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Changing distribution of flocking sea ducks as non-regenerating food resources are depleted

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ABSTRACT: Sutherland & Anderson (1993; J Theor Biol 160:223–230) considered how the distribution of consumers should change as prey resources fixed at the start of a period of exploitation are depleted by foraging activities. Their model predicts that consumers initially aggregate on a single or a few patches offering the highest feeding rate. As the prey density in those patches is reduced, the feeding rate declines to the level attainable at the next best patches, which are then also exploited. Therefore, an increase in the number of flocks and a decline in flock size should be observed as individuals spread out over the available feeding opportunities. Further, once occupied, a patch is exploited for the remainder of the winter. We tested these predictions with winter survey data on the number, size and location of flocks of common eiders *Somateria mollissima* and king eiders *S. spectabilis* wintering in Kvalsundet, a sound in northern Norway. Both species are benthivorous, and there is little or no growth or recruitment of their prey in winter at high-latitude sites. The green sea urchin *Strongylocentrotus droebachiensis* was the dominant prey of both species in Kvalsundet, and the density of this prey species declined over the winter in kelp beds, the preferred winter habitat of common eiders. Our data showed that both common and king eiders began their winter periods in Kvalsundet aggregated into a few large flocks. As the winter progressed, the distribution changed and birds gathered into more and smaller flocks. In the case of common eiders, flock locations remained fixed once a foraging location began to be exploited. King eiders formed a few large flocks early in the season which drifted in heavy tidal currents, but when these split up into smaller flocks in February, they started to exploit fixed locations. We interpret these results as consistent with the Sutherland & Anderson model.

KEY WORDS: Benthic ecosystem · Flocking behaviour · Distribution · *Somateria* · Foraging behaviour

INTRODUCTION

A central theme in ecology concerns the dispersion of consumers in relation to resources. Examples include territoriality, flocking, and the ideal free and ideal despotic distributions (Milinski & Parker 1991, Lessells 1995). Analyses of these situations usually assume, often implicitly, that resources are constantly input into the feeding system. For example, nectar in flowers is continually replenished, while in desert ecosystems, winds uncover seeds each day so that nocturnal rodents forage on a refreshed resource base each night (Ben-Natan et al. 2004). The distribution of foragers over the resource distributions can be predicted using established theoretical procedures and compared to observations. Less well studied is how the distribution of consumers changes in the common situation when resources are fixed at the start of a period of exploitation (e.g. winter) and are depleted by foraging activities. How does the distri-

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bution of the consumers change over time as the prey base is reduced?

Sutherland & Anderson (1993) developed a model of such a situation. To isolate the effect of depletion, they assumed that interference (which causes consumers to avoid each other) is low or negligible; that consumers are free to move between feeding locations; and that they have perfect knowledge of the feeding options available to them. Their model predicts that predators should initially aggregate in patches where the density of prey is highest, spreading out to occupy patches with successively lower prey densities as the prey density in the exploited patches is reduced.

In the present study, we measured the flocking behaviour of 2 species of benthivorous sea ducks (common eider *Somateria mollissima* and king eider *S. spectabilis*). Sea duck flock sizes are known to vary both temporally and spatially (Bourget et al. 1986, Guillemette et al. 1993, Bustnes & Systad 2001), but few attempts have been made to identify factors influencing flock dynamics of sea ducks (see Guillemette et al. 1993, Guillemette & Himmelman 1996). Prey of both species are patchily distributed (e.g. Guillemette et al. 1993, Bustnes & Lønne 1995, 1997, Hamilton 2000), and there is little or no growth or recruitment of their prey in winter at high-latitude sites (Guillemette et al. 1996). Several studies have demonstrated that eiders deplete their food resources over the winter, and eiders have been considered keystone predators in benthic communities (Guillemette et al. 1992, 1996, Bustnes & Lønne 1995, Hamilton 2000). Both king eiders and common eiders show great diet diversity, but often a few species dominate; i.e. in common eiders the blue mussel *Mytilus edulis* and the green sea urchin *Strongylocentrotus droebachiensis* are often high-volume prey, whereas in king eiders the green sea urchin and other echinoderms may dominate (Goudie & Ankney 1986, Bustnes & Erikstad 1988, Goudie & Ryan 1991, Bustnes & Lønne 1995, Guillemette et al. 1996, Hamilton 2000). Finally, interference is generally low among feeding sea ducks (Guillemette et al. 1993, 1996, Fox & Mitchell 1997a), so they appear to be species suited for testing model predictions.

The Sutherland & Anderson (1993) model predicts that upon arrival at the wintering site, birds feed in large flocks concentrated on the single or few patches offering the highest feeding rate. As the winter progresses, the prey density in those patches is reduced and the feeding rate declines to the level attainable at the next best patches, which are then also exploited. Therefore, an increase in the number of flocks and a decline in flock size should be observed as individuals spread out over the available feeding opportunities. Further, once exploitation begins, a patch is exploited for the remainder of the winter. We tested these predictions with winter survey data on the number, size and location of flocks of common and king eiders wintering in Kvalsundet in northern Norway. Kvalsundet is a narrow sound in which the number of eiders of both species was relatively constant over the winter (December to March) at the time of this study, except in the early fall and late spring (Bustnes & Lønne 1997, Systad et al. 2000). In addition, the underwater habitat use of the species was mapped, showing that common eiders forage mostly in kelp beds and more occasionally in other habitats, whereas king eiders feed mostly in open cobble/rock habitats (Bustnes & Lønne 1995, 1997). Moreover, since there are no large concentrations of blue mussels (mussel beds) in Kvalsundet, the most common prey for both eider species was the green sea urchin, comprising 30 % or more of the diet (Bustnes & Lønne 1995). Furthermore, monthly video footage of the same transects showed that urchin densities declined consistently over the winter in kelp beds heavily exploited by common eiders. Finally, it was shown that the diving effort (underwater time) of both eider species more than doubled from mid-winter until spring, suggesting that higher feeding rates were necessary as winter progressed (Systad et al. 2000). Hence, Kvalsundet is a good area for testing the Sutherland & Anderson (1993) model.

MATERIALS AND METHODS

The study area was in Kvalsundet, a sound near Tromsø, Troms County (69° 49′ N, 18° 50′ E), northern Norway, and data were collected during the winter of 1991 to 1992. Kvalsundet lies between the islands of Kvaløy and Ringvassøy. The study area is 7 km long, 600 to 2000 m wide, and about 9.6 km^2 in area, and the perimeter is entirely accessible by road (Fig. 1). Depths range up to 60 m. There are strong tidal currents, and the benthos consists of several community types. Due to the flow of the Gulf Stream, there is no winter ice formation in the main part of the sound. A full description is given in Bustnes & Lønne (1997).

In winter, Kvalsundet attracted up to 1000 common eiders and 1000 king eiders at the time of the present study (Bustnes & Lønne 1997, Systad et al. 2000). Common eiders foraged mostly in calm, shallow water (<10 m depth; mean diving depth 7.4 m), which in our case (see below) is distributed around the

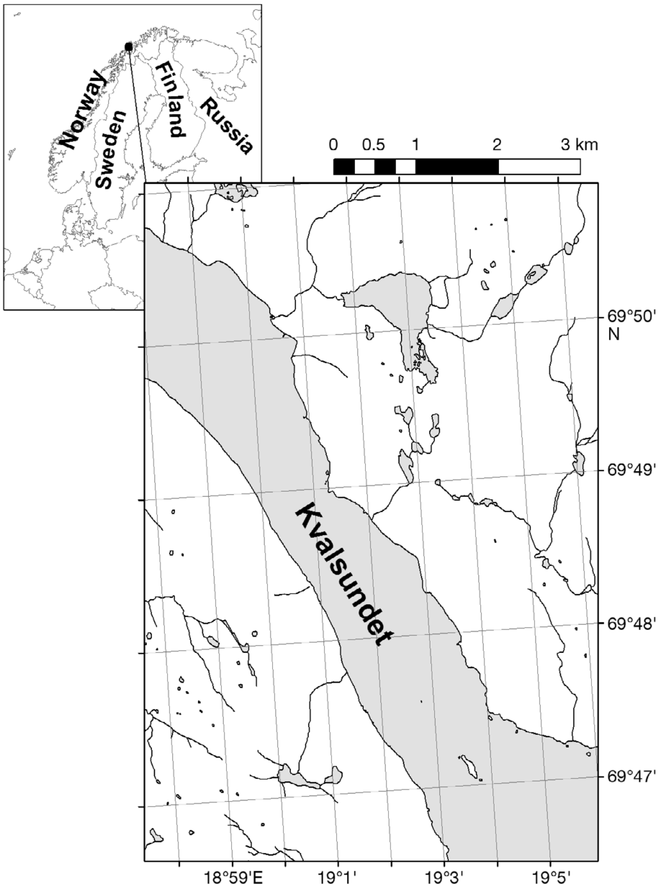

Fig. 1. Study area in Kvalsundet, northern Norway

perimeter of the study area. King eiders, in contrast, may dive as deep as 30 to 40 m (mean diving depth 20.4 m), in our study area located in the centre of the sound (Bustnes & Lønne 1997), where strong tidal currents may carry feeding flocks down the length of the sound; thus, while we expect that common eider flocks become fixed in location, the same should not necessarily be true of king eider flocks.

The diverse benthic habitats shallower than 10 m preferred by the common eider have an area of about 1.75 km^2, and the mean density during the winter of study was 347 birds km^{-2}. The density of king eiders during the same winter was on average 93 birds km^{-2} in the 6.8 km^2 of benthic habitat deeper than 10 m. Common eiders arrive in mid-September and leave in late April. King eiders arrive in early December and most have left by early April (Bustnes & Lønne 1997). However, for king eiders during our study, very few birds remained in April, and we therefore chose to remove the April data for king eiders.

Fieldwork was carried out from September 1991 to April 1992. Systematic surveys were made every second week from a vehicle, as the sound has roads close to the sea on both sides. All sea ducks were counted, and any aggregation (including lone individuals) distinctly separated from any other aggregations (~25 m), independent of density of birds within the aggregations, was considered a 'flock'. Mixed-species flocks were rare, but when encountered, we used the number of each species in separate analyses. Flocks were easily classified as feeding or non-feeding (resting, preening or swimming), as sea duck flocks generally alternate between bouts of feeding and resting (Guillemette 1994, Fox & Mitchell 1997b, Systad et al. 2000, Systad & Bustnes 2001). We used a detailed map and triangulation to assign the position of each observed flock to one of 957 blocks (1 ha each) covering the entire sound (see Fig. 1 in Bustnes & Lønne 1997). Flocks were observed from 2 points, with reference points on the opposite side of the sound (using a ruler on a map).

We used the following procedure to test whether flocks occupied a location continuously once it began to be used. We located for each flock on the nth survey the position of the nearest neighbouring flock on the following n+1th survey. The distance between these positions (called NNF for 'next nearest flock's location') was computed from the centres of the 1 ha blocks in which they were located. Thus, the centres of adjacent hectare blocks are 100 m apart, and the centres of cornering hectare blocks are 141.4 m apart. We compared the mean NNF measured on each survey with that expected if the positions of flocks were random on successive surveys.

To compute the random expectation, we took the number of flocks observed on survey n+1 and randomly chose (without replacement) that number of hectare blocks. We located the randomly chosen hectare block closest to that of each flock observed on survey n and computed the NNF for each flock. The actual NNF was then subtracted from the simulated NNF to calculate a difference in NNF. This procedure was repeated 10 000 times to generate a distribution of random NNF differences for each flock. The mean NNF difference for each flock from these 10 000 randomizations was extracted, and the distribution of these mean NNF differences was compared to see if it differed from 0. If flocks are positioned randomly on successive surveys, the difference between actual and simulated NNF should not differ from 0. However, if flocks tend to occupy (nearly) the same position on successive surveys, measured NNFs should be smaller than simulated NNFs. Because common eiders tend to congregate in shallow waters (Bustnes & Lønne 1997), we ran the above test procedure for both the whole sound and the depth zone <15 m. Simulations and statistical analyses were carried out using SAS (SAS Institute 2008).

RESULTS

A total of 9132 common eiders were counted on 14 surveys between 25 September 1991 and 23 April 1992. The data are summarized in Table 1. Numbers peaked during November to January (Fig. 2a). On average, 73.2% of the birds counted on a survey were in feeding flocks, and other than the low percentage recorded on the first survey (25 September), there was no seasonal pattern. The mean size (Fig. 2b) and the number of feeding flocks counted (Fig. 2c), however, both showed strong seasonal trends. Mean flock size declined steadily over the course of the winter ($r = -0.76$, $p < 0.01$) and number of flocks increased ($r = 0.74$, $p < 0.01$). The mean size of resting flocks also decreased, but the slope was shallower than that estimated for feeding flocks, and the correlation was weaker ($r = -0.59$, $p < 0.05$).

Common eider feeding flocks were positioned much more closely to the location of the nearest flock on the succeeding survey than expected on a random basis (Table 2). For example, 7 common eider feeding flocks were observed on the first survey, and the average distance from their positions to that of the closest feeding flock on the subsequent survey was 1318 m less than the distance to the position of the nearest randomly placed feeding flock. This difference was significantly negative on 12 of the 13 successive survey pairs. The result did not change significantly when restricting the analysis only to <15 m habitats (Table 2).

A total of 5487 king eiders were counted during 8 surveys (4 December to 22 March). The data are summarized in Table 3. Numbers peaked during November to January (Fig. 3a). On average, 77% of the birds counted on a survey were in feeding flocks, a value that remained approximately constant throughout the winter, although only 36% of the birds were feeding at the last count. The mean flock size (Fig. 3b) and the number of flocks counted both show strong seasonal trends (Fig. 3c). Mean flock size declined steadily over the course of the winter ($r = -0.74$, $p < 0.01$), while the number of flocks observed increased ($r = 0.96$, $p < 0.01$). The mean size of non-feeding flocks showed no seasonal trend (Table 3).

In December and January (Table 3), a few large flocks of king eiders fed in heavy tidal currents in the middle of the sound, and they were not observed at the same location on subsequent surveys (Table 4). In February, the large flocks split up into smaller flocks (Table 3), and for the next surveys (4 February to 4 March), the distances from the closest feeding flock on the subsequent survey were between 887 and 2000 m less than the distance to the position of the nearest randomly placed feeding flock ($p < 0.01$; Table 1). For the last survey, however, this distance was not significant (Table 4).

Table 1. *Somateria mollissima*. Number and size of common eider feeding and non-feeding flocks, in Kvalsundet, northern Norway, during winter 1991 to 1992

Date	Feeding flocks			Non-feeding flocks			Total	% feeding
	No. of flocks	No. of birds	Mean flock size	No. of flocks	No. of birds	Mean flock size		
25 Sep	7	158	22.6	20	392	19.6	550	28.7
11 Oct	15	340	22.7	8	173	21.6	513	66.3
26 Oct	13	544	41.8	13	93	7.2	637	85.4
13 Nov	25	752	30.1	17	137	8.1	889	84.6
4 Dec	25	739	29.6	8	134	16.8	873	84.7
18 Dec	24	846	35.3	6	35	5.8	881	96.0
8 Jan	27	760	28.1	11	124	11.3	884	86.0
21 Jan	23	315	13.7	22	234	10.6	549	57.4
4 Feb	28	555	19.8	14	181	12.9	736	72.4
19 Feb	34	726	21.4	14	82	5.9	808	89.9
4 Mar	41	435	10.6	29	330	11.4	765	56.9
22 Mar	23	239	10.4	18	215	11.9	454	52.6
6 Apr	26	266	10.2	22	131	6.0	397	67.0
23 Apr	32	175	5.5	6	21	3.5	196	89.3
Total	343	6850	21.5	208	2282	10.9	9132	73.2

DISCUSSION

Our data show that both common and king eiders began their winter periods in Kvalsundet aggregated into a few large flocks. As the winter progressed, the distribution changed and birds gathered into smaller flocks. In the case of common eiders, flock locations remained fixed once a foraging location began to be exploited, whereas for king eiders foraging positions were only fixed late in the season. We interpret these results as consistent with the depletion model of Sutherland & Anderson (1993), in which consumers initially occupy the best feeding patches. The result

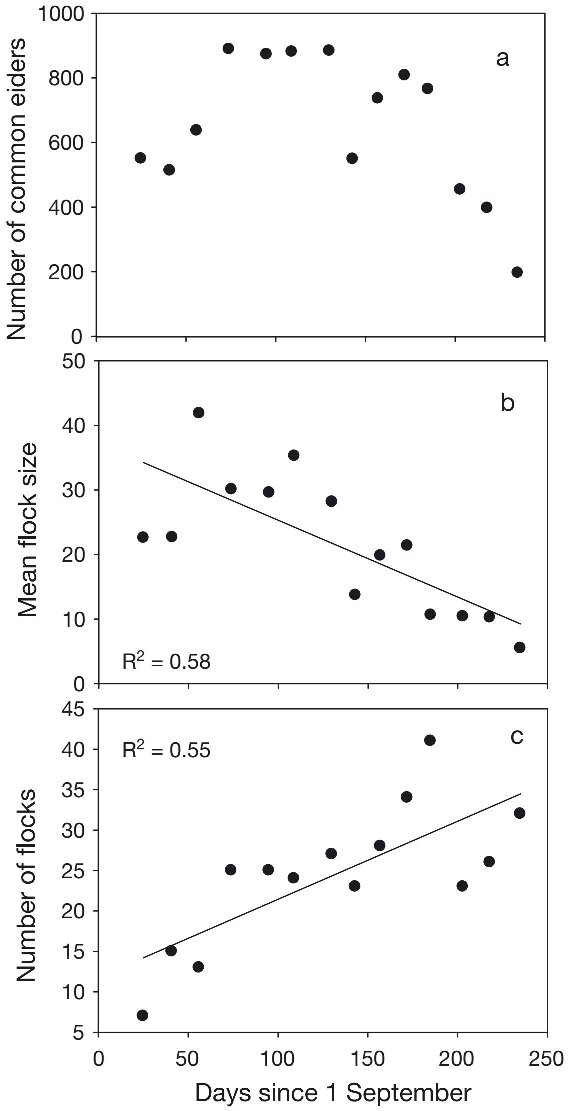

Fig. 2. *Somateria mollissima*. (a) Total number of common eiders, (b) mean size of common eider feeding flocks, and (c) number of common eider feeding flocks relative to number of days since 1 September. Data from 14 surveys in Kvalsundet, northern Norway, during winter 1991 to 1992 (see Table 1)

not predicted by the model (the random locations of king eider flocks on successive surveys in early winter) would seem to be accounted for by their habit of feeding in strong tidal currents, which transported flocks the length of the sound.

The eiders wintering in Kvalsundet match important assumptions of the Sutherland & Anderson (1993) model. Interference is low among feeding sea ducks (Guillemette & Himmelman 1996, Fox & Mitchell 1997a), so individuals influence each other mostly through exploitative competition, in which the consumption of food reduces the availability of food for conspecifics (Sutherland 1996). In Kvalsundet, eiders are free to move throughout the sound, as no territoriality or other aggressive behaviours of other eiders prevents them from feeding anywhere at all.

A strong, direct test of the Sutherland & Anderson (1993) model would measure prey density and feeding rate, predicting that these are highest at the start of winter, gradually fall as the winter progresses, and are equal in different patches. This was found in the classic work of Gibb (1958) on the predation by avian forest insectivores on *Ernarmonia* pupae. Gibb (1958) showed that the density of pupae was very unevenly distributed across blocks in the forest at the start of the winter, but by the end of the winter, density was overall lower and much more even over the study area. This arose because predation was more intense at high-density sites. However, measuring changing patch profitability in very complex benthic habitats such as those in Kvalsundet is extremely difficult due to the problems assessing availability and accessibility of large numbers of potential prey species (on the substrate, embedded in the substrate, under rocks, on kelp plants, etc.; i.e. dozens of potential prey species).

Nevertheless, many studies have demonstrated that feeding by sea ducks has profound effects on benthos populations, and wintering eiders seem to be particularly important predators (Guillemette et al. 1996, Hamilton 2000). The reasons for this are that the benthic invertebrates preyed upon by eiders neither grow nor reproduce during winter at these latitudes (Guillemette et al. 1996). Moreover, eiders have high energy needs when wintering in cold climates, and the prey have low energetic content; i.e. both molluscs and echinoderms mostly consist of exoskeletons that need to be digested by the ducks. As a result, eiders may consume 2 to 3 kg or more of benthos each day to meet their energy requirements (Bustnes & Erikstad 1990, Guillemette et al. 1992, Bustnes 1998). For common eiders in Kvalsundet, observations over the winter showed that 70% of the prey species brought to the surface were urchins (see Beauchamp et al. 1992 for methods). When including empty dives, urchins were brought to the surface in ~35% of the dives (n = 638; Bustnes & Lønne 1995), so the true urchin content in the diet may be as high as 40 to 50%. King eiders could not be observed from the shore, but in collected birds (n = 8), the green sea urchin was the most common prey species, making up ~30% of the diet (Bustnes & Lønne 1995). Based on calculations using energy requirements of the eiders

Table 2. *Somateria mollissima*. Feeding flock positions. Common eider feeding flocks are positioned much more closely to the location of the nearest flock on the successive survey than expected on a random basis. For example, on survey 1 (whole sound), 7 common eider feeding flocks were observed. The distance from their positions to that of the closest feeding flock on the subsequent survey is on average 1318 m less than the distance to the position of the nearest randomly placed feeding flock. The standard deviation in the next nearest flock's location of all 7 measured flocks is 1549, making the difference between the measured and randomly expected positions significantly less than 0. The procedure was run for both the whole sound and for habitats shallower than 15 m. See 'Materials and methods' for details of the randomization procedure

Survey	Whole sound				Depth <15 m			
	Frequency	Mean	SD	p	Frequency	Mean	SD	p
1	7	−1318	1549	<0.05	7	−1317	1548	<0.05
2	15	−142	294	<0.05	12	210	755	0.82
3	13	−4050	1519	<0.001	11	−4335	1321	<0.001
4	25	−833	1341	<0.01	22	−798	1333	<0.01
5	25	−1977	1616	<0.001	25	−1981	1620	<0.001
6	24	−1500	1941	<0.001	19	−1367	2052	<0.01
7	27	−1890	1678	<0.001	26	−1950	1676	<0.001
8	23	−1457	1859	<0.001	19	−1732	1938	<0.001
9	28	−2674	2210	<0.001	22	−2553	2190	<0.001
10	34	−2981	2206	<0.001	27	−2937	2174	<0.001
11	41	−728	1518	<0.05	38	−255	1300	0.12
12	23	−2715	1857	<0.001	20	−2772	1762	<0.001
13	26	−2075	2187	<0.001	25	−1998	2196	<0.001

and energy content of urchins, it was calculated that eiders removed between 6 and 16 urchins m^{-2} in Kvalsundet depending on size (15 and 25 mm test diameter, respectively; Bustnes & Lønne 1995). Moreover, high-resolution photographs showed that the density of visible urchins was much higher in open areas (cobble and bedrock) than in kelp beds but that most of the urchins were within the size categories eaten by eiders in both habitats (Bustnes & Lønne 1995). Furthermore, both eider species doubled their feeding effort (underwater time) from mid-winter to the spring, a strong indication that they needed to increase their search time for prey (Systad et al. 2000). Finally, video footage of a 150 m permanent transect in a kelp bed heavily used by common eiders (filmed monthly, 5 times) showed that urchin density dropped consistently over the winter (Bustnes & Lønne 1995). This made us conclude that common eiders, which preferred kelp beds (Bustnes & Lønne 1997), experienced prey depletion over the winter and that the flocking behaviour is consistent with the Sutherland & Anderson (1993) model.

In early winter, the king eiders fed in the middle of the sound and drifted in the tidal current, a pattern not predicted by the model. However, as the flocks split up and dispersed in February, flock locations remained more fixed once a foraging location began to be exploited. The differences between king eiders and common eiders may be caused by several factors. First, king eiders exploit a much larger proportion of the sound compared to the common eiders (~70 vs. ~30%, respectively; Bustnes & Lønne 1997) and in areas with much higher density of urchins and perhaps some other prey species. Hence, they may experience reduced prey densities later in the season than common eiders. Although a transect running through open king eider habitats did not detect consistent declines in urchin populations over the winter (Bustnes & Lønne 1995), the strong increase in feeding effort (increasing their underwater time from 57 to 161 min d^{-1}; Systad et al. 2000) strongly suggests that they experience prey depletion. In addition, other prey types are probably also important for king eiders, and they might have declined more consistently.

In the Sutherland & Anderson (1993) model, flocks occur because all individuals are free to move among feeding sites and aggregate on the relatively few sites offering the highest feeding rate. There is an assumption of low or no interference (i.e. individuals do not spread out to avoid each other), but assump-

Table 3. *Somateria spectabilis*. Number and size of king eider feeding and non-feeding flocks, in Kvalsundet, northern Norway, during winter 1991 to 1992

Date	Feeding flocks			Non-feeding flocks			Total	% feeding
	No. of flocks	No. of birds	Mean flock size	No. of flocks	No. of birds	Mean flock size		
4 Dec	4	271	67.8	2	84	42.0	355	76.3
18 Dec	6	812	135.3	2	22	11.0	834	97.4
8 Jan	10	502	50.2	1	70	70.0	572	87.8
21 Jan	9	869	96.6	6	45	7.5	914	95.1
4 Feb	10	680	68.0	16	270	16.9	950	71.6
19 Feb	17	715	42.2	12	165	13.8	880	81.3
4 Mar	18	416	23.1	21	165	7.9	581	71.6
22 Mar	21	145	6.9	25	256	10.2	401	36.2
Total	95	4410	61.3	85	1077	22.4	5487	77.2

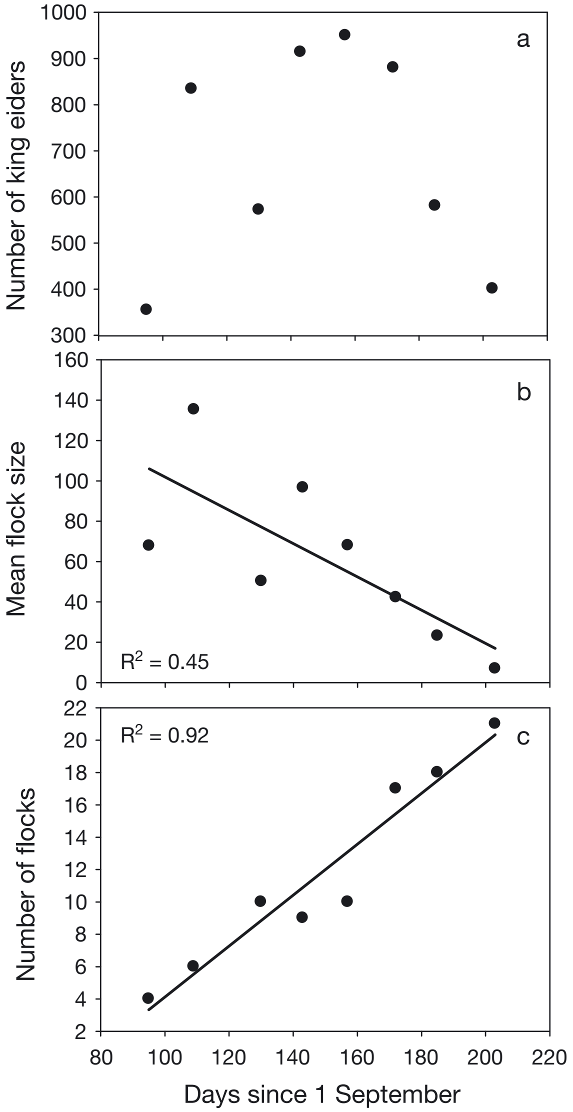

Fig. 3. *Somateria spectabilis*. (a) Total number of king eiders, (b) mean size of king eider feeding flocks and (c) number of king eider feeding flocks relative to number of days since 1 September. Data from 8 surveys in Kvalsundet during winter 1991 to 1992 (see Table 3). Counts made before king eiders arrived are not shown in the figure

Table 4. *Somateria spectabilis*. Feeding flock positions. King eider feeding flocks are positioned randomly with respect to the location of the nearest flock on the successive survey. For example, on survey 5, 4 king eider feeding flocks were observed. The distance from their positions to that of the closest feeding flock on the subsequent survey is on average 45 m greater than the distance to the position of the nearest randomly placed feeding flock. The standard deviation in the next nearest flock's location of all 4 measured flocks is 761, making the difference between the measured and randomly expected positions no different from 0. See 'Materials and methods' for details of the randomization procedure

Survey	Frequency	Mean	SD	p
5	4	45	761	0.54
6	6	359	230	0.99
7	10	−79	682	0.36
8	9	22	1057	0.052
9	10	−887	847	<0.01
10	17	−1736	1799	<0.001
11	18	−2000	1856	<0.001
12	21	−11	855	0.48

tions about other benefits of flocking for individuals, such as extra safety (so that individuals aggregate to gain these benefits), are not made explicit. Such flocking benefits might be important for sea ducks, as they are preyed upon by avian raptors (Watson et al. 1992, Sulkava et al. 1997, Lang et al. 1999, Stoeck 2000, Anderson et al. 2012) and possibly also by seals. Further, Guillemette et al. (1993) suggested that flocking in common eiders increased the ability of individuals to remain over profitable prey patches, as individuals alternate between diving and staying on the surface. Thus, there may be direct benefits to individuals from associating with conspecifics.

The fact that both common and king eider flocks became smaller and more numerous as the winter progressed indicates either that these benefits of flocking are unimportant in Kvalsundet or, more likely, that there are also costs to flocking that offset the benefits. For example, large flocks may attract kleptoparasitic gulls, forcing flocks to adopt defensive behaviours such as synchronised diving and surfacing, which reduce the attainable feeding rate (Schenkeveld & Ydenberg 1985). Interference in the form of avoidance manoeuvres (Beauchamp 1992) or spacing to access prey may become significant as food density declines, making smaller flocks better options.

LaCroix (2001) found that surf scoters *Melanitta perspicillata* wintering in rocky intertidal habitats in British Columbia foraged in large flocks on bay mussels *Mytilus trossulus*, which grow in discrete, densely packed beds. Flocks exploited a sequence of foraging sites over the course of the winter, completely stripping each site of all mussels over a few days or weeks. She provided evidence to support her hypothesis that this exploitation pattern was created by the dense packing and strong mutual byssal thread attachments that give bay mussels powerful communal defenses (see also Kirk et al. 2008). However, mussels are less well defended along edges and openings in the mussel mat; surf scoters forage along such openings, enlarging them and rendering the entire bed increasingly vulnerable, and the bed is then quickly consumed. This characteristic of these prey items therefore leads to a seasonal pattern of flocking very different from that observed in Kvalsundet.

Other factors may also affect the distribution of sea ducks. In a study of common eiders wintering in the St. Lawrence estuary in Canada, Guillemette & Himmelman (1996) concluded that the distribution of flocks over differently sized mussel beds was generally consistent with an ideal free distribution, although some beds were exploited less than expected and birds crowded into others. They suggested that higher predation danger in some patches led to lower usage. Guillemette et al. (1992) showed that variance sensitivity underlies the small flock sizes observed in one habitat type, in which eiders could forage for large though hard-to-catch prey (crabs). There are other, albeit probably minor, possible drivers of distribution of eiders over the course of the winter. One such driver is juvenile birds, naïve to the location, which preferentially join foraging flocks; as they become experienced with preferred foraging locations over the winter, however, they are less likely to congregate. The other is sexual behaviour; as courtship behaviours develop in the spring, birds may become more prone to isolate themselves.

In conclusion, the present study showed that aggregations of both king eiders and common eiders changed from a few large flocks to many small ones over the winter. For common eiders, the gradual expansion in patch use and depletion of green urchins in their main habitat was consistent with the predictions from the Sutherland & Anderson (1993) model. King eider distributions are probably also strongly affected by prey density, but this is more difficult to detect, as they feed in heavy tidal currents early in the season. Finally, aggregations of sea ducks are extremely vulnerable to a range of anthropogenic factors such as oil spills, fishing gear, habitat destruction and overfishing of shellfish, and the present study adds to the understanding of the critical factors influencing the size of aggregations.

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