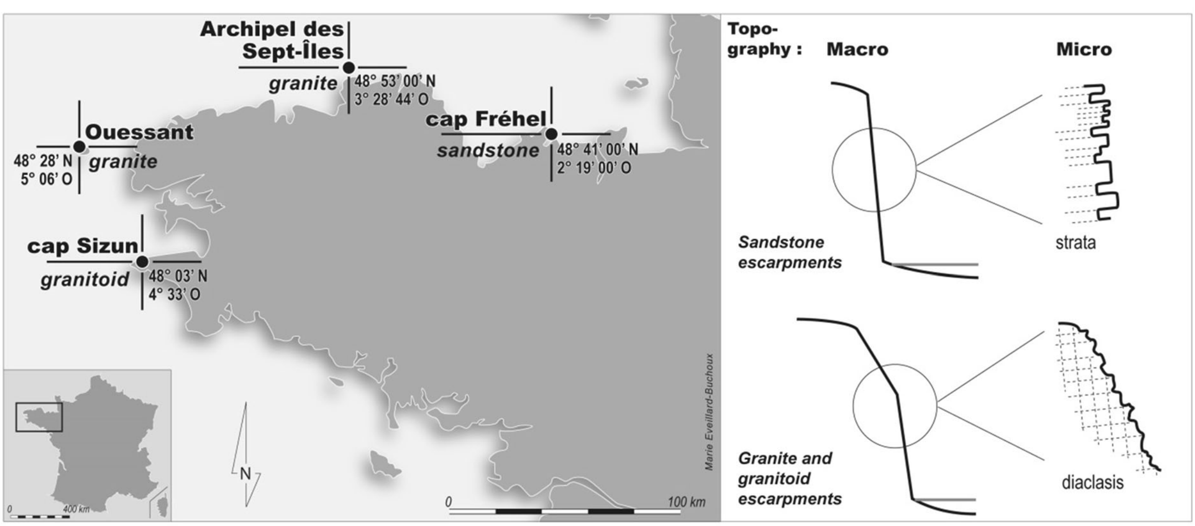

Fig. 1 Maps showing location of study sites in Brittany, France, and main geomorphologic characteristics for nesting: macro and micro-topography

somewhat smaller, at approx. 700 g, 37–43 cm length, 60–69 cm wingspan, with very cursory nests. Fulmar are close in size to Guillemot, at approx. 0.8–1 kg, 43–52 cm length, 100–117 cm wingspan, and very primitive nests. Kittiwake are the smallest of the four species, at approx. 300–500 g, 37–42 cm length, and 93–108 cm wingspan; in contrast to the other chosen species, kittiwakes construct elaborate nests from dried algae and terrestrial vegetation (Bedard 1985; Shealer 2001; Peterson et al. 2010; Svensson et al. 2015).

Characteristics of nesting sites

Nesting sites were initially identified from photographic surveys. For most locations, archive material was available for this purpose from the naturalist organizations 'Bretagne-Vivante' and 'Ligue de Protection des Oiseaux' (the French representative of Birdlife International), and original photography was performed at the remaining locations. Close-up images were obtained either by approaching the individual nests (where possible) or by long-range photography using a Canon EOS 500 with Sigma 150–500 f5-6,3 APO DG OS HSM. Nest site description was perfomed both *de visu* and from the photographs. The following geomorphological criteria were recorded for each nest site (Fig. 2): vertical position on the cliff, type of ledge, and degree of enclosure (number and orientation of enclosing surfaces). Percentages of nests presenting each of the criteria were calculated. A scoring system was devised to quantify the degree of enclosure, wherein points were incrementally attributed for increasing degrees of enclosure by both the nest site ceiling and side walls (see Fig. 2 for visual depictions of these terms).

Ledge considerations

Previous studies have highlighted the importance of ledge characteristics to seabird reproductive success (Birkhead et al. 1985; Harris and Wanless 1988; Olsthoorn and Nelson 1990; Gilchrist and Gaston 1997; Harris et al. 1997; Gilchrist et al. 1998; Mallory and Forbes 2011). The ledge is obviously a *sine qua non* requirement for all non-burrow vertical cliff-face nests; however, over the course of the extensive field work of the present study, it became apparent that accurate, objective, physical characterization of ledges was beyond the techniques currently available. It was thus decided that the only reliable ledge characteristic was the presence or absence of a stoop (a small, forward-projecting, lower 'step'), and that further interpretation of nest site characteristics should be based solely on vertical position and degree of enclosure.

A total of 1048 nest sites were examined (see Supporting Information Table S1), over three breeding seasons, from 2013 to 2015. The relatively small number of Razorbill nesting sites reflects the scarcity of this species on the Brittany coast (approx. 50 couples—Cadiou et al. 2015).

Results

Vertical distribution

While Kittiwake nests could be found throughout the vertical range, most nests were situated in the mid-level (43%) or low-level (40%) of the cliff formations. A small number of Kittiwake nest sites were observed at 3–5 m above sea level, some of which were destroyed during spring storms. Fulmar nests were located throughout the top half (49% at the highest level and 46% at the middle level), with some Kittiwake and Fulmar nests adjacent to the clifftop, and most located approx. 6 m below the clifftop. Razorbill and Guillemot nests were located in the bottom half of the vertical range (62 and 57%), although not as close to sea level as some Kittiwake nests (Fig. 3).

Nest site geomorphology: presence-absence criteria

All nest sites could be initially characterized according to the geomorphology of their front. Most Kittiwake, Guillemot, Razorbill and Fulmar nest sites presented a front precipice, while a small number had a front stoop, itself usually occupied by another nest. Nests could then be further characterized according to presence-absence enclosure criteria, i.e. presence or absence of a ceiling, and back and side walls.

All nest sites had ledges abutting the back wall of the nest site, which could be enclosed by a ceiling and/or by right and left side walls (see Supporting Information Fig. S1). It was not possible to further

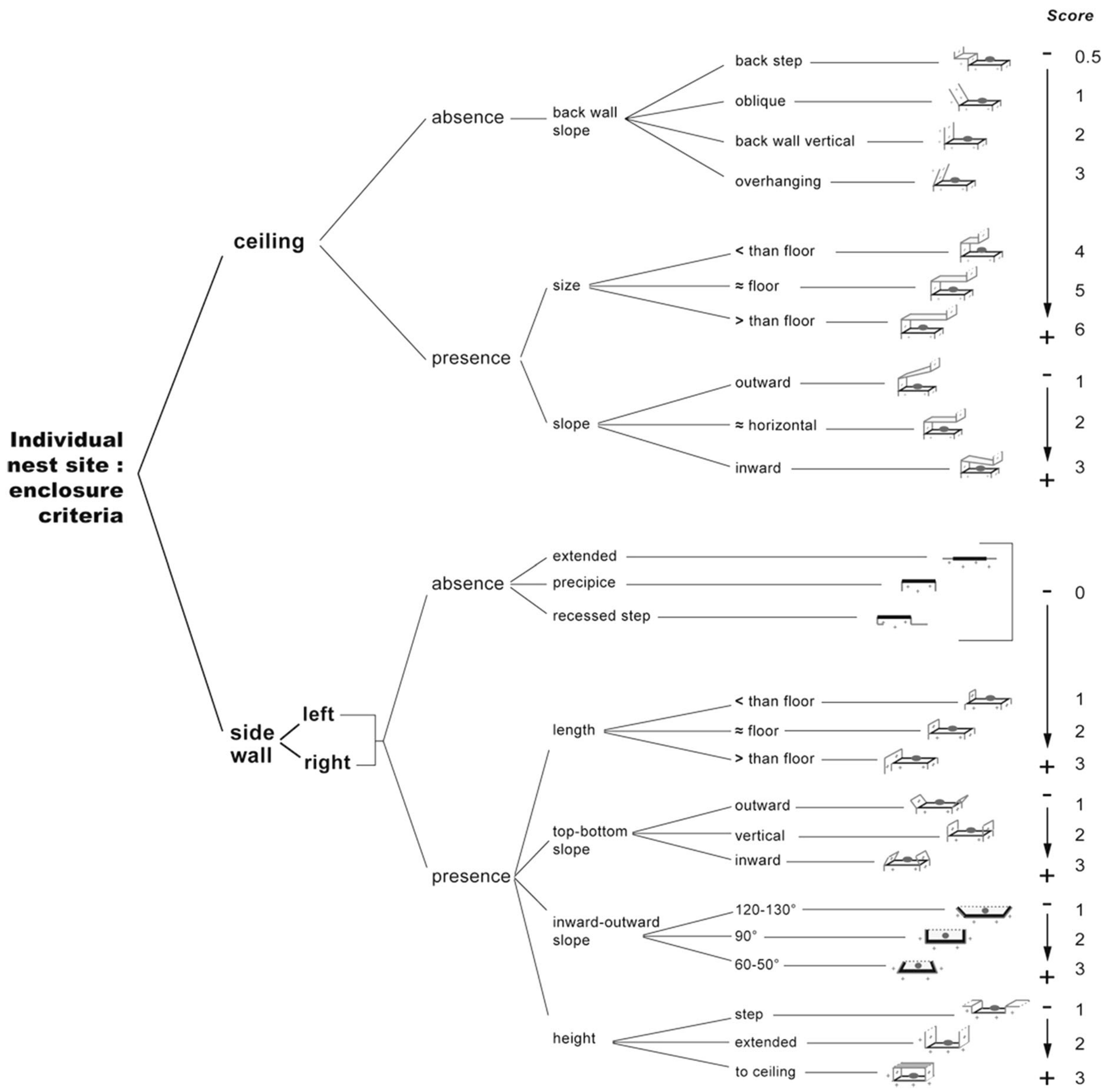

Fig. 2 Nest site enclosure criteria and scoring method

detail the ledge characteristics (slope etc.), since there were often old or occupied nests obstructing the view, and parallax problems were acute.

Most Fulmar and Kittiwake nest sites lacked ceilings (present at 18 and 16% of all nest sites, respectively); whereas ceilings were more frequently present at Guillemot and Razorbill nest sites (39 and 62% of all nest sites, respectively—Fig. S1A). Species nest sites were further differentiated according to their side walls: most Guillemot nesting sites had none (73%), whereas the most common situation for Fulmar (55%) and Kittiwake (46%) sites was one side wall, and the most common situation for Razorbill sites was two walls (45%—Fig. S1B).

Nest site geomorphology: ceiling characteristics

Characteristics of the ceiling size and slope are shown in Supporting Information Fig. S2 A and B. A distinct trend was evident with respect to ceiling size:

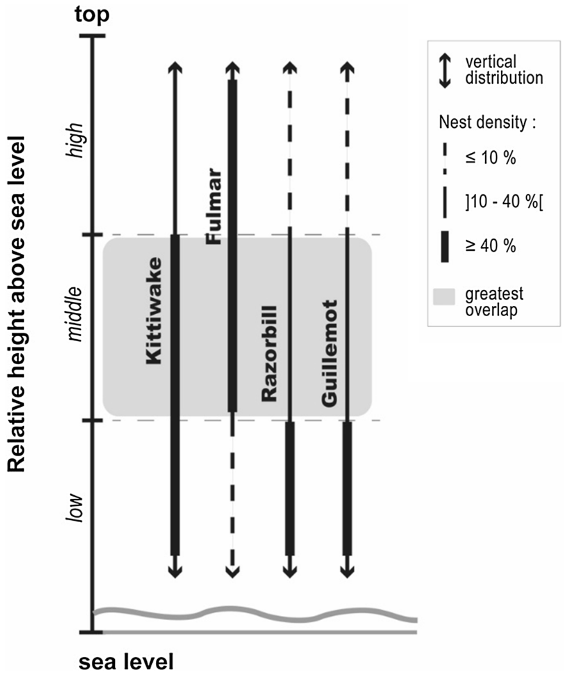

Fig. 3 Seabird nest—site vertical distribution

Razorbill + Kittiwake > Guillemot > Fulmar. An opposite sequence was observed with respect to ledge size compared to ceiling size (Fig. S2A). Two distinct trends were also evident with respect to ceiling slope. For horizontal preference, Razorbill > Guillemot > Kittiwake > Fulmar. For outward slope preference, Fulmar > Kittiwake > Guillemot > Razorbill (Fig. S2B). The dominant ceiling slope was horizontal for all species' nest sites except for Fulmar, which had an equal preference for both horizontal and outward slopes.

Nest site lateral characteristics

Nest site lateral characteristics could be grouped in the following categories: side wall close to nest location, precipice, extended lateral ledge surface, recessed step (Fig. S3). Side walls were most frequent for Fulmar and Razorbill (55 and 50%, respectively), whereas a precipice was most frequent for Kittiwake (39%) and an extended lateral ledge surface for Guillemot (67%).

Nest site geomorphology: side wall characteristics

When side walls were present, a distinct trend was evident with respect to the criterion 'side wall length > ledge length': Razorbill > Guillemot > Fulmar > Kittiwake. No distinct trend was observed for the less-frequent criterion: 'side wall length < ledge length' (Fig. S4A).

A distinct, dominant trend was also evident with respect to top–bottom slope (in relation to perpendicular from ledge): a vertical slope frequency was observed in the hierarchy Razorbill > Guillemot > Kittiwake > Fulmar. A minor inward frequency was observed in the hierarchy Guillemot > Kittiwake > Fulmar > Razorbill (Fig. S4B).

With respect to the side wall inward-outward slope, the perpendicular orientation was most often occupied by Razorbill, followed by Kittiwake and Fulmar. The opposite hierarchy was observed for an obtuse orientation (Fig. S4C). The degree of uncertainty in Guillemot observations precluded assigning formal values (this characteristic was often not discernable when observed from the foot of the facies).

With respect to side wall height, both Kittiwake and Fulmar were observed most frequently on sites with extended side walls, whereas Razorbills and Guillemots were most often observed at sites with lower ceilings (Fig. S4D).

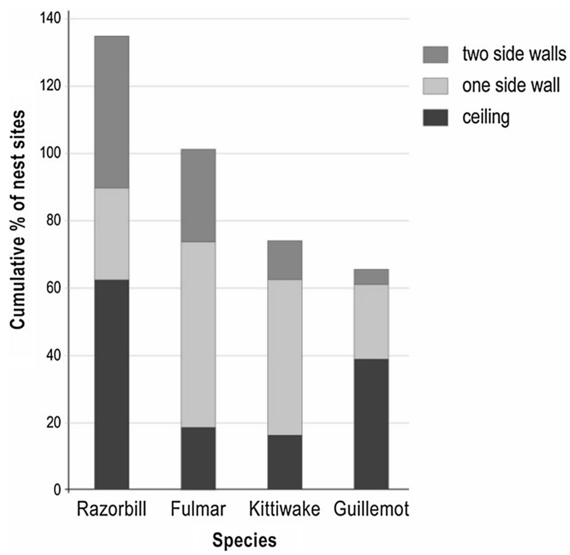

Fig. 4 Presence-absence enclosure criteria of nesting sites

Presence-absence enclosure criteria

Combining the results for the presence-absence enclosure criteria (Fig. 4), the most-enclosed nest sites were those of Razorbill (21% with ceiling and two side walls), while the least-enclosed nest sites were those of Guillemot and Kittiwake (< 5 and 8%, with ceiling and two side walls, respectively; 44 and 36% with no ceiling and no side walls, respectively). No dominant presence-absence enclosure characteristic was evident for Fulmars.

Scoring enclosure criteria

The results of the enclosure criteria scoring summarize and confirm those of the presence-absence criteria: Razorbill > Fulmar > Kittiwake > Guillemot.
Despite this hierarchical trend, the data also reveal a large degree of variability in enclosure tolerance for these four species (Fig. 5).

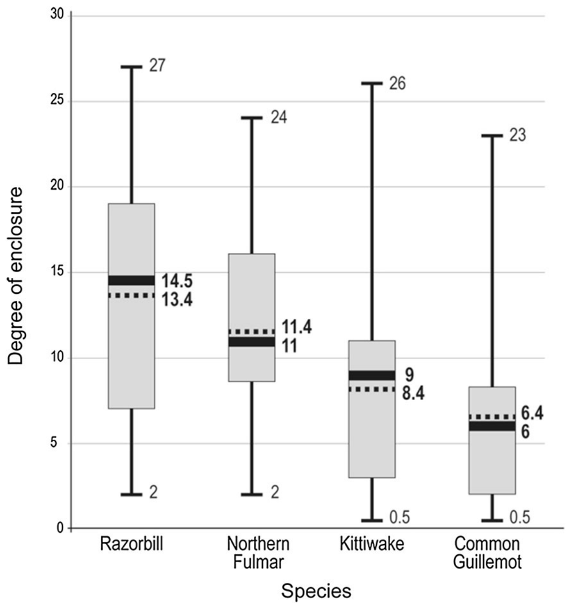

Fig. 5 Five-number summary plots for degree of nest enclosure scores. Dotted line = mean, solid line = median. Boxes represent the first and third quartiles, while whiskers represent the range values

Discussion

Vertical distribution of nest-sites

The results of the present study demonstrate species—specific nest-site cliff height preferences for the seabirds examined. Guillemot and Razorbill tended to avoid the highest reaches of the cliff, and Kittiwakes, although present in these areas, were also relatively rare. The upper cliff reaches are the most exposed to both terrestrial and avian predation (Harris et al. 1997; Massaro et al. 2001); indeed, breeding success in Guillemots has been shown to increase with distance from the cliff-top (Harris et al. 1997). Fulmars, well-known for their projectile vomiting defence mechanism, are less likely to be preyed upon, and this may explain why they are found mostly in the upper reaches of the cliff.

Degree of enclosure

The results of the present study confirm those previously, and succinctly, reported for Razorbills, Guillemots, and Kittiwakes at the Bullers of Buchan cliffs in Scotland (Olsthoorn and Nelson 1990), and extend these results to the complete geomorphology of nesting sites. Most notably, degree of enclosure appears to be a discriminating characteristic of the seabird nest sites for the four species examined in Brittany, with a clear hierarchy of enclosure preference. At the extremes of this characteristic, it is possible to include four other species: the Atlantic Gannet, which was regularly observed to nest on open sites (enclosure score = 0); and the Atlantic Puffin, Manx Shearwater and Storm Petrel, which nest in extremely enclosed sites (burrows or crevices, enclosure score > 33). We may therefore construct a hierarchy of enclosure preference for all eight species in Brittany (Fig. 6).

Quantifying the degree of enclosure, either by presence-absence criteria or by scoring, allows a graded ecological interpretation of the relation between nest site geomorphology and species preference. On the one hand, the low degree of enclosure preference observed in the Guillemot allows a high density of nesting couples (73% of the couples in Cap Fréhel were observed to nest in very dense groups in the present study; see also Birkhead 1977, 1978; Birkhead and Harris 1985; Harris et al. 1996, 1997;

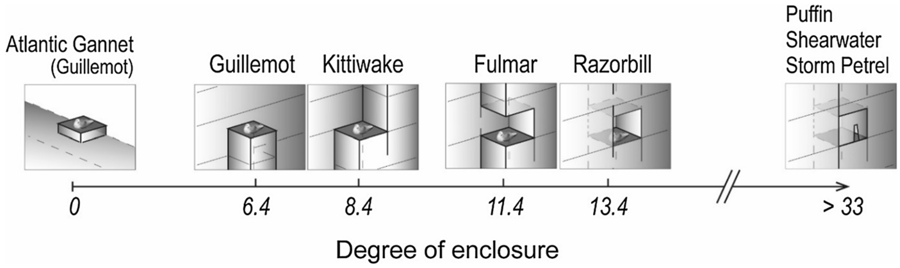

Fig. 6 Nest site enclosure score hierarchy, including extreme-scale Brittany seabird species

Kokko et al. 2004), increasing breeding success (Birkhead et al. 1985; Birkhead and Nettleship 1987; Olsthoorn and Nelson 1990; Hatchwell 1991; Harris et al. 1997). Similarly, high nest site densities in Kittiwake are correlated with fewer predatory seabird attacks (probably through more efficient predator alert and counter-measures—Cullen 1957; Birkhead et al. 1985; Gilchrist and Gaston 1997; Gilchrist et al. 1998; Regehr et al. 1998; Massaro et al. 2001). These observations mirror those found in continental cliff-nesting bird species (Anushiravani et al. 2016 (= Kestrel); Pfeiffer et al. 2016 (= Vulture); Lambertucci and Ruggiero 2016 (= Condor)). Moreover, it may be expected that larger seabirds such as the Atlantic Gannet, which require large landing spaces, will be virtually excluded from enclosed nest sites, and restricted to open sites, thereby also facilitating the social stimulation necessary for reproductive timing (Nelson 2002).

On the other hand, great degrees of enclosure may preclude high nesting densities, and may be expected to occur in less-gregarious species, such as Fulmars and Razorbills. Greater degree of enclosure is an alternate mode of protection from predation, which also provides increased protection from accidental falling for the eggs and chicks, and therefore contributes to greater reproductive success (Cullen 1957; Hudson 1982; Birkhead et al. 1985; Birkhead and Nettleship 1987; Mallory and Forbes 2011). Extreme enclosure is encountered in burrowing species, in which it has been suggested that reproductive success is linked to availability of suitable nest cavities (Ramos et al. 1997).

Despite a clear hierarchy of nest-site geomorphological preferences among the eight seabird species examined in the present study, a great degree of tolerance for nest-sites deviating from the 'most preferred' characteristics is also evident. For a large bird population, the number of geomorphologically 'optimal' sites is obviously more limited than the number of birds seeking such sites, and some birds will therefore choose sub-optimal sites, either due to competition or to differing proficiencies at evaluating nest site quality (Harris et al. 1997), and may even change sites over the course of the breeding season. This trade-off has been termed the 'win-stay, lose-switch' strategy (Kokko et al. 2004). These effects are more evident in nesting areas located well within the geographic limits of these species (e.g. Scotland, Iceland, Orkneys, Sheltands, Norway—see Eveillard-Buchoux et al. 2017), compared to the extreme margins of these geographic limits (e.g. Brittany). Similar observations have been made in Japan (Hasebe et al. 2012) and Maine (Parker et al. 2007). Appropriate nest site selection is obviously essential to reproductive success, especially in colonially-nesting species such as seabirds (Block and Brennan 1993; Jones 2001; Mallory and Forbes 2011); future studies could advantageously examine the relation between degree of deviation from the species geomorphological 'optimum' and reproductive success.

Nest-site geomorphology and seabird conservation

Seabirds are environmentally-emblematic organisms, important for their roles as ecological sentinels, in conservation awareness, and eco-tourism (Furness and Camphuysen 1997; Burger and Gochfeld 2004; Piersma and Lindström 2004; Frederiksen et al. 2007; Parsons et al. 2008; Mallory et al. 2010; Paleczny et al. 2015; Lindquist et al. 2016; Dunlop 2017), and the linking of terrestrial and marine ecosystems (Beninger et al. 2011).

Worldwide declines in seabird populations have been abundantly documented (Birdlife International 2004; Mitchell et al. 2004; Gilchrist and Mallory

2005; Ospar Commission 2010; Croxall et al. 2013; Paleczny et al. 2015; North American Bird Conservation Initiative 2016). The overarching importance of abiotic habitat characteristics in cliff-nesting bird conservation is widely recognized (Retief et al. 2013; Pfeiffer et al. 2016), and in particular the SNF (Ramos et al.1997; Mallory and Forbes 2011; Hjort et al. 2015; Lawler et al. 2015).

The results of the present study highlight the importance of cliff geodiversity to nest site choice in cliff-nesting seabirds. This geodiversity, in the form of SNF, constitutes a potentially crucial tool for the conservation of these seabird species, as has previously been suggested for continental cliff-dwelling species (Pfeiffer et al. 2016). In essence, cliff features may be evaluated for their suitability as nest sites for various seabird species. However, since nest site choice is necessarily effected by the birds themselves, special attention must be paid to nest sites previously occupied, and hence cliff formations, since there is a definite 'memory effect' (Harris et al. 1997; Kokko and Lopez-Sepulcre 2006). Colonization of new sites may be the result of overcrowding at, or forced displacement from, the favoured cliff formations (Danchin and Monnat 1992; Danchin et al. 1998; Nelson 2002), and it is the neighbouring, as-yet uncolonized formations, with their specific geodiversities, which may be most important conservation tools. New colonization is inherently risky for seabirds, and it may be possible to facilitate such colonization by the use of decoys on favourable cliff formations. Alternatively, in the absence of suitable neighbouring geodiversity, the installation of artificial nest sites with specific degrees of enclosure and ledge width may be explored.

Geodiversity, and especially SNF, are obviously important landscape features in habitats characterized by complex three-dimensional structure, exploited by species with precise small-scale geomorphological requirements, such as seabirds. Such small-scale landscape diversity is a *sine qua non* condition for population rebuilding and geographic extension in threatened seabird species (Parker et al. 2007; Hasebe et al. 2012) or even for threatened continental cliff species (Lambertucci and Ruggiero 2016; Pfeiffer et al. 2016). Although the present study focuses on the scale of the individual nest site, each site is just one component of the larger cliff facies, and, given the large degree of connectivity afforded by seabird flight, each cliff facies forms part of a much larger landscape unit. Indeed, it has recently been advanced that for oceanic seabirds, the entire European North Atlantic shelf system functions as one biogeographic spatial unit (Eveillard-Buchoux 2018).

SNF and seabird conservation

Although successful seabird conservation depends on many factors at multiple scales (Martin et al. 2007), the importance of geodiversity, and in particular SNF, has hitherto been overlooked. For threatened species which are highly dependent on SNF, it is thus of the utmost importance to identify and conserve suitable geodiversities, as an unconditional first step in biological conservation (Gray 2011, 2013; Hjort et al. 2015; Hunter et al. 2017). The data of the present study show that it is possible to fine-tune selection of site geodiversity for the SNF of particular seabird species, providing a new tool and opening a new avenue in seabird conservation.

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