*Wildfowl* (1973) 24:43–53

# A moulting population of non-breeding Mute Swans with special reference to flight-feather moult, feeding ecology and habitat selection

SVEN MATHIASSON

Mute Swans *Cygnus olor* are known to have gathered for moulting purposes in bays of the Swedish west coast during the 1960s (Mathiasson, 1973a,b). In 1971 the situation at the major moulting ground, Kungsbackafjorden (57.25N, 12.04E), was analysed in detail.

## General description of moulting flocks

From previous investigations (Mathiasson, 1963, 1973a,b) we know that the west coast gathering of moulting swans is an annual cyclic event. We also know that the range of these swans covers the coastal areas of the Skagerack-Kattegatt (including southern Norway, Jutland and the Danish Isles), middle and south-western Sweden (but not the eastern part of southern Sweden), and the westernmost part of the Baltic Sea (including the coasts of East and West Germany). The breeding area is restricted to the northern part, but wintering occurs all over the range. The moulting ground consequently forms a centre on which the non-breeding fraction of the geographic population concentrates once a year.

Six moulting grounds were found along the Swedish west coast in 1971 (Figure 1) with in all 1,572 non-breeding moulting swans.

The general build-up and decline of the moulting population at Kungsbackafjorden followed a normal curve (Figure 2). However, it was skewed towards the early part, indicating a rapid disappearance (between 3–9·8) of swans. The decrease in moulting numbers was more rapid in some haunts (Figure 1).

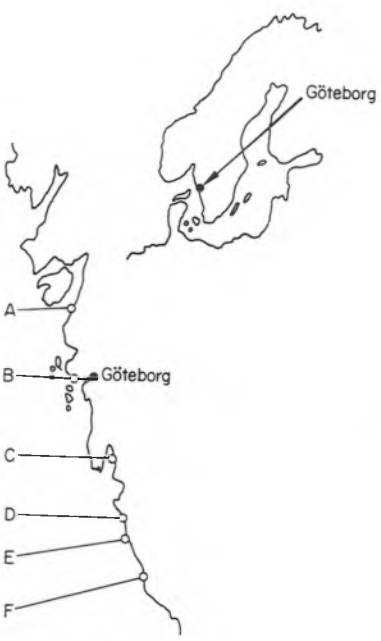
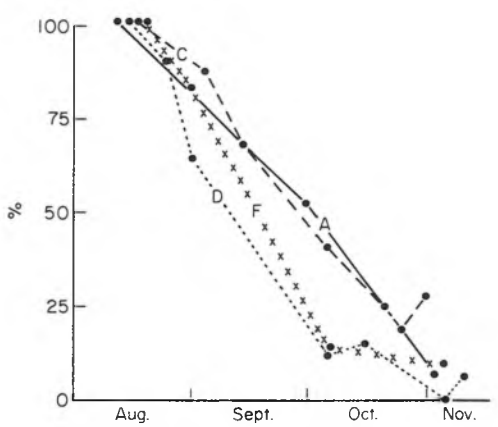



**Figure 1.** The moulting grounds (A–F) on the Swedish west coast. A, Ödsmals kile, 92; B, Torslanda, 220; C, Kungsbackafjorden, 921; D, Klosterfjorden, 93; E, Balgöfjorden, 63; F, Uteros-Lisereds skär, 183. The graph illustrates the decline from August to November (initial number = 100%).



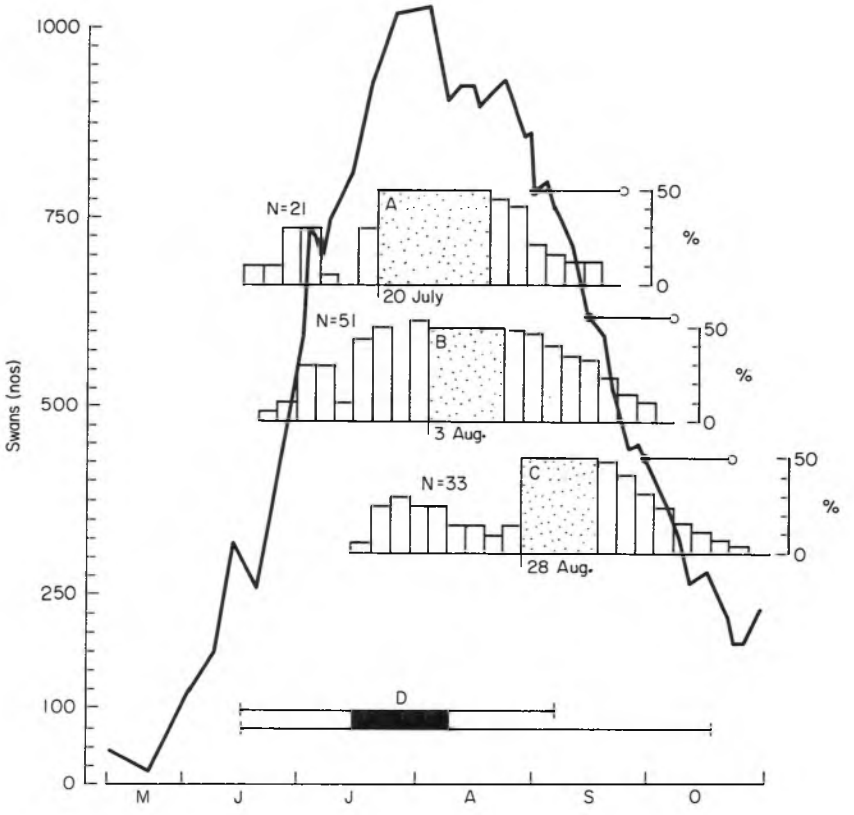



**Figure 2.** Numerical fluctuations (thick curve) of swans at Kungsbackafjorden. Diagrams A, B, and C illustrate the start of the moult and the regained ability to fly of samples of moulting birds caught on 20 July, 3 August and 28 August. The onset of moult in absolute numbers, in five day intervals is indicated to the left of the dotted central part which shows when the birds were still unable to fly. The right histograms present, in percent and pentads, the fractions of the population with fully grown flight feathers. To the right a ●, indicates all birds had regained their ability to fly; ○, that their flight feathers were full length. Diagram D shows (upper line) when birds started their moult, and the central black section when most did so. The lower line indicates when flightless birds occurred.

At Kungsbackafjorden, 138 swans were caught. All save thirteen (9·4%) were 2 years old or older. Twelve, previously ringed, had the following age distribution: 2 years, 1; over 3 years, 2; 5 years or more, 5; 7 years, 1; 9 years or more, 2; more than 10 years, 1. The percentage of males was: 68% ($n = 31$) between 5–21·7; 61% ($n = 51$) on 3·8; 64% ($n = 14$) on 17·8; 62% ($n = 40$) between 25–28·8. Calculations based on the sex ratio of birds starting their moult in different periods (Table 1) gave a male proportion of 65·8 for the same population. For later calculations of biomass an average of this value and that on 3·8 has been used, i.e. 63·3% males.

The stabilized July–August concentration had been 1,530 swans in 1970 whereas in 1971 there were only 939. The decrease can be explained in terms of reduced breeding in the summer of 1970 caused by the hard conditions of the preceding winter (Mathiasson, 1973a,b), which had the effect that sexually mature, but underfed swans which failed to breed joined the non-breeding, immature swans at the moulting grounds. The bad breeding success of 1970 is also reflected by the very low percentage of 1-year-old swans among the moulting swans of 1971 (only 9·4% against 29% on an average for the years 1964–1967).

In the early 1960s the Kungsbackafjorden moulting ground had more swans than nowadays (1961: 1,360 individuals;

**Table 1. Timing of started moults at Kungsbackafjorden moulting ground, calculated from the moult stage of swans caught**

| | 18–30 June | 1–15 July | 16–31 July | 1–15 Aug. |
|---|---|---|---|---|
| No. (and %) of started moults | 87 (9·8) | 209 (23·5) | 436 (49·0) | 157 (17·6) |
| No. (and %) of started moults of males | 46 (7·8) | 154 (26·3) | 305 (52·0) | 81 (13·8) |
| No. (and %) of started moults of females | 41 (13·6) | 52 (17·3) | 131 (43·7) | 76 (25·3) |
| Sex ratio (% males) of birds starting their moult | 52·9 | 73·7 | 70·0 | 51·8 |

1962: 1,850 individuals), the recent decrease is most probably explained by a shift of moulting ground (Mathiasson, 1973a,b).

The effect of different flock sizes on the behaviour of the moulting swans in respective years is poorly understood. We do not find any dead swans at the moulting grounds, not even when the moulting numbers reach their peaks. So either the food supply is superabundant or the birds are able to escape the 'moulting trap' (flightlessness for 5–6 weeks). On the other hand, the food supply may vary in abundance and availability and determine the numbers of moulting birds and their behaviour at an early stage.

## Moult

The moult is an annual cyclic event, which takes place in May (body feathers)–June–October (body feathers/flight feathers/tail feathers)–November (tail feathers/body feathers). The body feather moult often starts on the pre-moult haunts. The flight feather moult of non-breeding swans is normally performed at certain central moulting grounds, the breeding swans moulting at their breeding sites. The primaries are dropped some days before the secondaries.

The growth rates of the 5th primary and the 5th secondary of four swans (two males, two females) kept in captivity with superabundant food supply (*Zostera marina*, *Ulva lactuca*) were 5·5, 5·7, 5·9, 7·6 mm/day and 3·2, 4·1, 4·3, 5·8 mm/day. The growth rate of the 5th primary of three wild-living females at Kungsbackafjorden was 5·0, 7·4, 8·3 mm/day. The average growth rate of the renewed 5th primary is thus 6·5 mm/day ($n = 7$), the individual variation being rather large.

The longer primaries have a faster growth rate than the shorter secondaries so their replacement is synchronized. The growth rate of secondary 5th is 71·0% and its length is 70·2% of that of primary 4th! However, the 5th primary is full-grown in a day less than the 5th secondary (67 days in an adult male, having a 5th primary length 41·5 cm, against 66 days for the 5th secondary of 29 cm).

The length of the growing flight feathers (primary 4th) of 138 swans of the Kungsbacka-population was measured. Knowing the growth in mm per day, we are able to calculate when the flight feather moult started and when the flight feathers reached their full lengths.

Three diagrams (Figure 2A,B,C) give the essential information on the onset, continuation and termination of the moult in 1971. The flight feather moult started about 18–19 June. Of the swans which were moulting their flight feathers (and therefore unable to fly) on 3 August, 2% started the flight feather moult between 19–21 June (Figure 2B). On 3 August there were 890 unable to fly and an additional 183 flying. Thus, only 1·7% (eighteen birds) of that population started their flight feather moult between 1–21 June. Consequently, only 4·1% (eighteen out of 420 individuals) of the birds present at the moulting ground between 18–21 June were in flight feather moult at that time, against 83% of the swans present on 3 August.

Most birds started their flight feather moult between 14·7 and 7·8 (Figure 2 A,B), quite obviously with the culmination at the turn of the month. The first moulting swans regained their ability to fly around 3 August. But no less than 46% of the swans moulting flight feathers on 28 August had started the flight feather moult later than 3 August (Figure 2C). None of the birds which started their flight feather moult before 15 July (= 33% of the birds unable to fly in 3 August, i.e. 294) were caught on 28 August. That means that those birds had by then regained their ability to fly. The total number of swans present on 28 August was only about 914, which may imply that most (at least 159) of the 294 capable of flight had also left the moulting ground.

Sex distribution in samples of moulting

swans caught, indicate a stronger predominance of males in the moulting flocks at the beginning of the moulting period. More reliable, however, is the sex ratio of swans starting their flight feather moult in different periods, by calculating the start of the moult from the length of the 5th primary (Table 1). Between 18 June–15 July, almost an equal part of the males and females started their moults (34·1% of the males, 30·9% of the females). The culmination in 'started moults' occurred between 16 July–31 July for both males and females. In the period after the culmination, on the other hand. a higher proportion of the females than of the males started.

On 13 June there were 316 swans at Kungsbackafjorden–5 days later the first swan dropped its flight feathers. However, the increase in the number of swans actually unable to fly shows a 30 days' retardation compared to the influx of newcomers (Figure 3). The gap between arrival and

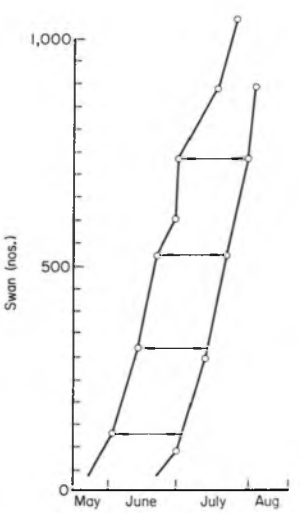



**Figure 3.** Increase in total numbers of swans at the Kungsbackafjorden moulting ground (left) in relation to numbers of swans having started their flight feather moult (right) at different dates in May–July. The arrowed lines indicate 30 days.

start of flight feather moult seems to be radically reduced (to 16 days) in the beginning of July.

The time required for the flight feathers of an adult male to achieve full length is calculated to be 66–67 days, for an adult female 6–7 days less. At least 55% of the males in a sample of forty swans caught between 25–28 August should have primary 5th 25–32 cm long. Actually there was only 4%. This indicates that the birds regain their ability to fly before the wing feathers are fully grown, when primary 5th reached a length of about 25–27·5 cm, i.e. 35–42 days after the start of the moult.

The number of swans at the moulting ground decreased in a clear relation to the time when the moulting swans regained their ability to fly (Figures 2 and 4). There was a clear tendency for more swans to depart sooner after they have regained their ability to fly in the beginning of the season than later (Figure 4). Thus, on 10

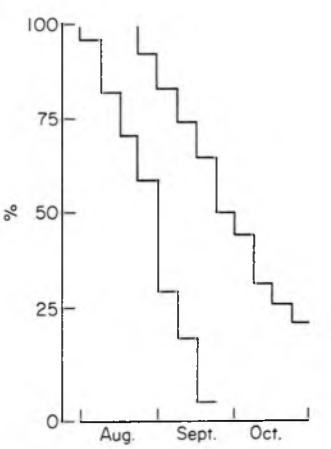



**Figure 4.** The relation between the decline in swans present at the moulting ground (right) and the fraction unable to fly (left). Expressed as percentages of numbers present in August.

September when all birds moulting on 3 August (890) had regained their ability to fly, 76% of the average August-moulting population was still on the moulting ground. The calculations indicate that all swans should be able to fly by 17 October. On 25 October all the 190 swans still in the haunt were indeed capable of flight.

There was a clear tendency for females to start the moult somewhat later than the males. This seems to be explained by the excess males (average sex ratio = 63·3% males) arriving at the moulting ground earlier in the season (males between 5 and 21 July = 68%). Of birds starting their moult between 1 and 5 July, 73·7% were males (cf. Table 1). However, in breeding swans the female is said to initiate the moult, the male not starting its moult until the female has completed hers, i.e. 6–8 weeks later (Hilprecht, 1970; Heinroth, 1928).

**Localization within the moulting ground**

The Kungsbackafjorden moulting ground is a sheltered coastal bay of about 53 sq. km. The shallow waters of less than 1·5-m depth provide accessible feeding places for the swans (cf. Figure 6). Under extreme low-water conditions some of the bottoms between 1·5 and 3·0 m are also accessible, extending the total feeding area to 21 sq. km.

We find (Table 2, Figure 5): haunt A was most important in May–June and again in October; haunt B was important all through the season, but especially in August–September; haunt C harboured most swans in July; haunt D was not used during May–August, but lodged comparatively high numbers in September–October; haunt E

**Table 2. Monthly and seasonal (22 May–31 Aug. 71) swan-days at different haunts in Kungsbackafjorden (see Figure 5)**

| Haunts | May | June | July | Aug. | Sept. | Oct. | Season |
|---|---|---|---|---|---|---|---|
| A | 280 | 3,060 | 4,538 | 576 | 5,157 | 3,664 | 17,275 |
| B | 220 | 2,088 | 2,681 | 11,044 | 8,839 | 2,644 | 27,506 |
| C | 160 | 2,147 | 14,501 | 4,716 | 1,000 | 316 | 22,840 |
| D | 0 | 516 | 3,983 | 11,079 | 1,129 | 204 | 16,911 |
| E | 0 | 8 | 1,004 | 1,690 | 1,868 | 347 | 4,917 |
| F | 30 | 7 | 0 | 0 | 1,440 | 1,335 | 2,812 |
| All | 690 | 7,826 | 26,707 | 29,105 | 19,423 | 8,510 | 92,261 |

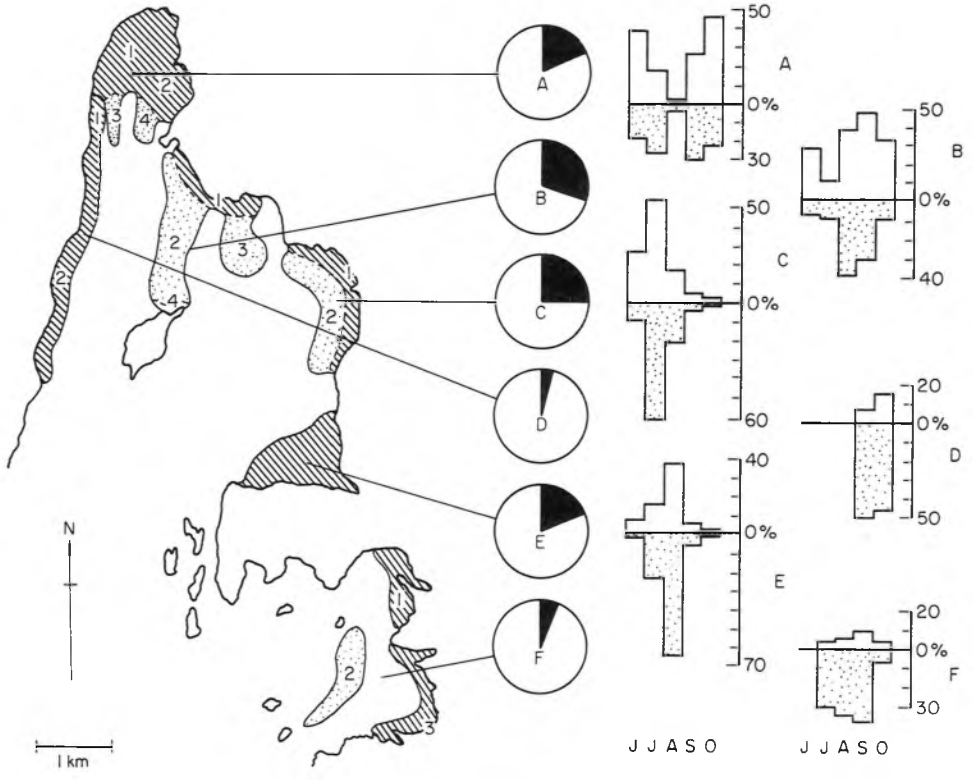



**Figure 5.** The Kungsbackafjorden moulting ground. The black sectors of the circle diagrams illustrate the proportion of the total annual moulting population (in swan units) which stayed at the different haunts. The histograms show (upper) the fraction of the monthly total of swan units at Kungsbackafjorden present at respective haunt, and (lower) the seasonal distribution of the total sum of swan units at the single haunts. See Table 2.

was dominant in August, haunt F was unimportant throughout the season.

The swans thus tended to move between haunts.

A comparison of the actual swan days for the shallow sections (high-water grazing areas = B1) of haunt B (cf. Figure 5) and those of the deeper sections (normal/low-water grazing areas = B2 and 3) for the period before the first extreme high-level situation (1·7–27·8) and after (28·8–25·10) gives the following values:

| | 1 July–27 Aug. | 28 Aug.–25 Oct. |
|---|---|---|
| Shallow sections Swan-days | 683 (7·0%) | 4,022 (33·1%) |
| Deeper sections Swan-days | 9,013 (93·0%) | 8,116 (66·9%) |
| Totals | 9,696 | 12,138 |
| Average depth and range at Forsbäck | 38 cm (18–57 cm) | 56 cm (25–100 cm) |

Thus, most swans occurred in shallow waters near the coast or in the shelf between Kalvö and the mainland (i.e. at depths less than 1·5 m). The normal low-water grazing area was favoured by the swans and formed their regular quarters (Figure 5). At high-water the swans moved to shallower sections close to the coast.

**Food and feeding habits**

The availability and abundance (biomass) of potential food organisms and the feeding technique of the swans limit the number of significant food organisms to the following: plants—*Zostera marina*, *Z. nana*, *Ulva lactuca*, *Enteromorpha intestinalis*, *Ectocarpus* sp., *Fucus vesiculosis*, and *Chorda filum*; animals—*Mytilus edulis*, *Cardium edule* and *Littorina littorea*. Figure 6 and Table 4 give the essential distribution of these species in the different haunts.

Feeding swans were specially observed with a telescope (× 25 or × 40) at certain haunts. The behaviour of the total flock at the location in question was noted, and as many birds as possible were individually checked for visible food items in the bill (Table 3). A clear preference was indicated for *Zostera marina*, which also entirely dominated the available crops of most haunts all through the moulting season. At high water levels and late in the season *Ulva lactuca* plays an important role. It must be stressed, however, that it was only possible to examine what was brought out of the water, and kept in the bill for a while, and also only items of a certain minimum size.

Samples of faeces were collected from the cloaca or rectum of thirty swans caught for ringing between 9 July and 6 September. Tissue fragments and cells were examined under the microscope. Two types of fragments dominated, *Zostera marina* (*nana*) and *Ulva lactuca*. The classifications were checked against fresh cell material collected at Kungsbackafjorden. Further, captive swans were fed the plants to provide faeces of known origin.

Technically it is difficult to distinguish between small cells of *Z. marina* and *Zostera nana*. However, *Z. marina* was completely dominant in twenty-four samples. Only in two samples could leaf fragments be referred definitely to *Z. nana*. Four samples had *Ulva* mixed with the *Zostera*. In most samples single threads of *Ectocarpus* sp. had obviously been consumed by accident when the swans were feeding on *Zostera*.

Four swans (three females, one male) were caught and killed. Throughout their alimentary tracts there was a predominant presence of *Zostera marina*. Thin threads of *Ectocarpus* sp. occurred in all specimens.

Four swans (two males, two females) were caught among the moulting swans at Kungsbackafjorden and brought to the Natural History Museum, where their food preferences were tested in a special basin offering eight choices (Figure 7 and Table 5). Again the indicated preference was for *Zostera marina*, with *Ulva lactuca* as second choice, in a series of fifteen experiments. The samples of these plants offered were nearly always totally consumed. This was also the case with *Zostera nana*. *Enteromorpha intestinalis* and *Ruppia maritima* were only partly taken when eaten at all. *Fucus vesiculosus*, *Chorda filum*, *Ectocarpus* sp. *Mytilus edulis*, *Littorina littorina*, *Cardium edule* were all ignored.

**Food consumption**

The daily (24 hours) food requirements of a moulting swan were determined for two males and two females individually under a superabundant food supply. As the moulting swans are unable to fly, and rather stationary, we may assume that in the test basin energy requirements do not differ too much from those under natural living conditions. The food plants offered were fresh, but blotted dry before weighing. Dry weight was determined after heating

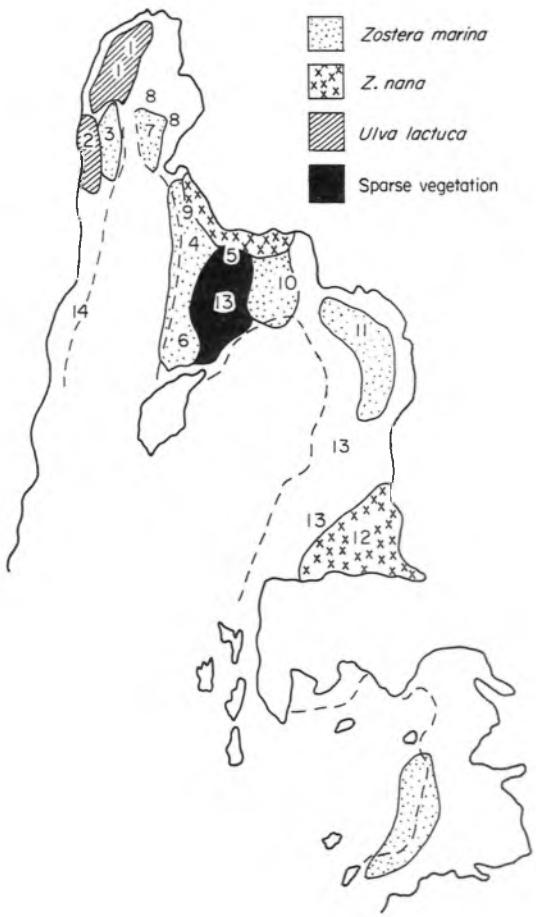



**Figure 6.** Food resources at Kungsbackafjorden. Areas below 1·5 m. water depth (broken line) have been investigated for the main distribution of the three dominant food items of the Mute Swans. The area of sparse vegetation is a shallow, sandy stony section. The figures refer to sample stations (see Table 4).

**Table 3. Observations on feeding swans and stated food items (see Figure 5)**

| Haunt | Date | No. of swans observed feeding | No. observed feeding on | |
|---|---|---|---|---|
| | | | *Zostera marina* | *Ulva lactuca* |
| A:4 | 2 July | 15 | 15 | — |
| B:2 | 5 July | 12 | 2 | — |
| A:3 | 9 July | 297 | 16 | — |
| C:2 | 9 July | 312 | 2 | — |
| B:3 | 15 Aug. | 235 | 3 | — |
| A:4 | 25 Aug. | 53 | 7 | — |
| A:3 | 10 Sept. | 216 | 9 | — |
| A:4 | 10 Sept. | 72 | 2 | — |
| A:1 | 22 Sept. | 148 | — | 2 |
| A:1 | 16 Oct. | 22 | — | 5 |
| A:1 | 16 Oct. | 97 | — | 1 |
| D:1 | 16 Oct. | 48 | — | 6 |
| A:4 | 25 Oct. | 89 | 2 | — |

**Table 4. Relative abundance of food organisms at sampling stations in Kungsbackafjorden (see Figure 6)**

| | Station | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| *Ulva lactuca* | +/++ | ++++ | — | | | | | + | | | — | | | |
| *Zostera nana* | | | | | | | | | | | | | | |
| *Zostera marina* | | | | | +++ | | | — | | | | ++++ | | |
| *Enteromorpha intestinalis* | — | | ++++ | +++ | | ++ | +++ | — | ++/++++ | ++ | + | | | |
| *Ectocarpus* sp. | — | | | | | | | — | | | | | | |
| *Fucus vesiculosus* | | | — | — | ++ | ++ | — | | — | +++ | ++ | ++ | ++ | |
| *Chorda filum* | | | | | | ++ | | | — | | | | — | |
| *Mytilus edulis* | | | — | | ++ | — | | | | +++ | | | | |
| *Cardium edule* | | | | | ++ | — | | | | | | +++ | | |

+ – + + + +, Degree of abundance;—, present but unimportant.

All stations investigated by complete bottom sample and by raking except 1, 7, 10, 14 (rake only).

**Table 5. Combined food preferences of four swans. Columns I-VI refer to sequential choices; the figures indicate how many food units were eaten in fifteen experiments; total of that food offered in one experiment was 100 units**

| Food | I | II | III | IV | V | VI | Total |
|---|---|---|---|---|---|---|---|
| *Zostera marina* | 1,180 | 300 | 20 | — | — | — | 1,500 |
| *Ulva lactuca* | 195 | 840 | 285 | 160 | — | — | 1,480 |
| *Zostera nana* | — | 200 | 410 | 400 | 90 | — | 1,110 |
| *Enteromorpha intestinalis* | — | 5 | 140 | 300 | 240 | — | 685 |
| *Ruppia maritima* | — | — | — | — | 70 | 10 | 80 |

for 1 hour at 100° C. The amount of food eaten was calculated by subtracting the weight of the amount left from the weight of the amount offered.

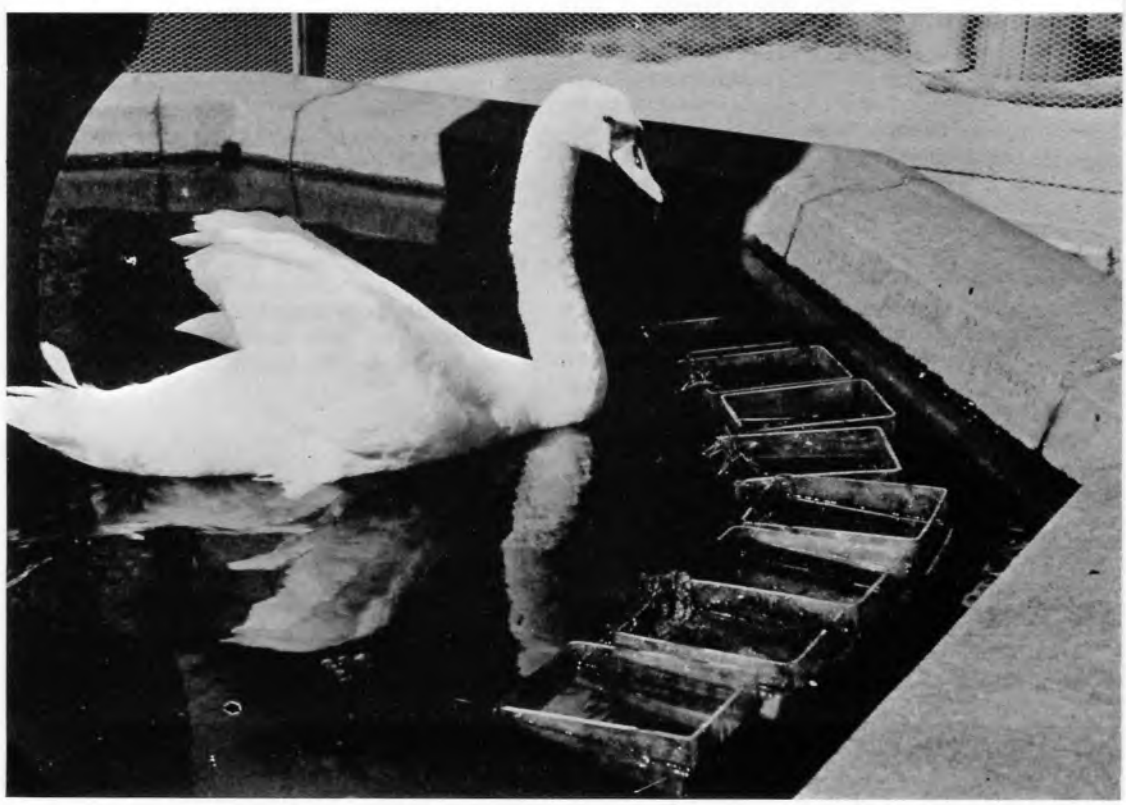
The consumption of the two essential food plants was expressed as kg food/kg body-weight/24 hours. The consumption of *Zostera marina* averaged 0·49 kg fresh weight, or 0·077 kg dry weight. That of *Ulva lactuca* averaged 0·54 kg fresh weight or 0·183 kg dry weight

The average consumption of fresh weight/swan/24 hours was 3·66 kg *Zostera marina* ($n$ = 4), and 4·03 kg *Ulva lactuca* ($n$ = 2).

The information collected tells us that the swans feed nearly exclusively on *Zostera* during May–August, while in September–October they also feed on *Ulva lactuca*. The faeces contain less than 0·5% of *Ulva* in all samples of a mixed composition. Observations, however, show that large flocks may feed exclusively on *Ulva* for some periods, predominantly in haunt F (northern part) and haunt A (inner, northern part).

The weight of moulting males (more than 2 years old) averaged 9·7 kg ($n$ = 10), that of females 8·1 kg ($n$ = 10). The accumulated biomass of the whole period 22 May–25 October was 861,715 kg (= the average biomass of each day × the total number of days), which is equivalent to 94,561 swans. In the period of more active moult, i.e. 15 July–31 August, the daily average swan number was 939, the accumulated number 45,074. Consequently, the accumulated biomass was 417,842 kg. The daily biomass of the stabilized average

**Figure 7.** Mute Swan and choices of food. *Sven Mathiasson*



August numbers (between 9–24 August) was 8,557 kg. The highest average daily biomass—9,660 kg—was found between 27 July–4 August.

Knowing the biomass of the moulting population and the daily food consumption of *Zostera marina* and *Ulva lactuca* respectively, we are able to calculate the total food need of the moulting flock. Thus, the theoretical food consumption (fresh weight) of the moulting population between 22 May and 25 October was 422,240 kg (based on *Zostera marina*) or 465,326 kg (based on *Ulva lactuca*).

In haunt F1, 1,775 swan-days occurred between 11 September–25 October in a section where nothing but *Ulva lactuca* was available, high water preventing grazing in the *Zostera* areas. Observations showed that the swans were feeding on *Ulva*. With a biomass of 15,990 kg, the total consumption (fresh weight) would be 8,635 kg. In the same period 2,885 swan-days occurred in the adjacent haunt A1 under the same conditions, and the birds were observed feeding on *Ulva*, which might have formed their predominant food (Table 3). Their biomass was 26,290 kg, their total food consumption 14,197 kg.

It seems justified to judge the true total consumption of food of the moulting swans between 22 May and 25 October to be the order of 401,523 kg of *Zostera*, and 22,832 kg of *Ulva lactuca*; 424,355 kg in all.

During June–July *Zostera* totally dominated, during September–October it only answered for 55·4% of the total food intake, the rest being *Ulva*. This means a consumption of 373,123 kg *Zostera* during June–August, against 28,400 kg during September–October, when 22,832 kg of *Ulva* was consumed as well.

## Food resources of Kungsbackafjorden

The distribution and relative abundance of different food organisms are shown in Figure 6 and Table 4. Three quantitative studies have also been made. The food item studied was manually collected by a frogman, within a frame of 50 × 50 cm, and put into plastic bags. Fresh weight and dry weight were taken.

### *Zostera marina*

Haunt A3 harboured the richest meadows and the largest plants of the moulting ground. The standing crop (root system, leaves, etc.) was 1,392 g/sq. m (fresh weight), equivalent to 204 g dry weight. The value is the sum of four samples 50 × 50 cm (235, 237, 390, 530 g fresh weight respectively).

### *Ulva lactuca*

Haunt D1 provided the richest supplies of this food. The standing crop was 1,030 g/sq. m (fresh weight), 348 g dry weight. The value is the sum of four samples of 50 × 50 cm (150, 232, 298, 350 g fresh weight).

### *Zostera nana*

The richest supplies of this plant were found in Haunt E. The standing crop was 550 g (fresh weight)/sq. m, which is equivalent to 383 g dry weight. The value is the average of two samples covering 1 sq. m each (525 g and 575 g).

Unfortunately there were no possibilities of making transects for quantitative studies nor to determine the productivity of these plants during this study period.

The total food consumption of swans staying in haunt F1 between 11 September–25 October was calculated to 8,635 kg of *Ulva lactuca*. The standing crop of this plant in the haunt was 1,030 g/sq. m in the middle of September. This means that the amount consumed converted to standing crop covered an area of 8,383 sq. m. This area is similar to the area used by the grazing swans, and the distribution of the *Ulva* supplies of the haunt. An investigation on 25 October showed that the entire *Ulva* crop (except within a narrow zone along the shore, covering about 800–1,000 sq. m) had been eliminated, leaving empty, sandy bottoms. The growth form of *Ulva* (without a root system) facilitates a total elimination of the plant by the feeding swans. The area is protected from heavy waves and strong currents so no other factors but the grazing could have been responsible. After the elimination of their food resources the swans abandoned the locality.

## Summary

The build-up of the moulting numbers at the moulting ground and their decline followed a regular, gradual curve. This implies a clear time relation between arrival and departure.

Individual swans started to moult about 30 days after the arrival, this span reducing to half at the later part of the influx period. Govern-

ing factors must include population density, available food supplies and hormonal condition.

Males start their moult somewhat prior to the females. The swans regained the ability to fly 3–4 weeks before the flight feathers achieved full length.

The rate of departure seems to be dependent on population density and available food supplies.

The swans shifted between haunts in relation to changed food supplies. The main food was *Zostera* during summer and early autumn, while *Ulva* was taken later. The swans totally eliminated *Ulva* in certain areas.

The moulting population consumed 425 metric tons, mainly of *Zostera*, but also some *Ulva*.

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Sven Mathiasson, Naturhistoriska Museet, 40030 Göteborg, Sweden.