

# Landscape features and sea ice influence nesting common eider abundance and dispersion

Keith G. Chaulk, Gregory J. Robertson, and William A. Montevecchi

**Abstract:** Factors that influence individual and colony spacing are still not well understood in many organisms. Common eiders (*Somateria mollissima* (L. 1758)) nest on coastal islands and forage in intertidal and shallow subtidal waters. We considered several biotic and abiotic factors, their interactions, and how these might influence the distribution of eider colonies at several spatial scales in Labrador, Canada. At the island level, nest abundance was not related to intertidal prey density. At the 104 km<sup>2</sup> grid scale, eider nest abundance and the coefficient of dispersion (CD; the variance to mean ratio of colony size or grid cell, where CD indicates population dispersion) were negatively related to the number of islands. Spring ice cover was positively related to the number of islands but was negatively related to eider nest abundance and to CD. Ice cover – abundance and ice cover – CD were significant at two spatial scales (104 and 455 km<sup>2</sup>, respectively), but other relationships were weaker at the larger spatial scale. We hypothesize that during the spring, archipelagos with many islands trap ice, providing terrestrial predators access to nesting islands by acting as bridges and that increased predation reduces habitat quality causing nesting eiders to disperse. Our findings suggest that eiders respond to landscape features, including ice cover, a feature that is being influenced by climate change.

**Résumé :** Les facteurs qui influencent l'espace des individus et des colonies restent encore mal connus chez de nombreux organismes. Les eiders à duvet (*Somateria mollissima* (L. 1758)) nichent sur des îles côtières et se nourrissent dans la région intertidale et les eaux peu profondes de la zone subtidale. Nous avons examiné plusieurs facteurs biotiques et abiotiques et leurs interactions afin de voir comment ils peuvent influencer la répartition de colonies d'eiders à différentes échelles spatiales au Labrador, Canada. À l'échelle des îles, la densité des nids n'est pas reliée à la densité des proies de la zone intertidale. À l'échelle d'une grille de 104 km<sup>2</sup>, l'abondance des nids d'eiders et le coefficient de dispersion (CD, soit le rapport variance à moyenne de la taille de la colonie ou cellule de la grille qui représente la dispersion de la population) sont en relation négative avec le nombre d'îles. La couverture de glace au printemps est en corrélation positive avec le nombre d'îles et en corrélation négative avec l'abondance des nids d'eiders et avec CD. Les relations de la couverture de glace – de l'abondance, ainsi que de la couverture de glace – de CD sont significatives à deux échelles spatiales (104 et 455 km<sup>2</sup>, respectivement), mais les autres relations deviennent plus faibles à l'échelle spatiale plus grande. Nous émettons l'hypothèse selon laquelle, durant le printemps, les archipels composés de plusieurs îles emprisonnent la glace, ce qui donne accès aux prédateurs terrestres en formant des ponts vers les îles de nidification; la prédation accrue réduit la qualité de l'habitat, forçant la dispersion des eiders en nidification. Nos résultats indiquent que les eiders réagissent aux caractéristiques du paysage, en particulier à la couverture de glace, une caractéristique qui est sous l'influence du changement climatique.

[Traduit par la Rédaction]

## Introduction

Many mechanisms influence the distribution of colonial species (Anderson and Titman 1992; Kaiser and Forbes 1992). Predator avoidance, increased vigilance, mating options, foraging opportunities and brood amalgamation have all been considered as possible benefits of group living (Powell 1974; Munro and Bédard 1977; Bertram 1978; Ainley

et al. 1995, 2003). However, many costs are also associated with group living, including disease transmission, brood parasitism, competition for mates and other resources, increased conspicuousness, and prey depletion (Ashmole 1963; Alexander 1974; Furness and Birkhead 1984; Birt et al. 1987; Cairns 1989).

Food availability is often seen as one of the most important factors influencing the distribution and size of bird colonies (Ainley et al. 2003). Furness and Birkhead (1984) and Cairns (1989) argued that food availability and competition were primary factors influencing the spacing of seabird colonies. However, for species that do not feed during incubation or that have precocial young, proximity to resources may be less important in the selection of nest sites.

Common eider (*Somateria mollissima* (L. 1758)) females do not feed during incubation (Milne 1976; Korschgen 1977; Parker and Holms 1990; Erikstad and Tveraa 1995) and experience extreme weight loss during incubation (Korschgen 1977). Christensen (2000) argued that the critical phases of eider egg formation occur just prior to laying,

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and if sufficient energy is not consumed, reserves may be insufficient for clutch formation. Yet, the demonstrated importance of food and habitat quality in the selection of eider breeding islands remains unclear (Christensen 2000). Schmutz et al. (1983) reported that food near breeding islands in Hudson Bay was unimportant, while in Europe the availability and quality of food near eider colonies is thought to substantially impact breeding success (Oosterhuis and van Dijk 2002).

Predation has also played an important role in the evolution of common eider nesting strategies (Quinlan and Lehnhausen 1982; Robertson 1995; Bolduc and Guillemette 2003). Prolonged nest incubation and fasting by eiders is also thought to have evolved to reduce predation by gulls and crows (Swennen 1983, 1989; Götmark 1989; Erikstad and Tveraa 1995). Furthermore, when approached by mammalian predators, incubating female eiders defecate on their nests to reduce egg palatability (Swennen 1968). In general, mammalian predators are sometimes considered to have a larger negative effect, because their presence often results in the decimation of all clutches in a colony (Goudie et al. 2000).

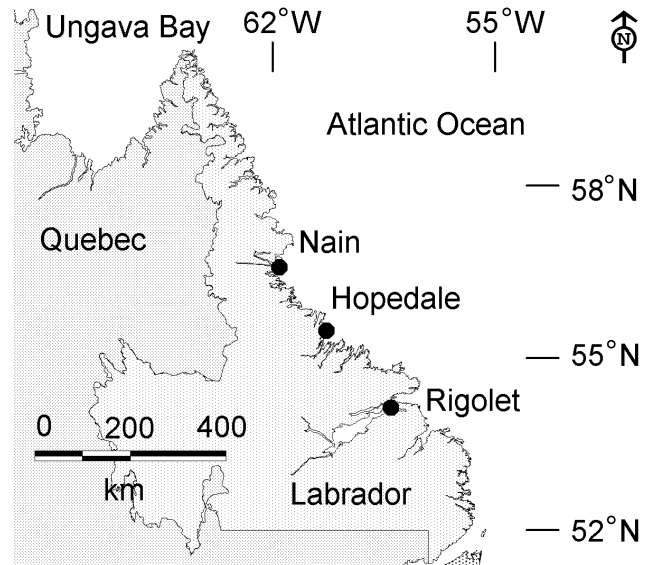
Huffaker (1958) suggested that populations in complex spatial environments persist in the presence of localized negative impacts (i.e., predators, disease) better than populations in continuous space. The reasoning is that discontinuous spatial arrangements act as barriers to the spread of the negative impacts (i.e., predators). In the context of nesting islands in northern areas, ice cover during spring can reduce spatial heterogeneity by increasing connectivity among islands for terrestrial predators (Parker and Mehlum 1991). Many researchers have suggested (although few have demonstrated) that eiders often delay nesting until ice bridges between islands and mainland have receded (Lack 1933; Ahlen and Andersson 1970; Quinlan and Lehnhausen 1982). Parker and Mehlum (1991) found that in years with late spring ice breakup, the number of available nesting islands was limited, resulting in higher nesting densities at ice-free colonies. Ice cover might also negatively influence habitat suitability by reducing access to nearshore foraging habitat, though Guillemette et al. (1993) reported that during winter, foraging eiders have a high threshold for ice obstruction.

We considered several biotic and abiotic factors that might influence the distribution of eider colonies in Labrador. We used intertidal sampling to examine relationships between resources and common eider abundance. We also used geographic analysis to explore relationships among landscape features (including ice cover), eider abundance, and dispersion at two spatial scales. We hypothesized that landscape continuity and heterogeneity might influence the size and distribution of eider colonies.

## Materials and methods

Archipelagos near the communities of Nain, Hopedale, and Rigolet in northern Labrador were surveyed for nesting common eiders between 2002 and 2003 (Fig. 1). All regions shared similar environmental characteristics, including a northern maritime climate. All three archipelagos are classified as coastal barrens (Lopoukhine et al. 1978) and are considered to have a high-boreal ecoclimate (Meades 1990) in a

**Fig. 1.** Study area for nesting common eider (*Somateria mollissima*) in northern Labrador, surveys conducted 2000–2003.



low Arctic oceanographic regime (Nettleship and Evans 1985). Islands in this region were typically barren with sparse vegetation composed primarily of mosses, lichens, forbs, and grasses, providing very limited nesting cover, so both hens and unattended nests were easily detected. Islands were originally selected for study based on random sampling (see Chaulk et al. 2004 for details), and island that were visited in more than 1 year were randomly chosen from the larger survey set (Chaulk et al. 2005). Eiders in Labrador typically nest on small barren islands, so we limited our searches to islands <30 ha (Chaulk et al. 2004). Ground censuses were conducted using standard search methods employed by the Canadian Wildlife Service (Nettleship 1976; Chaulk et al. 2004).

## Intertidal sampling

In 2003, we randomly selected a subset of previously surveyed islands, consisting of 27 islands in the three archipelagos. At these islands we sampled intertidal habitat and censused nesting eiders. Intertidal sampling was conducted between low and mid-tide only, primarily in the lower mid-littoral zone. Direction of movement around the island was chosen randomly by a coin toss. Four to nine rectangular quadrats (1280 cm<sup>2</sup> each) were sampled at each island (163 quadrats in total); in rare cases sampling was halted because of weather conditions or rising tide. Each quadrat was separated by ~20 m. Final location of each quadrat was determined by tossing the quadrat in the direction of movement. The purpose of this sampling was to assess broad-scale relationships between intertidal resource density and eider nest abundance.

Where possible all organisms in each quadrat were identified to species using field guides (Gosner 1978; Kavanagh and Leung 2001); if not, organisms were identified to genus or family. Percent ground cover per quadrat was estimated for most species; when possible, invertebrates were counted individually. Because of the three-dimensional nature of the sampling area, total combined ground cover could exceed

100%; however, this was rare. Throughout our analyses, we used average ground cover (or number of individuals) of intertidal species/island to compensate for unequal sampling effort, as the actual number of sampled quadrats varied per island.

In some cases, variables were log-transformed to normalize distributions. We used a general linear model (GLM) to test colony nest count (log) in 2003 against the density (log) of three intertidal species: blue mussel (*Mytilus edulis* L., 1758), common periwinkle (*Littorina littorea* (L., 1758)), and knotted wrack (*Ascophyllum nodosum* (L.) Le Jol.), which are important food sources for adult eiders and ducklings (Guillemette et al. 1992; Goudie et al. 2000; Hamilton 2000, 2001). We hypothesized that eider nest abundance would be highest in areas with highest prey densities (mussel, periwinkle) and (or) habitat features (knotted wrack).

### Coastal Landscape

To examine relationships with landscape features, we used common eider nest census data collected in 2002, our most intensive sampling year. Two rectangular grid systems were created: one grid was composed of numerous 104 km<sup>2</sup> cells (10 km × 10 km grid cells, with distortion due to earth curvature), and the second grid system was composed of numerous 455 km<sup>2</sup> cells (20 km × 20 km grid cells with distortion). Only cells containing three or more censused islands were used in the analysis; this was to ensure we had at least the minimum sample size needed to estimate the mean and variance of abundance; these statistics were then used to calculate the coefficient of dispersion (CD).

These two grid cells sizes were chosen to maximize both island and grid cell sample size. For example, grid cells smaller than 104 km<sup>2</sup> often meant that many cells contained less than three surveyed islands, while cells larger than 455 km<sup>2</sup> grid cells meant that the number of grid cells used in the total analysis was reduced. The grid systems were created using a spherical projection system and randomly superimposed on the surveyed islands in a geographic information system (Mapinfo 7.5). Structured query language was used to reduce the grid network to cells containing surveyed islands. Mean eider abundance was calculated based on colony sizes of censused islands within each grid cell, while the landscape features (number of islands, total shoreline) were based on all islands located within each grid cell. For the context of the analysis, colonies also include surveyed islands that had zero or one nest.

We used the simplest method to assess colony size distribution: the variance to mean ratio or the coefficient of dispersion (CD; Taylor 1961). CD was calculated by dividing the variance of colony sizes for surveyed islands per grid cell by the mean colony size (i.e., abundance) for each grid cell. When CD = 1 the distribution is random; when CD < 1 the distribution is uniform; when CD > 1 the distribution is aggregated. We used a GLM to test relationships between number of islands, eider abundance and dispersion. We hypothesized that eider abundance and dispersion would be negatively related to number of islands.

### Ice cover

A satellite photo (8 June 2002, Fig. 2) of the study area was downloaded in raster format and geo-referenced in

MapInfo (NASA 2002). This photo was selected because of geographic coverage and because the image date coincided well with the study and general eider nest initiation dates in northern Labrador (12 June ± 12 days, range = 21 May to 9 July; Chaulk et al. 2004). Ice cover was estimated at the two grid scales used to evaluate other landscape features (104 km<sup>2</sup>, 455 km<sup>2</sup>; see above).

The same grid systems described above were superimposed on the satellite image. Percent ice cover was estimated for each grid cell and was converted to total ice cover per grid cell in hectares (ha). Using GLMs, we tested whether ice cover was related to eider abundance and CD in 2002. We hypothesized that ice cover would be positively related to the number of islands within a given area and that eider abundance and dispersion would be negatively related to ice cover.

### General statistics

We used MINITAB 14 (Minitab, Inc. 2003) for all statistical testing and graphing. We used GLMs to test relationships between landscape features and eider population variables; all variables included were continuous, so essentially these tests were forms of regression. Scale (104 km<sup>2</sup>, 455 km<sup>2</sup>) was not considered in the models as a separate term, but rather they were analyzed separately to examine whether relationships across the two scales were comparable. When appropriate, we used a sequential Bonferroni adjustment (Rice 1989) for multiple tests. Residuals were checked for all models, and all tests were two-tailed with initial critical  $\alpha$  set to 0.05; all ± values are standard errors. To avoid confusion with the coefficient of dispersion in the text and tables, we use the term slope instead of the term regression coefficient ( $\beta$ ).

## Results

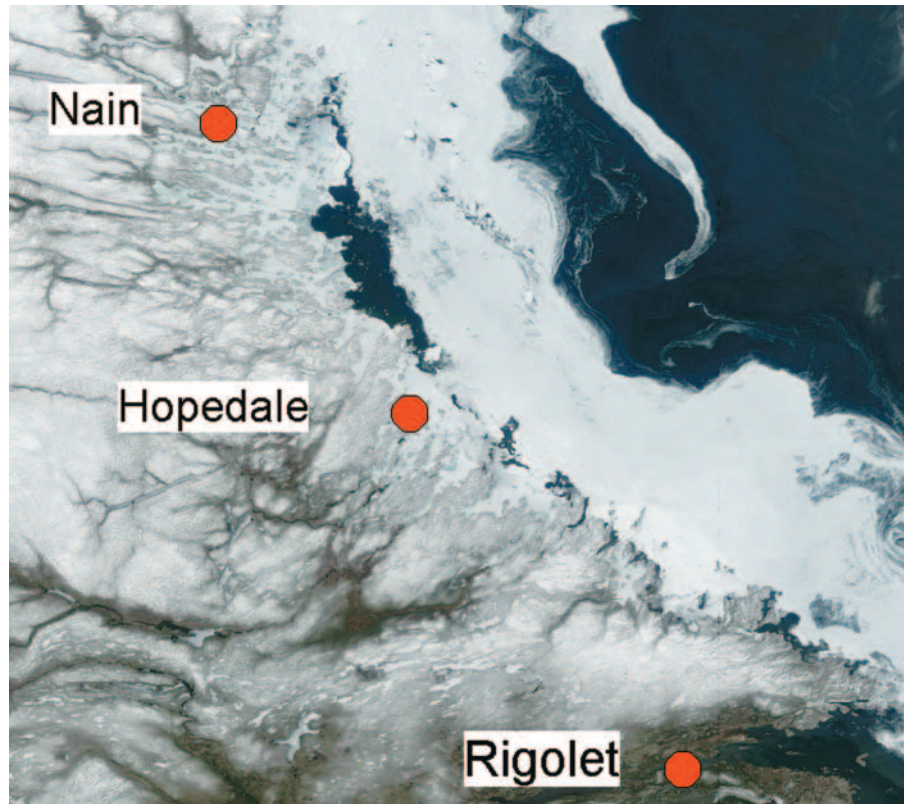
### Intertidal

Sampling effort and geographic coverage varied by study component (Table 1). In 2003, we sampled 163 quadrats on 27 islands and identified 19 species, 9 of which were found on two or fewer islands. The GLMs revealed that neither mussel, periwinkle, nor knotted wrack had a significant relationship with log of colony nest count (mussel:  $\beta = -0.10 \pm 0.14$ ,  $P = 0.47$ ,  $F_{[26]} = 0.54$ ,  $R^2 = 2.12\%$ ; periwinkle:  $\beta = 0.05 \pm 0.18$ ,  $P = 0.80$ ,  $F_{[26]} = 0.07$ ,  $R^2 = 0.28\%$ ; knotted wrack:  $\beta = 0.23 \pm 0.12$ ,  $P = 0.06$ ,  $F_{[26]} = 3.90$ ,  $R^2 = 13.50\%$ ).

### Landscape (104 km<sup>2</sup> scale)

In 2002, we sampled 89 islands within 18 grid cells at the 104 km<sup>2</sup> scale (Table 1). Not surprisingly, the length of shoreline and the number of islands in each grid cell were positively related (slope =  $0.96 \pm 0.16$ ,  $F_{[17]} = 33.9$ ,  $P < 0.001$ ,  $R^2 = 0.68$ ). To simplify the data presentation, we report tests based on the number of islands, but note that relationships with shoreline length were similar. We found a significant negative relationship between mean eider abundance and number of islands within a grid cell (Table 2; Fig. 3). We also found a significant negative relationship between the CD and number of islands, with dispersion becoming random (CD = 1) at the highest island densities

**Fig. 2.** Satellite image of the Labrador coast taken on 8 June 2002 (NASA 2002). Average eider nest initiation for this region is 12 June (see Chaulk et al. 2004).



(Table 2; Fig. 3). Also at the 104 km<sup>2</sup> scale, ice cover was positively related to the number of islands in a grid cell (Table 2; Fig. 3). We also found a significant negative relationship between mean eider abundance and ice cover in a grid cell (Table 2; Fig. 3). There was a significant negative relationship between CD and ice cover in a grid cell (Table 2; Fig. 3).

#### Scale effect

Using data from 2002 at the 455 km<sup>2</sup> scale, we ran the same analyses listed above. At this larger scale, two tests were significant. Ice cover was a significant negative predictor of mean abundance and CD (Table 2; Fig. 4). These findings suggest a scaling effect, with islands playing a more important role at smaller spatial scales and ice cover being important across spatial scales.

#### Discussion

It has been long recognized that physical landscape features influence animal and plant distributions (Wallace 1878). Yet there are few investigations on the role of the physical landscape with respect to the distribution and abundance of bird colonies. Findings from other bird species suggest geographic dispersion of colonies is not always the case (Ainley et al. 1995), but when colonies are dispersed these patterns are often explained by interactions with local food resources (Furness and Birkhead 1984; Cairns 1989) or site limitations (Kaiser and Forbes 1992).

#### Intertidal prey

Throughout the Subarctic, common eiders generally prefer to feed on blue mussel, but females and young often feed extensively on amphipods and periwinkles (Goudie et al. 2000; Hamilton 2001). Knotted wrack is an important habitat feature for ducklings, apparently because of increased prey abundance (Hamilton 2001). We found that eider nest abundance was not related to intertidal resource density. It is possible that during the prenesting period eiders overgrazed intertidal invertebrates around sampled islands, a form of prey depletion (Ashmole 1963; Birt et al. 1987). Alternatively, common eiders may not select breeding islands based on the local food supply. For example, preflight ducklings are known to follow hens to foraging areas that are located over 80 km from the nest (Cooch 1965). Posthatch dispersal behaviour may enable eiders to select nest sites on features other than proximity to food. It should be noted that the spatial (i.e., island) and temporal (i.e., 4 weeks) scale of our food study could have obscured relationships that exist at other scales and time periods.

#### Landscape and foraging

Deep water can reduce eider foraging efficiency especially for ducklings (Ydenberg and Guillemette 1991; MacCharles 1997), and a negative relationship between eider abundance and water depth has been previously suggested (Guillemette et al. 1993). Common eiders are generalists and typically feed at depths <10 m (Goudie et al. 2000; Larsen and Guillemette 2000) and at much less than that for

**Table 1.** Summary of sampling effort and major landscape features by study component for 2002–2003 among eider nesting islands on the north Labrador coast ( $\pm$ SE).

	Landscape and ice (2002)		
	Intertidal (2003)	104 km <sup>2</sup>	455 km <sup>2</sup>
Grid cell size	1280 cm <sup>2</sup>	104 km <sup>2</sup>	455 km <sup>2</sup>
Quadrats or grid cells	163	18	11
Islands surveyed	27	89	79
Islands in grid system		1 349	2 116
Average no. of islands		75 $\pm$ 36	192 $\pm$ 36
Average island area (ha)		1 548 $\pm$ 395	6 561 $\pm$ 1 988
Average mainland area (ha)		1 231 $\pm$ 487	15 239 $\pm$ 3 145
Average ice cover (ha)		7 928 $\pm$ 1 095	41 943 $\pm$ 1 607

**Table 2.** Summary of statistical tests, organized by spatial scale, predictor, and response.

Scale	Predictor	Response	Slope ( $\beta$ ) $\pm$ 1 SE	F	df	P	R <sup>2</sup>	Bonferroni sequence
104 km <sup>2</sup>	Islands	Abundance	-0.47 $\pm$ 0.16	8.5	17	0.010	0.348	5*
		Dispersion	-0.38 $\pm$ 0.13	8.0	17	0.010	0.333	5*
		Ice	75.81 $\pm$ 25.71	8.7	17	0.009	0.352	3*
	Ice	Abundance	-0.004 $\pm$ 0.001	15.6	17	0.001	0.494	2*
		Dispersion	-0.004 $\pm$ 0.001	43.0	17	0.000	0.729	1*
		Abundance	-0.06 $\pm$ 0.22	0.1	7	0.809	0.010	4
455 km <sup>2</sup>	Islands	Dispersion	0.02 $\pm$ 0.53	0.0	7	0.973	0.001	5
		Ice	-4.12 $\pm$ 14.87	0.1	10	0.788	0.008	3
		Abundance	-0.023 $\pm$ 0.006	13.4	7	0.011	0.691	2*
	Ice	Dispersion	-0.06 $\pm$ 0.01	28.5	7	0.002	0.826	1*

**Note:** For all models, we present the regression slope ( $\pm$  1 SE), degrees of freedom (df), and P values of tests. A Bonferroni sequence adjustment (Rice 1989) has been applied to the multiple tests shown in this table.

\*Indicates a significant test after Bonferroni sequence adjustment (Rice 1989). Note that the 104 km<sup>2</sup> scale was treated separately from the 455 km<sup>2</sup> in terms of the Bonferroni adjustment.

young eiders (Hamilton 2001). Given these factors, positive relationships between shoreline length, shallow foraging habitat, and eider abundance might be expected. However our data, at the scale of tens of square kilometres, suggest the opposite, in that abundance is negatively related to the number of islands and hence the amount of shoreline. These findings suggest that general landscape features, which are thought to be related to foraging habitat, can influence colony size, but not in the expected way. It should also be noted that water depth and subsurface contouring (bathymetry) likely influence foraging suitability. However, because of the limited quality and coverage of hydrographic charts for this remote region, we were not able to investigate the role of bathymetry as a landscape feature.

**Landscape and ice**

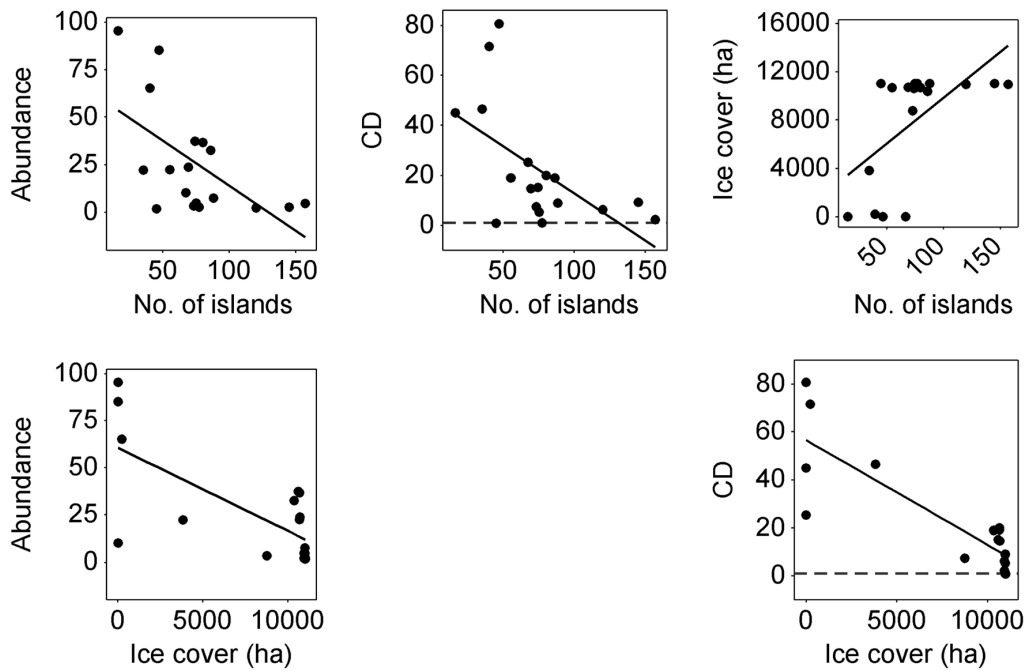
According to accounts by local residents of the Labrador coast, the spring of 2002 was an unusually heavy and late ice year. Preliminary analysis by the senior author of Radar-sat Images (provided by the Canadian Ice Service) for the 6-year period 1998–2003 support this finding (K.G. Chaulk, unpublished data). As such, 2002 is an ideal year for evaluating the impacts of ice on eider ecology, since any ice effects are likely to be most pronounced in heavy ice years.

In general, we found that the number of islands and ice

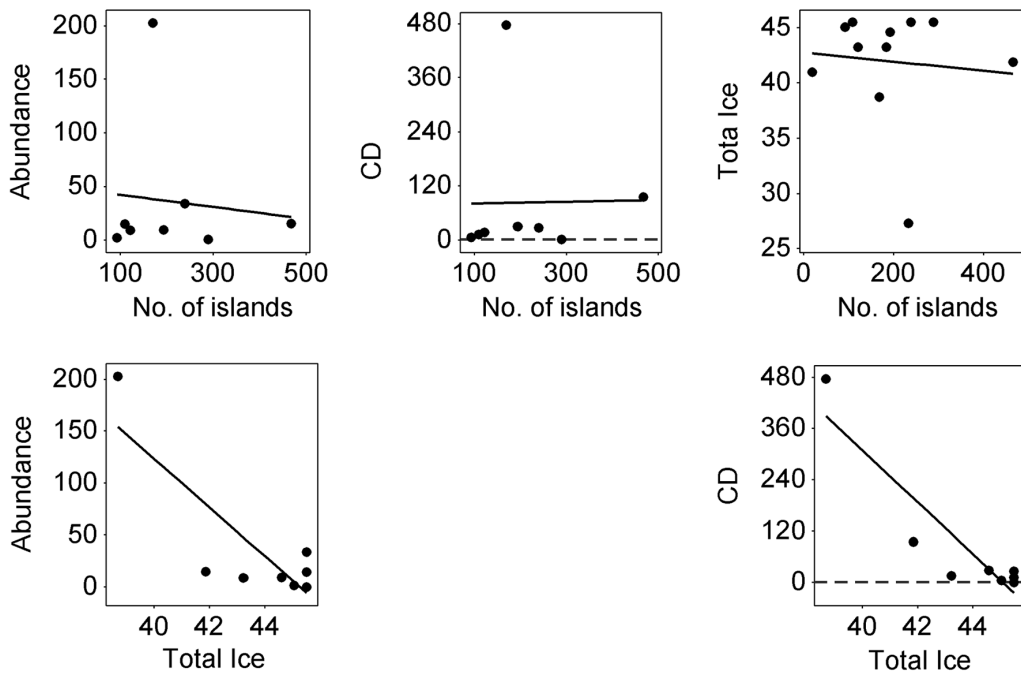
cover were negatively related to eider abundance and dispersion. Of these two predictors, ice cover was important at both spatial scales, while the number of islands was significant at the smaller scale. To explain why abundance is negatively related to island density and ice cover, we suggest several general explanations. First, we suggest that as the numbers of islands increase, so too does the tendency to trap ice. Increased ice in turn could reduce the overall attractiveness to nesting eiders, because ice bridges between islands and the mainland provide mammalian predators access to the nesting islands. Second, eiders are facultative colonial nesters, and as more islands are available and (or) as habitat quality declines, nesting females disperse, consistent with an ideal free distribution (Fretwell and Lucas 1970) or source sink population dynamics (Pulliam 1988).

In Finland, higher eider nest densities were positively related to island isolation, which in turn was related to reduced predation and earlier ice breakup (Laurila 1989). Parker and Mehlum (1991) reported that late breakup of sea ice limited the number of islands available for nesting, while Robertson (1995) found that nests on islands distant from the mainland were less likely to be depredated by arctic foxes (*Alopex lagopus* (L. 1758)). Johnson and Krohn (2002) investigated numerous habitat characteristics for nesting common eiders in the southern portion of their range.

**Fig. 3.** Relationships among landscape features, ice cover, and eider nesting abundance and dispersion. All data are based on 18 grid cells at the 104 km<sup>2</sup> scale, and ground surveys were conducted on the Labrador coast in 2002. In plots including the coefficient of dispersion (CD), the broken horizontal line indicates CD = 1, where the population is randomly dispersed.



**Fig. 4.** Relationships among landscape features, ice cover, and eider nesting abundance and dispersion. All data are based on 11 grid cells at the 455 km<sup>2</sup> scale; ground surveys were conducted on the Labrador coast in 2002. In plots including the CD, the broken horizontal line indicates a CD = 1, where the population is randomly dispersed. Total ice cover is in hectares × 10<sup>3</sup>.



They found that eider presence was positively correlated with distance to large islands (>50 ha) and with nest cover. These examples suggest that nearby landscape features can influence colony distribution and that reduced exposure to predators is important. The authors have noted four instances over the 6-year study period when signs of mammalian presence (bears, foxes, etc.) were associated with the decimation of individual eider colonies (K.G. Chaulk, unpublished data).

It should be noted that increased ice could be correlated with colder conditions and (or) reduced access to food resources. For example, heavy ice during winter is known to lead to starvation in eiders (Barry 1986; Fournier and Hines 1994) and has been suggested as a cause of population decline (Robertson and Gilchrist 1998). Similar processes could occur in response to heavy ice during the early nesting phases and could affect colony distributions. Unfortunately our study could not differentiate whether predation, colder conditions, and (or) reduced access to food were causing these landscape–abundance–distribution patterns; in fact all of these factors could play interactive roles. Regardless, landscape features, as they relate to the dynamics of spring ice breakup, appear to influence the abundance and dispersion of nesting common eiders. We suggest that our findings are consistent with early spatial models (Huffaker 1958) that demonstrated that landscape heterogeneity can have positive effects on population processes.

The behaviour of ice (trapped or deflected, land-fast or pack) relative to archipelago structure is influenced by many interacting factors such as temperature, wind, ice pan size, interisland distance, tides, and ocean currents. Therefore, heavy ice might not be expected in dense archipelagos every year. Furthermore, the type of ice (pack versus land-fast) may play important roles. For example, eiders may delay nesting in response to heavy land-fast ice; however, if sea conditions (wind and currents) cause pack ice to return, ice pans could act as bridges, allowing predators access to breeding islands. Therefore both intra- and inter-annual variation in ice cover could influence eider nesting patterns.

Alternating patterns of ice could change the attractiveness of a given archipelago to breeding eiders; this could lead to different nesting distributions across years and in some areas could reduce natal and breeding philopatry (Parker and Mehlum 1991; Bustnes and Erikstad 1993). These interactions are likely to be further complicated by the common eiders' tenacity to specific nest sites (Cooch 1965; Parker and Mehlum 1991). Consequently, over long time scales we predict the highest nest abundances in archipelagos with a combination of low average ice cover and low variance in ice cover during spring.

### Dispersion

CD was negatively related to the number of islands, meaning that when island numbers were low, eiders were highly aggregated, but at the highest island numbers, common eiders were randomly distributed. These landscape–dispersion patterns might be expected if colonial behaviour serves to reduce individual predation risk (Schmutz et al. 1983), but predation risk and subsequent antipredator strategies change with island density. For example, we suggest that terrestrial predators are likely to be of greater risk in high island density

archipelagos, because of increased connectivity, while at low island densities, avian predators, such as gulls, may be a greater threat and aggregated nesting may deter gulls from depredating nests (e.g., Kruuk 1964; Götmark and Åhlund 1984; Swennen 1989) or reduce predation risk through a dilution effect.

Such relationships are consistent with findings in Norway, where coloniality was found to be facultative, in that when more islands were available eider distribution increased, decreasing nest densities (Parker and Mehlum 1991). However these landscape–dispersion patterns might also be expected if eiders mirror the distribution of food resources, though we found no evidence for this. Finally, the dispersion patterns we detected could also arise if the island numbers directly influence distribution patterns by increasing the number of potential nest sites (Kaiser and Forbes 1992).

### Conclusion

We suggest that habitat quality decreases with island density because of bridging effects by ice and increased predator access. Overall, our findings suggest that landscape features influence marine bird distributions, but the relationship may not be as simple as expected, especially in high latitude regions where ice may play an important role. Studies involving sea ice effects on animal distributions will be of particular value in assessing the biological consequences of climate variability and change.

Our results have implications for the management of other gregarious organisms, especially in regions where habitat availability is low and colony size or population density are high. A key result is that habitat availability may not be a simple function of habitat area. Instead, availability may be mediated by spatial connectivity, especially in systems that are regularly influenced by predators, disease, and seasonal events such as fire or ice. In some southern portions of the eiders' range, spring ice may play a less important role, and this may explain why southern colonies tend to be very large, since the occurrence of ice and terrestrial predation may be less severe, although variation in the availability of nesting islands could also play a role in these regional differences (Brown and Bomberger Brown 2001). Our findings are highly relevant to considerations of ocean ice conditions and climate change, since links between animal ecology, climate change, and ice have been suggested for other species in northern marine ecosystems (Stirling et al. 2004).

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