Wintering diving duck populations and available food resources in the Baltic

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Introduction

During recent years a large number of studies on various aspects of the functioning of Baltic ecosystems have been presented or initiated. These studies have estimated biomass and production within different communities and in different areas of the Baltic and also tried to put the information together into energy flow models (Ankar 1977; Jansson 1972). They have only to a very limited extent or not at all considered the role of waterfowl in Baltic ecosystems.

The Baltic is an important breeding area for large numbers of diving ducks and a wintering area for large numbers of these ducks and other species migrating into the area. The food habits of the diving ducks in the Baltic are also fairly well known. The present paper tries to bring together the information about numbers, distribution and feeding habits of the Baltic wintering diving ducks and analyse it in relation to the data on the availability and production of food animals in order to evaluate the role of wintering diving ducks in the Baltic ecosystems.

Material and methods

Data on wintering waterfowl populations were obtained from the International Waterfowl Research Bureau's winter Counts. In Denmark aerial surveys were used to a very large extent. In Sweden the counts were made in a combination of ground counts, aerial surveys and counts from coastguard patrol boats. The counts in Schleswig-Holstein, Mecklenburg, Poland, and Estonia were undertaken mostly from the ground but aerial surveys were undertaken to some extent in Estonia and Latvia.

Complete census data from aerial surveys in Denmark are available for November 1967–1969, January 1968–1971 and 1973 and March 1969 (Joensen 1968, 1974). Swedish January surveys (ground, boat and aerial) were complete for Baltic areas except offshore waters in January 1971–1973 and were fairly complete for January 1975–1978 (Nilsson 1975, 1978). Offshore waters were extensively covered in all winters but complete coverage in one single January survey could not be obtained. In November 1971 complete coverage was obtained for southernmost Sweden, and fairly extensive coverage in November 1970, 1972 and 1973 (Nilsson 1977). In March 1976–1978 counts were undertaken on selected localities in south Sweden (Nilsson 1978).

From Schleswig-Holstein data on counts from the shore covering the entire Baltic coast in January 1963–1969 and 1975 and in February 1964, 1976 and March 1963, 1966 and 1969 were obtained from G. A. J. Schmidt. Moreover the International Midwinter Count data from Schleswig-Holstein were obtained from R. K. Berndt. These counts do however not cover the entire coast on each occasion.

Data from January counts on the coasts of Mecklenburg from the shores for January since 1963 and for some other months have been published by Nehls (1963, 1967, 1968, 1969, 1971, 1972, 1974). More unpublished data were obtained from H. W. Nehls.

From Poland count data were obtained from K. A. Dobrowolski. For Latvia, Viksne (1972) has published an account of midwinter counts. From Estonia data were obtained from E. Kumari but midwinter count data are also available in the International Midwinter Count files.

The food consumption of diving ducks was calculated according to two methods. The Standard Metabolic Rate (SMR) was calculated according to Lasiewski & Dawson (1967) using values of weights of the different species taken from Cramp & Simmons (1977). The SMR $\times$ 3 was used to estimate the daily food consumption of the birds (Nilsson & Nilsson 1976) whereas Laughlin (1973) in a study of Tufted Ducks *Aythya fuligula* used SMR $\times$ 2·5.

The existence energy (EE) was also calculated according to Kendeigh (1970) for 0°, which is close to normal monthly mean temperatures in the Baltic in the winter. Following Wiens & Innis (1974) the daily food consumption was estimated to be EE $\times$ 2. The values obtained by the two

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methods are presented in Table 1.

In the present study the values obtained by taking EE × 2 were used, as being closer to Baltic conditions in winter. Values obtained by SMR × 3 are appreciably lower, probably due to temperature effects.

Actual studies on the energy requirements of waterfowl are rare. Owen (1970) found an existence energy of about 100 kcal/24 hours for the Blue-winged Teal *Anas discors*, weighing 300–400 g. This corresponds to 200 kcal/24 hours in field conditions. Wooley & Owen (1978) estimated the total daily energy expenditure of Black Ducks *Anas rubripes* in summer to between 130 and 160 kcal/24 hours.

Swennen (1976) estimated a daily consumption of captive Eiders *Somateria mollissima* weighing about 2200 g to be 750 kcal/24 hours. This might however be appreciably higher than the consumption by birds under natural conditions. Cantin *et al.* (1974) obtained a consumption of 621 kcal/24 hours for the Eider. The values obtained in these studies were higher than the calculated values presented in Table 1.

The estimated food consumption as kcal/24 hours was transformed into grams fresh-weight of important food animals by using the data on calorific contents of various animals presented by Ankar & Elmgren (1976).

General characteristics of the southern Baltic as a waterfowl habitat

The present study considers the Baltic south of a line from the northernmost part of the Stockholm archipelago to the Estonian coast (Figure 1), including Öresund between Sweden and Denmark and the sounds between the Danish isles.

The general characteristics of the Baltic have been presented by Jansson (1972) and may be summarized. See also Table 2.

The salinity ranges from 6‰, in the northernmost parts of the area considered here, to between 10 and 20‰ in the southwest sounds. In relation to this salinity gradient the macrofauna becomes impoverished to the north even if the species remain numerous. Moreover the growth rates for most species is lower in the northern parts.

The Swedish areas in the northernmost part of the study area (regions O–S, Figure 1) are occupied by vast archipelagos of numerous small islands and skerries. Farther south on the Swedish coast moraine shores alternate with sandy beaches but there is also a smaller archipelago of rocky islands in the southeast corner (K, Figure 1). The southern and southeastern coasts of the Baltic are more lowlying with large expanses of sandy beaches and moraine shores, though there are some rocky areas.

The shallow areas outside lowlying coasts have mainly sandy bottoms except for smaller areas of mud that occur in sheltered positions. The sandy bottoms extend out over the whole depth interval considered here and often have large amounts of gravel and smaller boulders. Areas of larger boulders occur south of Scania (H), in areas around Öland and Gotland (M, N) and on the shallow banks in the middle of the southern Baltic.

The sand fauna is dominated by molluscs, mainly *Macoma baltica* with large

Table 1. Estimated energy consumption based on SRM × 3 (Lasiewski & Dawson 1967) **and EE × 2 for 0°C** (Kendeigh 1970; Wiens & Innis 1974) **for various diving ducks.** Weights for the different species according to data in Cramp *et al.* (1977). The energy consumption in Kcal (according to EE × 2) has been recalculated into the equivalent quantity of important food animals according to Ankar & Elmgren (1976).

Species	Weight (g)	Kcal per 24 hours according to SMR × 3	EE × 2	Estimated consumption fresh weight/24 hours if entirely consumed as Mytilus	Macoma	Hydrobia	Nereis	Crustacea
Aythya marila	1,200	270	371	1,625	1,430	872	—	—
Aythya fuliqula	900	218	319	1,397	1,229	750	—	—
Aythya ferina	1,000	240	337	1,476	1,299	—	—	—
Bucephala clangula	970	230	332	1,454	1,280	780	379	345
Clangula hyemalis	730	190	286	1,253	1,102	—	—	297
Melanitta fusca	1,760	354	455	1,993	1,754	—	—	—
Melanitta nigra	1,110	253	357	1,564	1,376	—	—	—
Somateria mollissima	2,230	420	516	2,260	1,989	—	—	—

Figure 1. Map of the southern Baltic showing the division into regions. 1–9 denote offshore banks: 1 = Kriegers flak, 2 = Rönne bank, 3 = Odder bank, 4 = Slupsk bank, 5 = S. mid bank, 6 = N mid bank, 7 = Hoburgs bank, 8 = Kopparstenarna, 9 = Vinkova bank.

Table 2. Total area (km²) of shallow water in the southern Baltic. (For division into sectors and delimination of the area considered see Figure 1.) For some areas with open coast and only few islands the total shore length (km) is also given. For the archipelagos the part lying in the outer zone is shown in brackets.

Area		Shore length	Total area of bottom in depth interval				
			0–6 m	6–10 m	0–10 m	10–20 m	0–20 m
Soviet Baltic states		781	?	?	?	?	12,865
Poland (A)		447	?	?	1,330+	4,040	5,370+
DDR: Open coast (B)		347	?	?	1,055	3,465	4,520
Bodden (B)		809	?	?	1,370	—	1,370
Schleswig-Holstein (C)		384	?	?	500	1,240	1,740
Denmark	D	?	?	?	2,115	1,600	3,715
	E	?	?	?	990	1,660	2,650
	F	?	?	?	590	510	1,100
Sweden	G	120	204	115	319	210	529
	H	250	198	245	443	818	1,261
	K	?	157	79	236	157	393
	L	?	377	160	537	448	985
	M	360	?	?	558	656	1,214
	N	536	?	?	731	698	1,429
	O	?	190(80)	?	?	?	?
	P	?	298(96)	?	?	?	?
	R	?	188(50)	?	?	?	?
	S	?	678(261)	?	?	?	?
Offshore banks		—	?	?	430	2,150	2,580
Total		?	?	?	11,390++	17,790++	42,045++

numbers of *Mytilus edulis* on the gravel and boulder areas. The mud fauna is dominated by molluscs such as *Cardium* spp. and *Hydrobia* spp. Annelid worms such as *Nereis diversicolor* and crustacea such as *Gammarus* are also important. For a more detailed description see Ankar & Elmgren (1976).

In the archipelagos, large sheltered areas with shallow water are occupied by vegetation of *Phragmites, Chara, Ruppia, Myriophyllum* and similar vascular plants. *Zostera* also occurs. The fauna of these areas is rich in invertebrates suitable as food for diving ducks. In the more exposed areas and along the moraine shores the shallows are occupied by *Fucus vesiculosus* and *Fucus serratus*. This community has a rich fauna of crustacea such as *Gammarus* and *Idothea* and the stones often have rich populations of *Mytilus*. Below the *Fucus*-belt there is a Red algae belt which also has rich populations of *Mytilus*. For further details see Jansson & Kautsky (1977).

The abundance and biomass of food animals

Several studies have been undertaken to elucidate the abundance, biomass and production of benthic macrofauna in the Baltic. These studies have only to some extent covered depth intervals utilized by deep-diving species such as the Long-tailed Duck *Clangula hyemalis*, the Scoters *Melanitta* spp. and the Eider. In recent years some studies have also been undertaken in more shallow areas mostly utilized by diving ducks. Unfortunately, due to sampling problems, most studies have been restricted to soft bottom areas and few deal with the important hard bottom and *Fucus* fauna.

Demel & Mulicki (1958) made a survey of the entire Baltic north to 56° 45′ and west to 12° 30′, and presented density maps and estimates of the total biomass for the more important items in the macrofauna. They did not cover the shallowest areas. The highest biomass values were found for *Mytilus* with up to 3 kg/m^2 in the most favourable conditions. High biomass values were noted for the Middle banks and the Slupsk bank. The overall biomass of the species was estimated to 3,400,000 tons without shells (4,400,000 tons including shells). *Macoma baltica* another important food animal had a mean biomass of 39 g/m^2 fresh weight and a total estimated biomass of 837,000 tons (without shells).

Löwe (1963) made a similar study of the abundance and biomass of the benthic macrofauna of the Arkona sea, i.e. the part of the Baltic bordered by the coasts of the DDR and Scania, extending from Falster and Mön in the west to Bornholm in the east. As in the other study the stations were restricted to depths of more than 10 m but the shallowest depth interval studied coincided with important feeding areas for the Long-tailed Duck.

Mean biomass values for larger areas of shallow water ranged between 405 g/m^2 fresh weight for Kriegers Flak (Figure 1) and 74 g/m^2 fresh weight for Prorer Wiek. The total biomass of important molluscs were estimated at 94,000 tons for *Cardium*, 370,000 tons for *Macoma baltica* and 1,300,000 tons for *Mytilus*.

Recently Persson (1977) studied the benthic macrofauna of Hanöbukten on the southeast coast of Sweden, this being an important area for wintering Long-tailed Ducks. Overall biomass values for the depth interval 5–19 m were 44·5 g/m^2 fresh weight and for the interval 20–29 m 132 g/m^2. Most stations were on sandy shores with some stones and gravel. The most important species were *Mytilus* with 17 and 80 g/m^2 and *Macoma* with 19 and 49 g/m^2, respectively. Much higher biomass values of *Mytilus* occur locally on stony grounds.

In the Askö area in the archipelago of region R on the Swedish coast extensive studies covered the macrofauna of the soft bottom areas. Biomass values for muddy and sandy bottoms on 10–20 m depth ranged from 100–1,000 g/m^2 fresh weight with *Mytilus* and *Macoma* dominating (Ankar & Elmgren 1976). The hard bottom fauna showed much higher biomass values. Jansson & Kautsky (1977) found maximum values of 500 g/m^2 dry weight for depths of about 4 m, the biomass for shallow water generally being over 250 g/m^2 dry weight. In the red algal belt at Askö, Kautsky (1974) found biomass values of up to 27 g/m^2 for the animals living among the algae. Including the fauna of the bottom substrate (rocks and boulders) biomass values of up to 150 g/m^2 shellfree dryweight were found, the difference mainly being due to the occurrence of large numbers of *Mytilus* on the bottom substrate. Values of up to 3,000 g/m^2 fresh weight of *Mytilus* have been reported from the archipelago by Berg (1974).

The macrofauna of the *Fucus* zone has been little studied. From Gotland, Larsson *et al.* (1972) reported preliminary values of 50–300 g/m² dry weight.

The shallow soft bottom communities (depth less than 3 m) have been little studied. Göthberg & Rondell (1973) reported overall biomass values of 83–640 g/m² fresh weight for the macrofauna of the *Zostera* zone in the Askö area. Gastropods (*Hydrobia* and *Theodoxus fluviatilis*) were common, but *Mytilus edulis* dominated even here. The same was the case for the Zostera zone in the Öresund, where Nilsson (1969, 1972) found biomass values of between 110 and 330 g/m² fresh weight.

The productivity of food animals

The productivity of the Baltic macrofauna has been studied by some authors. For *Macoma* Berg (1974) found a P/B (Production/Biomass) ratio of 0·4. For *Mytilus* the P/B ratio varied between 0·3 and 2·0 (Birklund 1975), 0·9 being a typical value for large parts of the Baltic (Persson 1977). For *Nereis diversicolor* the P/B ratio is about 3 (Ankar & Elmgren 1976), whereas a P/B ratio of about 2 has been used for crustacea (Persson 1977).

Size of wintering diving duck populations

The results from the International Waterfowl Counts have clearly shown the importance of Danish waters for wintering diving ducks (Atkinson-Willes 1976, 1978; Joensen 1974). It is thus only possible to estimate the total wintering populations of the Baltic when there is relatively good coverage of Denmark, Sweden and the two German states, i.e. January 1969, 1970, 1971, 1973. Numbers wintering in the other Baltic states are only a small porportion of the total population for all species except the Long-tailed Duck. On the basis of these counts and information from other sources the mean populations of the different species of diving ducks in the Baltic for these years have been calculated (Table 3). Details on the distribution and numbers in different regions will be found in the national reports referred to above, so only some general comments will be given here.

As has been discussed at length in the national reports from Denmark and Sweden (Joensen 1974; Nilsson 1975) the results of national surveys of wintering ducks are influenced by a number of different factors. For most species aerial surveys will only record a proportion of the birds actually present, this proportion varying between species and areas and also between different observers. For some species in Sweden it has proved possible to correct for aerial survey efficiency whereas no such corrections were undertaken in Denmark. For some species the results given will thus be underestimates but they will give the right order of size.

In the Baltic the counts of inshore species, i.e. Tufted Duck, Pochard *Aythya ferina* and Goldeneye *Bucephala clangula*, will yield good results in most years. The aerial survey efficiency is mostly fairly high for these species. The Scaup *Aythya marila* occurs in large flocks at sea that are easily detected from the air but involve counting problems. The sea ducks proper, the Long-

Table 3. Midwinter populations of diving ducks in the Baltic. The figures for the individual years show the numbers counted in Denmark, Sweden, FDR, DDR and Poland. In the estimated mean totals data from other sources are also included (see text). For the Long-tailed Duck no data are presented for the individual years as numbers counted do not represent numbers present in the area.

Species	Numbers counted 1969	1970	1971	1973	Estimated mean winter population
Aythya marila	72,400	90,750	64,000	72,000	75,000
Aythya fuligula	192,000	274,000	230,000	194,000	225,000
Aythya ferina	4,500	9,400	3,700	6,300	6,000
Bucephala clangula	56,000	54,000	54,000	64,700	60,000
Clangula hyemalis					1,000,000
Melanitta fusca	3,000	11,600	1,600	2,600	5,000
Melanitta nigra	26,000	27,000	7,100	17,100	20,000
Somateria mollissima	175,700	196,000	100,100	178,300	160,000
Mergus serrator	8,900	11,800	16,600	11,200	>12,000
Mergus merganser	17,300	27,000	19,800	16,400	25,000
Mergus albellus	680	720	1,110	720	800

tailed Duck, the Velvet Scoter *Melanitta fusca*, the Common Scoter *Melanitta nigra* and the Eider stay far out at sea and counts from the shore will yield no reliable estimates of total populations. The Eider mostly stay in Danish waters and as they are fairly easily seen from the air the figures are considered to be correct. The same applies to the Scoters but they are more difficult to count from the air.

For the Long-tailed Duck it is not possible to calculate total populations from the ordinary waterfowl count data. The species occur far out at sea and national surveys require extensive aerial counts that have only so far been undertaken in Denmark and Sweden. Moreover the species is difficult to count from the air except in favourable conditions that are rare in the Baltic in the winter. The highest annual total reported is only 113,000 (Atkinson-Willes 1978), the majority being counted in Swedish waters.

The Long-tailed Duck pass Finland on the migration into the Baltic in the autumn and leave the Baltic on a concentrated spring migration over the Finnish Bay. Bergman & Donner (1964), by means of radar observations, estimated the numbers arriving into the Baltic in the autumn to be about 1 million and the numbers leaving in spring to be about 500,000. Bergman (1974, and pers. com.) later estimated the strength of the autumn migration at about 2 million with a spring migration of about 1 million. An estimate of 500,000 in spring was considered unrealistically low. In normal winters most of these birds seem to remain in the Baltic (Berndt, pers. com.; Schmidt 1966). The Long-tailed Ducks wintering off the coasts of Scotland and Norway (Mathiasson 1970) probably pass to the north of Norway and then move south.

Nilsson (1975) estimated the total population of Long-tailed Ducks in Swedish waters to be about 150,000 in January 1973–1974 (see also Nilsson 1980). This corresponds to a density of 21 individuals per km^2. Counts in other winters indicate that numbers sometimes are appreciably higher. As the total area available for the Long-tailed Duck in the southern Baltic is about 42,000 km^2 (depth less than 20 m, Table 2) the density with an estimated population of 1 million will be about 25 individuals per km^2. This is consistent with experience from Swedish waters.

The mergansers will not be specially discussed in this paper but have been included in Table 3. The Red-breasted merganser *Mergus serrator* occurs well offshore and as it is difficult to count from the air the totals obtained are probably underestimates. The Goosander *M. merganser* and the Smew *M. albellus* occur inshore and counts are considered to be fairly accurate. Appreciable numbers of Goosanders occur in some areas not covered by the counts.

Exploitation of food resources

Regular counts of resting and wintering diving ducks in restricted areas (Figure 2) around the coasts of southern Sweden made it possible to calculate the exploitation rate by the ducks for these areas (Nilsson 1972) using the values in Table 1. The calculated rates of exploitation ranged between 1·8 and 42·6 kcal/m^2/winter (Table 4). Expressed as *Mytilus*, the favourite food of the diving ducks in the Baltic, this corresponds to 8–187 g/m^2 wet weight.

The highest rate was for sector Gl:e which is situated near the former outlet of untreated sewage from the city of Malmö. Later, when the discharge was stopped, the number of ducks (Tufted Ducks and Goldeneyes) decreased markedly and the rate for 1970/71–1973/74 was only 62 g/m^2 counted as *Mytilus*.

High consumption rates were also found for some other shallow areas in the Öresund (Table 5) and for stony inshore areas on the south coast. Large parts of the south coast are however fairly unproductive sandy beaches, with only a little duck food near the shore. In the two archipelago areas K2 and K3 the highest rate of consumption was noted for K3 which is characterized by vast areas of shallow bottom with low vegetation and a rich fauna, utilized mainly by Tufted Ducks. K2 is a more exposed area, although the production of food animals is probably higher there.

Unfortunately it has not been possible to obtain quantitative samples of the food resources of these areas except for Glc (Table 5). From the data referred to above it will however be clear that the consumption will certainly be less than 10% of the standing crop of *Mytilus*. Moreover, several other important food animals occur in these areas.

Nilsson (1969) studied the rate of exploitation of diving ducks on the bottom fauna for area Glc. Table 5 summarizes these data together with the calculated production of important food animals based on the P/B ratios given by Ankar & Elmgren (1976) and Persson (1977). The food choice of Scaups and Tufted Ducks in the area was also studied by Nilsson (1972). Data on the food choice of the Goldeneye were obtained from another area with similar bottom fauna. Applying the percentage composition of the diet obtained in this study to the data in Table 5 and the individual consumption of the ducks estimated according to Table 1, the overall estimated consumption of the diving ducks using the area amounted to 26% of the calculated annual production of food animals. For *Hydrobia* the entire annual production was probably consumed by the Tufted Ducks. The original estimates by Nilsson (1969), based on insufficient information about energy requirements of the ducks, were lower.

The figures presented can only be taken as rough estimates. Firstly the available knowledge does not admit more than rough values on the production of the

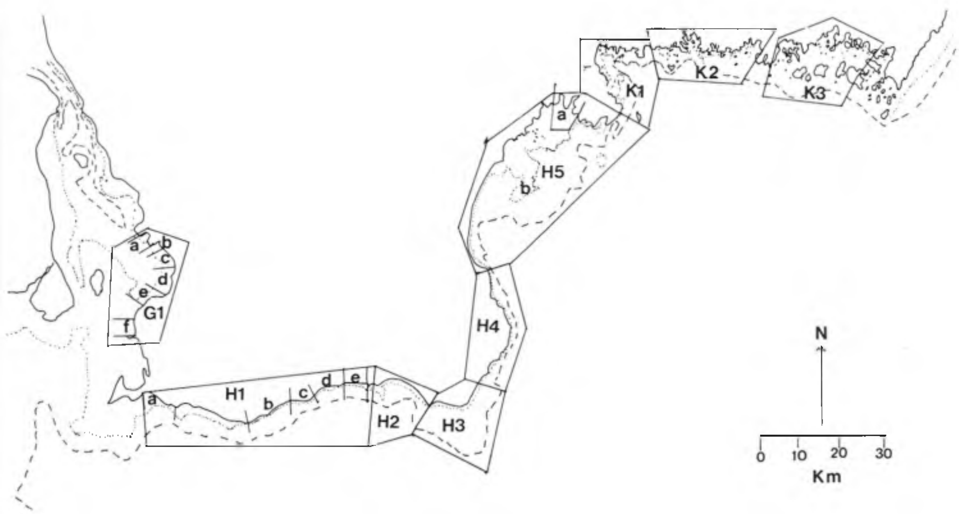

Figure 2. The south coast of Sweden with division into study areas. Capital letters denote the main regions in Figure 1.

Table 4. Calculated exploitation of bottom fauna by resting and wintering (Sept.–April) diving ducks in different areas on the coasts of south Sweden. Values for G:1, H:1 and H:5 recalculated from Nilsson (1972). Maximum depth interval included is 0–3 m for G:1 and 0–6 m for the other areas.

Sector	Area (km^2)	Mean number of bird days	Consumption/m^2/winter Kcal	*Mytilus* (g fresh weight)
G:1a	2·70	16,500	2·09	9
G:1b	0·48	26,800	18·85	83
G:1c	4·10	193,400	15·06	66
G:1d	10·90	278,400	8·38	37
G:1e	3·70	437,000	42·61	187
G:1 total	40·90	1,128,200	8·99	39
H:1a	4·30	23,100	1·81	8
H:1b	2·20	110,200	11·20	71
H:1c	3·00	122,200	12·69	56
H:1 total	31·90	436,800	4·32	19
H:5a	17·00	213,000	3·96	17
K:2	29·00	271,000	3·00	13
K:3	58·05	1,230,000	6·60	29

Table 5. Total estimated standing crop (tons) and annual production (tons) for important food animals in the entire Bjärred area (G:lc in Fig. 2) for 1966/67 together with calculated consumption by diving ducks (data from Nilsson 1969, 1972). For calculation of annual production and of duck food consumption see text. The total area is 4·10 km² of which 2·30 km² consists of muddy bottoms with a depth less than 1 m and 1·80 ha consists of *Zostera* community on sand at depths of 1–3 m.

Food animals	Total standing crop (tons) November	April	Production tons	Consumption by diving ducks (tons) *Aythya marila*	*Aythya fuligula*	*Buceph. clangula*	Total	% of production
Bird days × 10³	—	—	—	15·4	88·4	74·2	178	—
Crustacea	49	26	88	—	—	—	—	—
Nereis	80	93	217	—	—	16	16	7
Cardium	88	26	35	+	23	+	23	66
Mytilus	428	119	190	16	38	32	86	45
Hydrobia	39	7	17	—	19	+	19	100+
Total	684	271	547	16	80	48	144	26

various animals to be calculated. Secondly, the diet of the three species might have been more varied than apparent from the samples studied. Thirdly the composition of the diet of the Goldeneye was based on studies in another although similar area.

The food consumption of Long-tailed Ducks during the winter was calculated for various areas on the south coast of Sweden based on boat survey data presented by Nilsson (1980). The highest consumption rates (as *M. edulis*) were obtained for inshore areas on the south coast with 29 g/m² and 22 g/m² out of a total diving duck consumption of 71 g/m² and 56 g/m², respectively. For offshore areas the consumption rates equalled between 2 and 11 /g² of *Mytilus* for different areas.

In Hanöbukten (H5, Figure 2) mean densities of Long-tailed Ducks in winter were 72 individuals/km² for the central part (18 km²) and 24 individuals/km² for the other areas (478 km²) out to a depth of 20 m. This corresponds to 1,400,000 bird day units during the entire winter season. The calculated annual food consumption was 1,700 tons or 11% of the calculated production of *Mytilus* and *Macoma* (Persson 1977). This will however be an overestimate as the values for biomass and production are probably too low as some important stony grounds could not be adequately sampled (Persson, pers. com.).

The highest densities of Long-tailed Ducks in Swedish waters were found off northern Öland with 235 individuals/km² (Nilsson 1980), similar values were obtained from northern Gotland. This corresponds to a calculated consumption of 21 g/m² of *Mytilus* per winter which is small compared to the available resources on these stony grounds.

Based on the counts from Mecklenburg (Nehls, pers. com.), Schleswig-Holstein (Schmidt, pers. com.) and Denmark (Joensen 1974 for 1968/69) and available Swedish data from the counts in November, January and March, the mean number of bird-day units per km² was calculated for the different regions (Table 6). The mean densities for December and February were considered to be between the values for November–January and January–March, respectively. For counts made from the shore densities were expressed as individuals/km of shore line. Doubling these values (i.e. assuming a visual range of 500 m) will give fairly accurate estimates of actual density. However, by doing so the values for the totally covered regions will be low in the comparisons because even in these areas most ducks are concentrated inshore even if the entire areas were included in the calculations.

The estimated regional rates of food consumption by the diving ducks calculated as *Mytilus* ranged from 3 g/m² to 32 g/m². The actual rates of consumption for extensively used inshore areas will certainly be several times higher.

By using the population estimates presented above the total food requirements of Baltic diving ducks during the winter were calculated (Table 7). As seen from this table the total requirements if satisfied with *Mytilus* would amount to 329,000 tons for the entire period of November–March. In these calculations it is assumed that the January numbers are relevant for the entire period which will probably be true for normal winters when no winter movements out of the Baltic occur and as most migration inland occurs from April onwards.

Table 6. Calculated regional exploitation of bottom fauna by wintering (November–March) diving ducks in the Baltic. S = areas covered from the shore. Calculations are related to shore length and later recalculated to area assuming a coverage of 500 m from the shore. T = total coverage of region (aerial surveys or aerial + boat + shore surveys). Calcualtions are related to total area of a depth less than 10 m (6 m in Swedish archipelagos).

Region	Coverage	Total water area of depth less than 10 m (x = 6 m) km²	Total shore length km	Mean density ind./km² ind./km (°) November	January	Bird days per km² + = per km shore	Estimated consumption per m² Kcal	Eq.*
B	S	2,425	1,156	—	59°	8,200+	2·7	12
C	S	500	384	—	150°	20,300+	7·4	32
D	T	2,115	—	107	135	15,700	6·9	30
E	T	990	—	16	31	3,700	1·2	5
F	T	590	—	23	66	5,900	2·0	9
G	T	320	120	19	41	4,900 (13,100+)	1·5	8
H	S	440	250	55°	65°	8,100+	2·5	11
K	T	240	—	55	82	9,700	3·1	14
L	S	540	—	9	17	2,100	0·7	3
M	S	560	360	30°	31°	4,700+	1·5	7
N	S	730	536	26°	39°	4,600+	1·5	7
O	T	190x	—	86	52	8,600	2·8	12
R	T	190x	—	86	25	6,200	2·0	9
S	T	680x	—	70	50	8,000	2·6	11

*Eq. = Equivalent quantity of *Mytilus* g fresh weight incl. shells.

Table 7. Estimated wintering populations of diving ducks in the Baltic based on the International midwinter counts in January 1969–1971 and 1973 together with data on calculated food consumption. For the estimation of the numbers of Long-tailed Ducks see text.

Species	Mean wintering population	Bird-days $\times 10^6$	Food consumption Kcal $\times 10^9$	Equivalent quantity of *Mytilus* fresh weight tons $\times 10^3$
Aythya marila	75,000	11·3	4·2	18
Aythya fuligula	225,000	33·8	10·8	47
Aythya ferina	6,000	0·9	0·3	1
Bucephala clangula	60,000	7·0	3·0	13
Clangula hyemalis	1,000,000	150·0	43·0	188
Melanitta fusca	5,000	0·8	0·4	2
Melanitta nigra	20,000	3·0	1·1	5
Somateria mollissima	160,000	24·3	12·5	55
Total	1,550,000	157·7	53·6	329

As the estimate for the wintering population of the Long-tailed Duck is uncertain, the estimated food consumption will be rather uncertain. With a winter population of 1·5 millions (this corresponds to an autumn population of 2 millions and a spring population of 1 million, cf. p. 136) the estimated food consumption would be increased by 90,000 tons. If on the other hand the winter population of the species is only 500,000 it should be reduced accordingly.

From the data presented in the papers by Demel & Mulicki (1958) and Löwe (1963), discussed above, the total estimated standing crop of *Mytilus* in the 42,000 km² of southern Baltic with a depth less than 20 m would be 5 million tons (119 g/m²). A further 0·9 million tons of *Macoma* (23 g/m²) should be added. The annual production of these species is estimated to be 4·5 million tons of *Mytilus* and 0·5 million tons of *Macoma*. The estimated consumption by the diving ducks will thus be 6·6% of the annual production of *Mytilus* if all energy demands are filled by this food species.

Discussion

In the calculations above the food requirements of the diving ducks of the Baltic were expressed as *Mytilus*. As shown by Madsen (1954) and Nilsson (1972), *Mytilus* is the most important food item of the wintering diving ducks of the Baltic constituting a large proportion of their food intake. Besides *Mytilus* the diving ducks to some extent also fed on other food animals. *Macoma* was important for several species. The Goldeneye and Long-tailed Duck also fed on crustacea to a large extent. The diet was even more varied on shallow areas in the sounds, where large quantities of *Hydrobia, Cardium* and *Nereis diversicolor* were utilized by the diving ducks.

Studies on the food consumption of diving ducks from other marine areas have shown that they feed on a wide variety of different food species and often feed on the most abundant species.

The biomass values referred to above of course only relate to potentially available food for diving ducks. The sizes of the different food animals will limit the utilization of more than part of the food resources. According to Madsen (1954; also Pehrsson 1976) the maximum length of *Mytilus* used are for Goldeneye 10 mm, Long-tailed Duck 20 mm, Tufted Duck 25 mm, Scaup and Velvet Scoter 30 mm, Common Scoter 40 mm and Eider 80 mm.

Data from Hanöbukten (H5, Figure 2) by Persson (1977) show that only 4% of *Mytilus* were larger than 20 mm and that only 18% were larger than 10 mm, i.e. above the limit for the Goldeneye. Similarly most *Mytilus* measured on Gotland by Pehrsson (1976) were within the limits utilized by the Goldeneye. In the Öresund *Mytilus* grows bigger. In Lommabukten between 10 and 18% were larger than 25 mm, i.e. the limit for the Tufted Duck and only 35% were within the limits for the Goldeneye. Even if the mussels often grow too big for some diving ducks in the southwest of the Baltic, part of the mussels here will be utilizable even by Goldeneye. Moreover, these productive areas offer several alternative food animals of more suitable sizes. In the major part of the Baltic most *Mytilus* are well within the size limits utilized by all diving duck species.

In the Baltic the ice conditions in the winter limit the extent to which the food resources will be utilizable by the diving ducks. In normal winters most of the Baltic north of the areas considered here is ice covered and cannot be used by diving ducks. November counts in the Swedish part of the Bothnian bay are low even one month before the start of freezing. Similarly the larger part of Finnish archipelagos and Estonian waters will be covered by ice in winter. The same applies to large areas in the inner parts of the Swedish east coast archipelagos.

In normal winters part of the southern Baltic will not be utilizable by feeding diving ducks but this will probably have little effect on the total rates of exploitation calculated above as most areas will still be available. The effect will of course be most marked in the inferior divers such as Pochard, Tufted Duck and Goldeneye, whereas a superior diver such as the Long-tailed Duck will not be affected in normal years. The marked preponderance for this species among Baltic diving ducks must be seen in relation to its excellent diving abilities (see also Nilsson 1972, 1975).

The macrofauna of the bottom will not only be utilized by diving ducks but also by various fishes. In the Kiel Bay, Arntz & Brunswig (1976) calculated a food consumption by fishes of 24 kcal/m^2/year compared to a food consumption of 7 kcal/m^2/year by diving ducks for the inshore, most exploited, 500 m. However, according to Löwe (1963) *Mytilus* is not much used as fish food and there will thus be no competition with birds. On the other hand important food animals on shallow water such as *Nereis diversicolor* are much used as fish food (SKU 1976).

The primary production in the Baltic is estimated to be 2,200 kcal/year/m^2 for the Kiel Bay (Arntz & Brunswig 1976) and 1,440 kcal/year/m^2 for the Askö-Landsort area (Ankar 1977). The total estimated food consumption by the diving ducks in the southern Baltic during winter corresponds to 0·31 kcal/m^2 calculated for the total area or 1·81 kcal/m^2 for the shallow areas utilized by diving ducks. This is 0·2‰ and 1·0‰ respectively of the primary production taking this as the mean of the two cited values. Evans (1973) estimated the energy demands of sea birds of the North Sea to be less than 0·1‰, whereas Holmes & Sturges (1973) estimated the consumption of birds in deciduous forest to be 1·2‰. Nilsson & Nilsson (1976) estimated that birds of a south Swedish lake consumed about 3–6‰ of the primary production. When comparing these figures it should be remembered that the Baltic figures presented here only refer to part of the bird community and only to the winter months.

Local studies relating the calculated food consumption to the available food resources have been published for the Eider. Brun (1971) found that Eiders near Tromsö balanced the production of *Chlamys* in one study area. In the St Lawrence Bay, Canada, Cantin *et al.* (1974) estimated that the feeding Eiders used about 10–30% of the available *Littorina* spp. during the summer. For the Dutch Waddensea Swennen (1976) calculated a consumption of 6·2 kcal/m^2/year by the Eider or 17·5 g/m^2 *Cardium* fresh weight.

The distribution of diving ducks in the Baltic was related to differences in feeding ecology and diving abilities by Nilsson (1972, 1975). Pehrsson (1976) also discussed factors behind the winter distribution of diving ducks and related it to the occurrence of the preferred food. He stated that the occurrence of the preferred food for the Common Scoter and the Eider is insufficient in the Baltic compared to the Danish waters and the west coast.

The total population of Eiders leaving the breeding areas in the Baltic in the autumn is estimated to be 700,000–800,000 (Alerstam *et al.* 1974). This is approximately 600,000 more than the winter population of the southwest Baltic. Moreover an appreciable number of Common Scoter pass the Baltic on migration in the autumn. Atkinson-Willes (1978) estimates the west palaearctic population of the Common Scoter to be about 400,000–500,000, considerably less than the 1·2 millions estimated by Bergman & Donner (1964).

If 600,000 Eiders plus 450,000 Common Scoters stayed in the Baltic for the winter they would require about 320,000 tons of *Mytilus*, increasing the total demand on the food resources by diving ducks to 13% of the annual production of *Mytilus*. It should be remembered that the discussion hitherto has been limited to the five months November–March. Large numbers of diving ducks will still be present in the Baltic in the summer using the same food resources. As stated above, the diving ducks in winter utilize other food sources than *Mytilus* but these contribute only a relatively small part of the total food with the possible exception of other mussels. In summer the situation is different with the majority of the diving ducks concentrated in the archipelagos both in the part of the Baltic considered here and in areas farther to the north. The areas in the southern Baltic have only small diving duck populations in summer.

When considering the winter distribution of diving ducks in relation to available food resources, it should be remembered that diving duck populations probably were larger in former days. On the other hand the food resources were probably not larger than at the present especially as *Mytilus* to some extent is encouraged by sewage discharges.

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Summary

The wintering populations of diving ducks in the Baltic in 1969–1973 are estimated on the basis of the data gathered during the International Waterfowl Counts and from some other sources. The calculated food consumption of these diving ducks in different parts of the Baltic and in the entire Baltic are compared with published information about the abundance and production of suitable food animals, especially *Mytilus edulis*. Some data on the consumption of food in Swedish study areas are discussed. The wintering diving ducks use a rather small proportion of the available food resources. Calculated for the entire Baltic the consumption by the diving ducks in winter amounts to 6·6% of the annual production of *Mytilus* in shallow water (depth less than 20 m) if the entire consumption is taken out as *Mytilus*. This compares to about 1‰ of the primary production of these areas.

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