The food and feeding of common eiders in the St. Lawrence estuary in summer

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The study was conducted in the St. Lawrence estuary during 1969 and 1970. The food abundance in the intertidal zone was measured in four sampling stations located on the south shore of the river; the measurements revealed that over 95% of the available food of the common eider (*Somateria mollissima*) consisted of *Littorina* spp., *Mytilus edulis*, and *Gammarus oceanicus*. Both adult and young birds showed a distinct rhythm of feeding activities associated with tidal level. During the prenesting period, herring eggs and *Nereis virens* made up most of the food of adult common eiders. When accompanying ducklings, females ate mostly *Littorina* spp. and amphipods. *Littorina* spp. made up between 30 and 97% of the diet of the ducklings, the importance of this gastropod growing with age of the bird. Energy requirements during maximum growth were evaluated at about 460 kcal/bird per day on ducklings (age 54 days) fed natural foods, while between week 3 and week 8 it stood at about 520 kcal/bird per day in ducklings fed "turkey starter." These figures were used to assess the importance of the food removed by the eiders from the intertidal zone during the summer. We conclude that between 10 and 30% (according to the area) of the standing-crop biomass of *Littorina* alone (in July) is removed by the ducklings and the females accompanying them. At various moments through the season, these birds remove between 40 and 100 metric tons of mollusks per day from the intertidal zone.

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La présente étude a été faite dans l'estuaire du Saint-Laurent durant 1969 et 1970. Quatre stations d'échantillonnage situées sur la rive sud de l'estuaire furent choisies pour y accomplir un échantillonnage de la nourriture disponible dans la zone des marées; cet échantillonnage a révélé que chez l'eider commun (*Somateria mollissima*), seulement trois invertébrés, *Littorina* spp., *Mytilus edulis* et *Gammarus oceanicus*, constituent plus de 95% de la nourriture disponible. Tant les adultes que les jeunes exhibent un rythme d'activité alimentaire périodique et lié au cycle des marées. Avant et pendant la nidification, *Nereis virens* et les oeufs de hareng constituent les principaux éléments de la diète des adultes. Plus tard dans la saison, les femelles accompagnées de canetons consomment surtout des littorines et des amphipodes. Enfin, *Littorina* spp. constituent entre 30 et 97% de la diète des canetons durant la période d'élevage. Les besoins énergétiques durant la période de croissance maximum ont été évalués à 460 kcal/oiseau par jour chez des oiseaux (âgés de 54 jours) nourris d'invertébrés provenant de la zone des marées tandis qu'on obtenait une valeur moyenne d'environ 520 kcal/oiseau par jour chez des individus dont l'âge variait de 21 à 56 jours et nourris d'une moulée commerciale contenant 18% de protéines ("Début-dindons" Purina). A l'aide de ces mesures de besoins énergétiques, il nous a été possible d'estimer la quantité de nourriture prélevée par les eiders dans la zone intertidale. A eux seuls, les canetons et les femelles les accompagnant prélèvent une proportion variant de 10 à 30% (selon la place-échantillon) de la biomasse disponible (en juillet) de *Littorina*. Ceci représente une quantité variant, selon le moment de la saison, de 40 à 100 tonnes métriques de ce gastéropode par jour.

Introduction

Most of the literature on feeding habits of the common eider (*Somateria mollissima*) refers to the European subspecies *S. m. mollissima* and mainly describes the diet in different locations (e.g., Evans 1909; Soot-Ryen 1941; Segestråle 1947; Madsen 1954; Player 1971). More recent studies have turned attention to the amounts of food present in the feeding areas and the rate of uptake by the birds (e.g., Dorosch 1953; Pertsov and Flint 1963; Marriott 1966; Pethon 1967; Milne 1968; Nilsson 1969; Brun 1971; Milne and Dunnet 1972). In North America, far less information is available on the food and feeding of the American subspecies *S. m. dresseri*, the work of Cottam (1939) and McGilvrey (1967) being the most noted.

Most observations have been made in winter, when the main food species is the mussel *Mytilus edulis*, whereas work in the Kandalaksha Reserve

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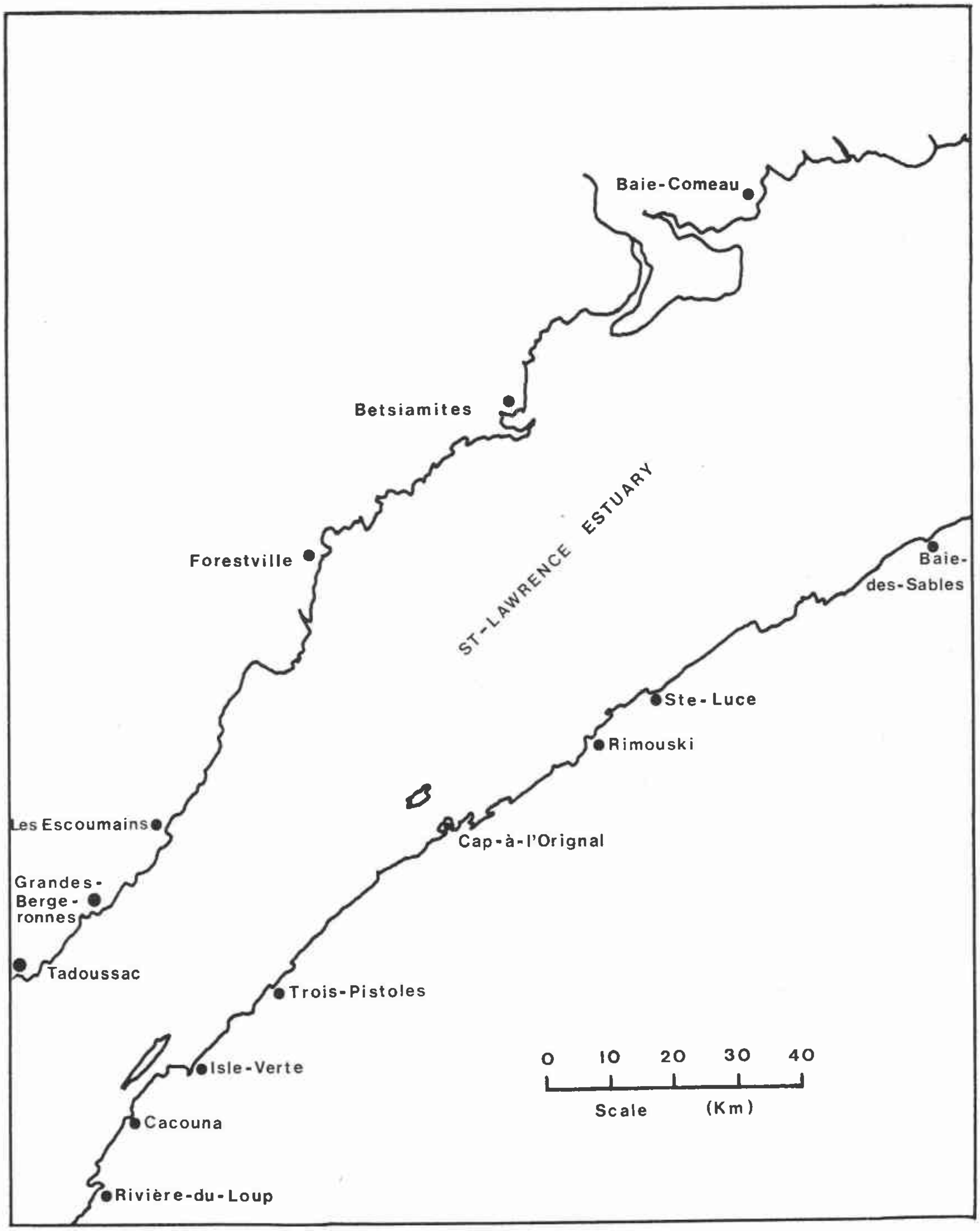

FIG. 1. The study area.

in the White and Barents Seas by Russian workers (Gerasimova and Baranova 1960), and the study by Pethon (1967) in Norway, have established the diet of ducklings and attendant females during the summer months.

The present study was aimed at describing the diet of females and ducklings in the St. Lawrence estuary through the summer months, at assessing the amounts of food present in the feeding areas, and at considering the relationship between the amount of food present and the amounts eaten by the eiders.

The Study Area

The study areas were located on the south shore of the estuary of the St. Lawrence river between Rivière-du-Loup and Baie-des-Sables, a section of about 150 km of coastline (Fig. 1). In this region, the tidal amplitude has a mean of 3.7 m at Rivière-du-Loup and 3.0 m at Rimouski, with maximum tides of 5.7 m and 4.6 m, respectively. The salinity of the water on the intertidal zone varied from 21.9‰ to 28.5‰ (Lavoie 1970), and may be considered typically coastal marine.

The bedrock consists of schists, sandstone, quartzite, conglomerate, and limestone dating to the Ordovician period, but the most common substrata are of clay schist and sandstone.

Methods

(A) Food Abundance

In 1970, sampling stations were set up on transects across the shore at Cacouna, Trois-Pistoles, Cap-à-l'Orignal, and Ste-Luce. These stations were located at each of the four areas in such a position as to give comparable periods of exposure (Table 1). The type of substratum for each station was described and, generally, three samples of $\frac{1}{16}$ m^2 were taken at each. From mid-May through September, quadrat sampling was carried out at 2-week intervals.

On each occasion, the percentage cover by algae (brown algae of the genera *Fucus* and *Ascophyllum* make up the bulk of these), the mean length of the algae, and the numbers and volume of organisms present on the algae and on the substratum were recorded. To calculate standing-crop biomass of *Littorina* from the numbers and volumetric measurements, the size distribution of the gastropods was established on fresh material collected in 1972 at Cap-à-l'Orignal; we assumed that size distribution was the same in 1970 and was also the same on all four study areas.

TABLE 1

Location of sampling stations according to the height of the tide, in meters

Station	I	II	III	IV
Cacouna	3.77	3.15	2.54	1.93
Trois-Pistoles				
Cap-à-l'Orignal	3.06	2.44	1.83	1.22
Ste-Luce				

(B) Feeding Behavior

Observations were made on feeding birds with the aid of a 30× telescope to determine the daily pattern of feeding, the numbers of birds present in each period of observation, and the degree of use of different parts of the shore for feeding purposes. Selected broods of ducklings were followed through entire days to establish the amount of time spent feeding. Every 2 weeks, a total count of all birds in each of the four stations was carried out.

(C) Food Analyses

Samples of birds were collected at regular intervals throughout the summer (June–September), and their gut contents examined for identification of the food items present. A total of 407 birds (19 males, 143 females, and 245 ducklings) were examined during the summers of 1969 and 1970. The volume of whole organisms found in the oesophagus and the gizzard was measured by displacement of water in a graduated cylinder, while partly digested items were identified and recorded in the diet lists; this particularly applied to soft-bodied forms such as insects and amphipods. Following Pethon (1967), an "Index of Importance" was established by expressing, in percentage, the product of frequency of occurrence (in percentage) and volumetric importance (also in percentage) for any one food item in either the total diet or, else, in the total food available on the beach.

Ducklings were aged according to their body weight and plumage development, following criteria described by Pethon (1967).

(D) Feeding Trials

During the month of May 1972, pipped eggs were incubated in the laboratory until hatching; groups of four ducklings were formed so as to represent birds hatched early and late in the season. Birds were fed commercially available "turkey starter" and feeding trials lasted for 72 h. During these, the birds were held in pens, 1.2 × 1.2 × 1.0 m, raised about 1 m above ground surface; a screen bottom allowed excreta to be collected in a removable pan. Standard, oxygen-bomb calorimetry was used to obtain calorific values of faeces and of appropriate food samples.

Results

1. Habitat

The physical nature of the beach was different in each of the four study areas. At Cacouna, the intertidal zone was very wide and muddy with a few scattered boulders. At Trois-Pistoles, there was much more gravel and sand on the beach and less mud than at Cacouna. The two sampling stations higher on the beach at Cap-à-l'Orignal were located on a large, flat rock platform with rock pools; algae growing on the platform were stunted presumably because of wave action and ice scouring. The other two stations, at Cap-à-l'Orignal, were in habitat similar to that

TABLE 2

Summary description of the intertidal zone at each of the four study areas

	Cacouna	Trois-Pistoles	Cap-à-l'Orignal	Ste-Luce
Length of shoreline, km, within the study area	3.5	2.6	6.6	8.0
Surface area of intertidal zone, km²	2.25	1.95	1.69	1.39
Substratum, % frequency of occurrence in samples				
A. Sand, mud, or clay	37	8	4	0
B. Boulders without sand	23	17	15	4
C. Rocks and gravel	16	41	17	5
D. Gravel and sand	22	29	24	10
E. Gravel	0	2	0	20
F. Slate rock	0	0	33	41
G. Slate rock with gravel or sand	0	0	4	16
H. Other	2	3	3	4
Mean length of algae, cm, followed by % cover, ( )				
Stn. I	6.1 (1)	10.0 (1)	1.6 (2)	0.0 (0)
Stn. II	45.4 (80)	24.0 (12)	14.7 (1)	8.9 (12)
Stn. III	33.4 (10)	44.1 (5)	47.6 (35)	13.6 (25)
Stn. IV	32.6 (10)	47.8 (45)	39.7 (50)	24.2 (50)
Distance between Stn. I and Stn. IV, m	550	250	100	120
Presence, +, or absence, −, of *Spartina* on upper shore	+	+	−	−

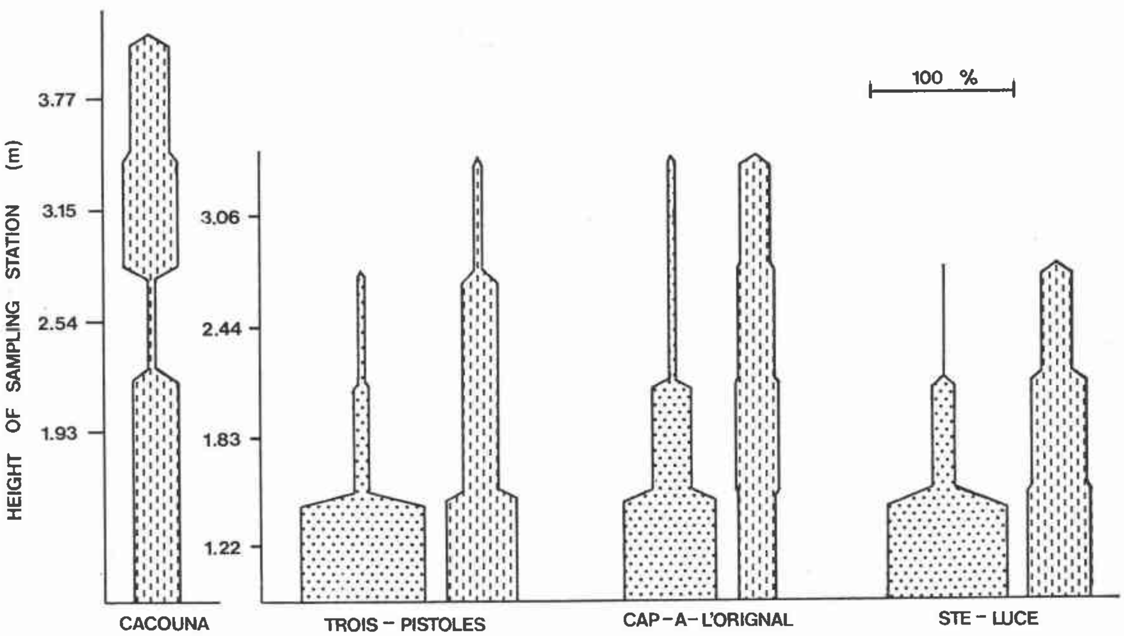

FIG. 2A. Comparative distribution of the two major food items, *Littorina* spp. and *Mytilus*, in the intertidal zone of the four study areas. Height is above the zero tidal level. *Mytilus* is absent in Cacouna at the height sampled. Values for 1970 only. The bar represents 100% or total volume over the whole season.

found at Trois-Pistoles and algae grew in tussocks reaching considerable length. Ste-Luce has a very exposed rocky beach with an evenly spread carpet of short algae; ice scouring in winter and spring must be relatively more important than wave action, for, in the spring, virtually no algae are present. But by early fall, a fairly thick mat has had time to develop even in presence of wave action.

The physical characteristics of the four study areas are summarized in Table 2.

2. *Food Supplies*

The muddy substratum at Cacouna was not suitable for *Mytilus* attachment, and only *Littorina saxatilis* and *L. obtusata* were found on the algae and the few boulders. The more varied habitat at Trois-Pistoles and Cap-à-l'Orignal favored equally *Mytilus* and *Littorina* spp. whereas at Ste-Luce, the rocky substratum was more favorable for *Mytilus*, which composed about 85% of the fauna by importance (Table 3).

TABLE 3

Index of "food importance" in the four sampling localities

	Cacouna (118)	Trois-Pistoles (140)	Cap-à-l'Orignal (95)	Ste-Luce (111)
Littorina spp.	94.77	44.34	47.83	13.93
Mytilus edulis	0.04	51.46	47.03	84.79
Amphipods	2.50	3.10	4.00	0.10

NOTE: Only *Littorina*, *Mytilus*, and amphipods are considered since they conistently make up more than 95% of all the food present on the beach. (See text for explanations on the calculation of the index.) The number in parenthesis indicates the total number of $\frac{1}{16}$-m² quadrats obtained at the four sampling heights throughout the season and used in the computations.

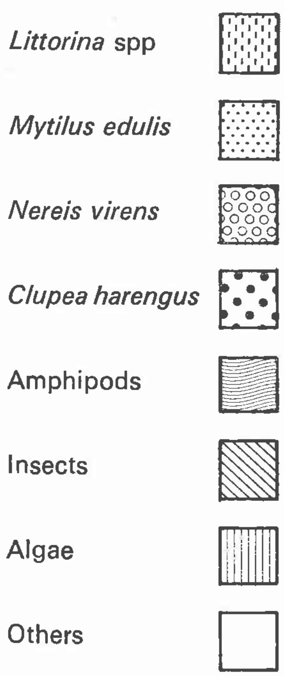

FIG. 2B. Code for all figures.

At all stations, *Mytilus* was confined to the lower half of the beach while *Littorina* was found more widely dispersed and with only a slight preference for a lower distribution on the beach in some of the areas (Figs. 2A and 2B). *Littorina saxatilis* was more abundant higher on the shore, whereas *L. obtusata* was found more among the *Fucus* and *Ascophyllum*. These observations are in agreement with those of Stephenson and Stephenson (1954), Berry (1961), and Barkman (1955), but we never attempted to systematically separate the two species during the surveys.

There was a direct relationship between the volume of *Littorina* spp. and the amount of cover at each of the four sampling areas, and the pooled data are presented in Fig. 3.

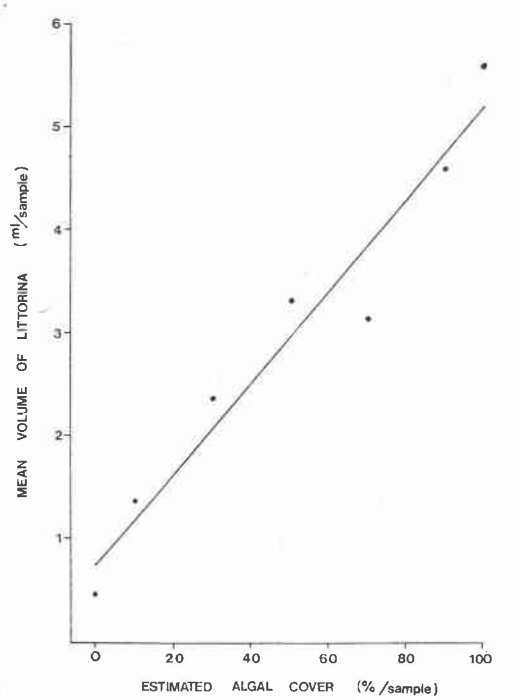

FIG. 3. Mean volume of *Littorina* spp. per sample as a function of algal cover. Date for all sampling stations (N = 464) for 1970 have been pooled. Each point on the graph is a mean for a selected class of algal cover. Regression equation for the line is $Y = 0.0445X + 0.763$.

At Ste-Luce, the volume of amphipods present on the shore increased through the summer, and the highest values were obtained by the beginning of September when sampling ceased (Fig. 4).

3. Feeding Behavior

Both adults and young showed a distinct rhythm of feeding activity associated with tidal level; most of them fed at low water, especially on the ebbing tide, irrespective of time of day (Figs. 5 and 6), but during daylight hours only.

In the spring, the females fed mainly by diving but, later, when associated with ducklings, they fed entirely by dabbling or up-ending in shallow water near the shore. Those females which played no part in the rearing of the young dispersed "seaward" (i.e., farther out into the estuary) where they were not observed feeding

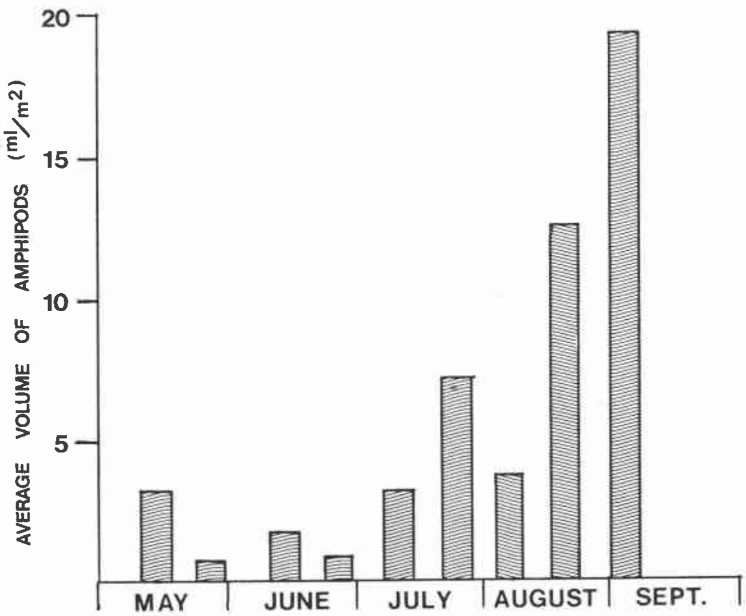

FIG. 4. Seasonal changes in average volume of amphipods per square meter for the Ste-Luce study area during the 1970 summer.

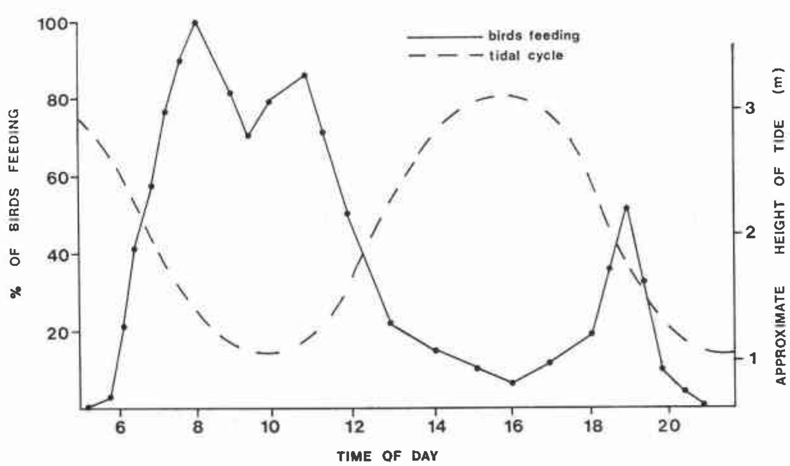

FIG. 5. Pattern of feeding activity of adult eiders with low tide in the morning, at Trois-Pistoles. Maximum number of birds observed, 166. May 3, 1969 and May 21, 1970.

by us; however, a few birds collected from that area had fed upon *Mytilus* which they must have obtained by diving.

Only one of the incubating females examined had any food remains in her gizzard, and since the birds lost about 45% of their gross body weight during laying and incubation (Fig. 7), we conclude that they do not feed regularly during this time. Part of the weight loss observed resulted from atrophy of some muscles, in particular, the breast muscles and those of the gizzard (Table 4). These findings are similar to those of Belopol'skii (1957) in Russia, Milne (1963), Gorman and Milne (1971), and MacDougall (1971) for the subspecies *S. m. mollissima* in Scotland.

The young ducklings fed by dabbling in the shallow water at the edge of the tide or among the fronds of algae floating on the surface of the water. Seldom did they come out on to the intertidal zone when it was exposed at low tide. By the time they were 15 days old, much of their feeding was effected by diving in shallow water.

4. The Diet

(A) Seasonal Changes in Adults

In the adult birds, herring eggs (*Clupea harengus*) formed over 40% by volume of the diet during the prelaying period in May (Fig. 8). At that time, the diet of both males and females was very similar and consisted of mainly herring eggs, *Nereis virens*, and assorted algae (Table 5). Later in the season, however, *Nereis*, *Littorina* spp., amphipods, and algae were found to occur with greater frequency. By the end of June and early July, herring eggs had almost disappeared from the diet while *Nereis* became a very important item to adult females. In late July and early August, *Littorina* became the most important food item with amphipods increasing in importance in late August and September (Fig. 8). This late-season diet is remarkably similar to that of ducklings (Fig. 10) but our adult sample was largely obtained from attending females. A few observations of adults of both sexes (in the absence of young) feeding in the infralittoral zone indicated that *Mytilus* was being consumed.

TABLE 4

Weight of the gizzard in adult eiders, in grams

	N	$\bar{x}$	SD
Males	12	80.3	11.9
Females (before laying)	6	80.3	16.3
Females (during last days of incubation and first days of chick rearing)	13	32.0	5.1

TABLE 5

Importance of various food items in the diet of adult eider, from late April to mid-June, 1969 and 1970. The value is an index of food importance (see text)

	N	Herring eggs	*Nereis virens*	Algae	Other
Males	19	81	14	1	4
Females	18	75	15	8	2

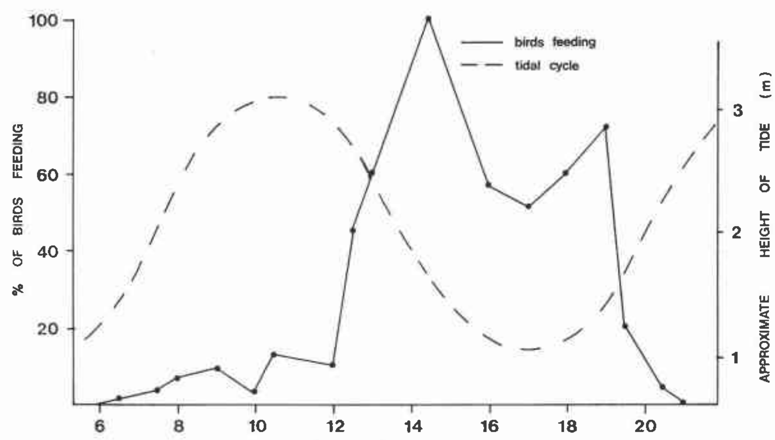

FIG. 6. Pattern of feeding activity of adult eiders, with low tide in the afternoon, at Trois-Pistoles. Maximum number of birds observed, 121. May 26, 1969.

(B) Changes with the Age of Ducklings

Littorina formed between 30% and 97% of the diet of the ducklings, depending upon their age, and tended to mask the other food items (Fig. 9 and Appendix 1). The food of the very young ducklings was more diversified than that of the older ones, but insects were a notable and surprising part of the diet during the first 2 weeks of life (Fig. 9). The bulk of the insects identified in their crop belonged to the family Bibionidae. When the ducklings were in their 2nd week of life, *Littorina* increased rapidly in importance from about 30% up to about 75% in their 3rd week; by their 5th week, it had reached about 90% and remained the predominant item from that point in time onwards.

In September, unfledged young were more attracted to amphipods than they were during the earlier part of the summer, perhaps as a result of the increasing abundance of that particular food type (Fig. 10).

(C) Electivity

We have investigated whether the ducklings showed selection for any particular food item, using the formula derived by Ivlev (1961):

$$E = (r_1 - P_1)/r_1 + P_1$$

where r_1 = percentage of this element in the diet

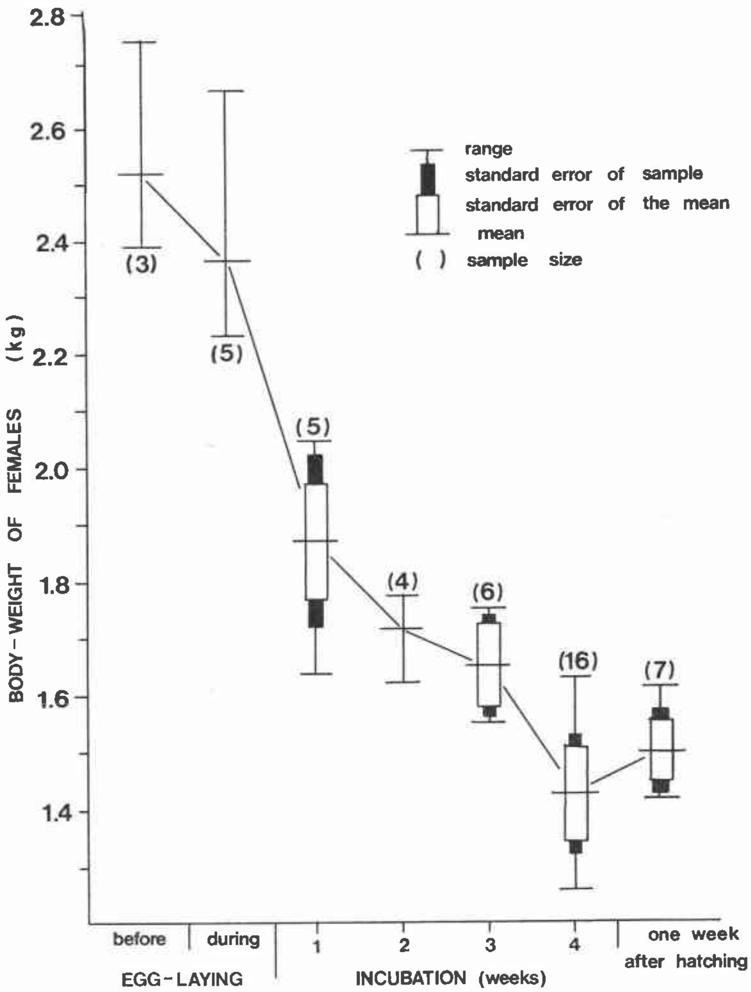

FIG. 7. Changes in body weight of adult female eiders during egg-laying and incubation. Stage of incubation is established by examination of embryos, while females designated "1 week after hatching" were so described by aging the ducklings accompanying them.

and P_1 = percentage of this element in the environment. Values of the index range from −1 (when an element is completely ignored), to +1 (element highly selected). Values around zero indicate that the element is present in the diet in the same proportion as it is found in the environment. The indices calculated in Table 6 suggest that the ducklings completely ignored mussels which were abundant in their feeding areas while they showed selectivity for *Littorina*, at Ste-Luce, and to some extent at Cap-à-l'Orignal.

The mean size of *Littorina* eaten by ducklings increased as the birds grew older (Fig. 11), implying that size selection by ducklings occurred, but the critical comparisons between sizes present on the beach and those present in the diet were not made at the time.

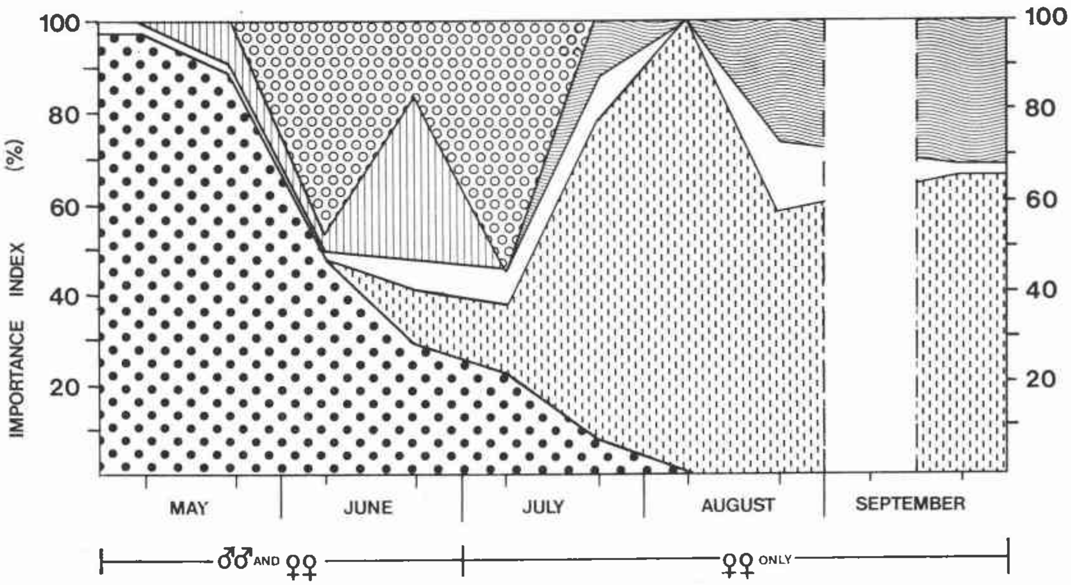

FIG. 8. Variations (in the index of food importance) in the diet of adult eiders with season, 1969 and 1970. Samples in July, August, and September are from females only; key as in Fig. 2B.

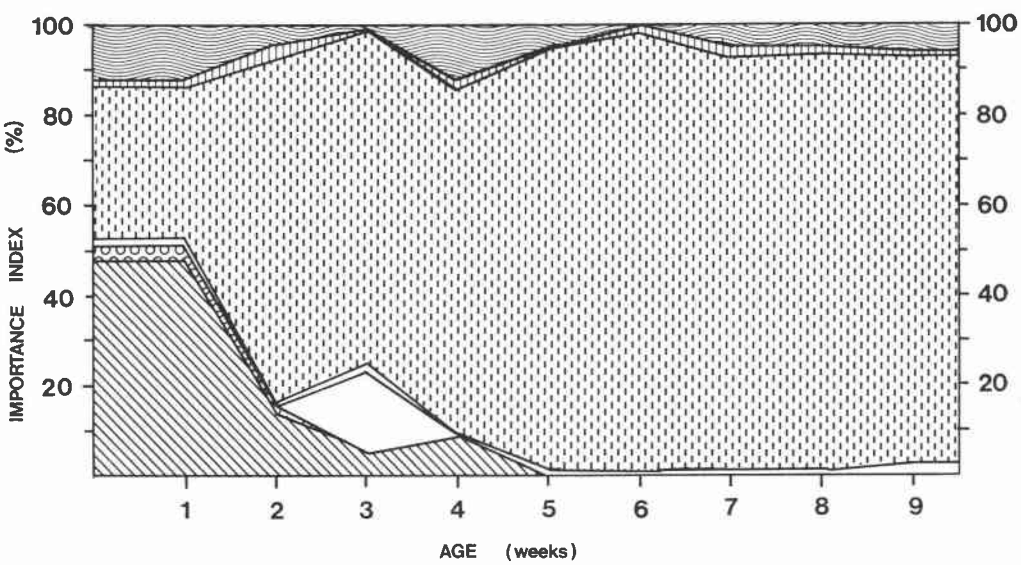

FIG. 9. Variations (in the index of food importance) in the diet of eider ducklings with age. Key as in Fig. 2B.

5. Energy Requirements

(A) Requirements of Captive Birds

The daily food consumption of growing ducklings and of adults was estimated from a series of trials carried out with birds of known age, held in captivity. These trials indicated that consumption and assimilation by ducklings reached the same levels as those of adults by the 3rd week in life (Table 7). The slight decrease at the end of the growing period has yet to be explained. As can be seen from Table 7, consumption values for ducklings, fed turkey starter, ranged from about 250 kcal/bird per day at 9 days of age, to around 720 kcal/bird per day during the rapid growth period from week 3 to week 8, and then declined to about 475 kcal/bird per day at fledging. After correction for faeces, these give corresponding assimilation values of about 200, 510, and 350 kcal/bird per day.

Similar feeding trials, on growing ducklings aged 54 days, were carried out in 1971, using mixtures of *Littorina* and *Gammarus* as food. Between feeding trials, experimental birds were kept on a mixture of "natural" foods, namely mollusks or crustaceans. These trials gave an estimated consumption value of 516 kcal/bird per day while faeces amounted to a mere 50 kcal, assimilation being therefore 466 kcal/bird per

TABLE 6

Electivity indices (see text for details of computation) for eider ducklings and their major prey items, *Mytilus* and *Littorina*, in the four study areas

	Cacouna	Trois-Pistoles	Cap-à-l'Orignal	Ste-Luce
Littorina				
Available*	94.77	44.34	47.83	13.93
Eaten*	97.02	31.67	76.61	89.53
Electivity index	0.01	−0.16	0.25	0.72
Mytilus				
Available*	0.04	51.46	47.03	84.79
Eaten*	0.43	0.00	0.06	0.67
Electivity index	†	−1.00	−0.99	−0.98

*Values are expressed as an "index of importance."
†Numbers of *Mytilus* too low to warrant calculations.

TABLE 7

Consumption and assimilation rates from feeding trials with captive eiders hatched in captivity, summer of 1972. Birds are fed commercial turkey starter. Feeding trials lasted 72 h; age given is the age at the beginning of the trial

Age, days	No. of birds in group	Energetics, kcal/bird per day: Consumption	Faeces	Assimilation
9	4	195.0		
11	4	240.6	43.2	197.1
14	4	522.1	208.7	313.4
24	8	763.1	249.3	513.8
26	8	742.7	199.8	542.9
33	8	673.2	147.8	525.4
38	8	687.7	230.9	456.8
52	8	726.2	204.7	521.5
64	4	469.9	112.7	357.2
79	8	480.3	140.0	340.3
"Adults"	2	682.7	166.6	516.1

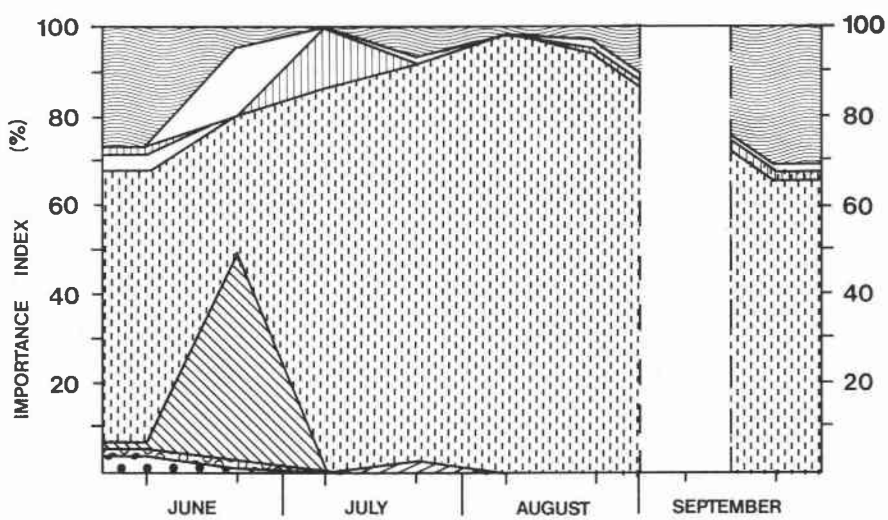

FIG. 10. Variations (in the index of food importance) in the diet of eider ducklings with season. Key as in Fig. 2B.

day. These two values for consumption (521 kcal at age 52 days (Table 7), and 466 kcal) obtained from birds kept on radically different diets were considered close enough to warrant confidence in applying the values from "turkey starter" feeding trials to the field situation.

(B) Computation of Food Intake in Nature, and Impact on Food Supplies

The numbers of birds feeding in our study areas were determined by counts conducted at least every 2nd week. The number of "duck-days"[3] for each area was then calculated (Table 8). After August 1, it was difficult to distinguish between adult females and young birds in the field, and they have been lumped together for the purposes of calculating duck-days after that date.

To estimate the total amount of *Littorina* being consumed in the study areas by the eiders,

[3]The number of "duck-days" is the product of the number of birds present feeding and the number of days they spent in the area.

TABLE 8

Estimation of number of "duck-days" spent by eiders feeding on *Littorina* at Cacouna, June–September 1970

Time period		Mean no. of birds present	Total "duck-days"*	% *Littorina* in diet	Corrected "duck-days"†
1–15 June	Y	28	420	60	252
	A	77	1155	1.5	17
16–30 June	Y	198	2970	30	891
	A	147	2205	13	287
1–15 July	Y	70	1050	80	840
	A	147	2205	16	353
16–31 July	Y	120	1920	97	1862
	A	134	2144	68	1458
1–15 Aug.	Y & A	180	2700	99	2673
16–31 Aug.	Y & A	127	2032	80	1626
1–30 Sept.	Y & A	58	1740	65	1131
Totals			20541		11390

NOTE: The values for percentage of *Littorina* in the diet are derived from Figs. 9 and 12. Calculations are presented as an example; similar calculations have been done for the other three study areas and only the summary values for these are presented in Table 10. Y = young; A = adults.

*"Ducks-days" are the number of ducks present × number of days (15) in time interval.

†"Corrected duck-days" are the number of duck-days feeding solely on *Littorina* obtained from the product of "duck-days" and percentage *Littorina* in the diet for each time period.

TABLE 9

Estimated consumption of *Littorina* by eiders at Cacouna, June–September 1970

Time period		Energy requirements, kcal/bird per day	Corrected "duck-days"	Total consumption in kcals	Total consumption in kg of *Littorina**
1–15 June	Y	170	252	42 840	79.2
	A	683	17	11 611	20.1
16–30 June	Y	493	891	439 263	760.6
	A	683	287	196 021	339.4
1–15 July	Y	546	840	458 640	794.2
	A	683	353	241 099	419.5
16–31 July	Y	719	1 862	1 338 778	2 318.2
	A	683	1 458	995 814	1 724.4
1–15 August	Y & A	661	2 673	1 766 853	3 059.5
16–31 August	Y & A	621	1 626	1 009 746	1 748.5
1–30 Sept.	Y & A	621	1 131	702 351	1 216.2
		Totals	11 390	7 203 016	12 479.8

NOTE: Calculations are presented as an example; similar calculations have been carried out for the other three study areas and only the summary values for these are presented in Table 10. A = Adults; Y = Young.

*The conversion of kilocalories to kilograms live weight of *Littorina* is based upon the calorific value of dry-flesh weight of *Littorina* taken as 3391 cals/g, and on the ratio of total fresh weight/dry-flesh weight being established as 5.9:1.0.

we have multiplied the values of duck-days for each 2-week period by a corresponding coefficient for the percentage of the diet represented by *Littorina* during that same period. From this value, and that of the daily requirement, we estimated the consumption of *Littorina* from each of our four study areas during the summer (Table 9).

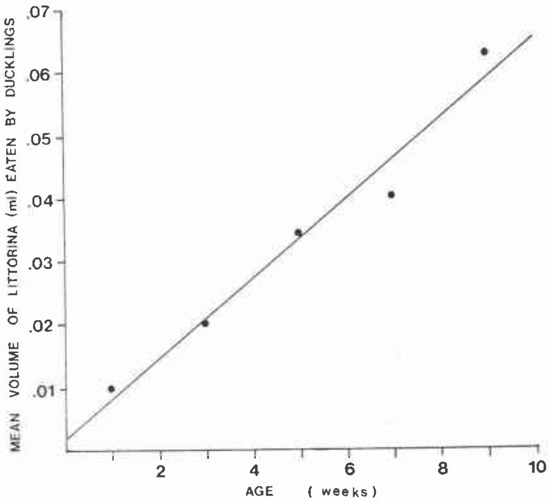

FIG. 11. Relationship between the mean volume of individual *Littorina* taken by eider ducklings and the age of the ducklings. Equation for the regression line is $Y = 0.063X + .0020$. The value for "r" is 0.982, which is significant at the 99% level.

From our estimates of densities of the food species and measurements of the surface area of each study beach, we also have calculated the total standing crops of *Littorina* in each area (in July). Assuming all of this material to be available to the birds as food, it becomes possible to estimate the proportion of their food being consumed by the birds during the summer (Table 10). These calculations indicate that the eiders were taking about 10–15% of the *Littorina* at Cacouna, Trois-Pistoles, and Cap-à-l'Orignal but were probably taking nearer 30% of the standing-crop biomass of this gastropod for food at Ste-Luce. It is important to appreciate that in this table we have estimated only the consumption of *Littorina* from the four study areas; the total energy requirements for the birds during the summer will be much higher and will be met by their consumption of other food organisms in their diet.

Finally, the numbers of ducklings per square

TABLE 10

Estimates of the proportion of the standing-crop biomass of *Littorina* eaten by eiders in the four study areas, June–September 1970

	Cacouna	Trois-Pistoles	Cap-à-l'Orignal	Ste-Luce
Total "duck-days"	20 541	22 760	29 035	50 820
Corrected "duck-days" for *Littorina*	11 390	10 228	15 035	33 038
Estimated total energy intake, kcal	7 203 016	6 577 763	9 497 833	20 422 782
Estimated total consumption of *Littorina*, kg	12 480	11 390	16 466	35 364
Estimated standing-crop biomass of *Littorina*, kg	127 906	106 903	103 204	107 813
% of standing-crop biomass consumed by eiders	9.7	10.7	15.9	32.8

TABLE 11

Abundance of *Littorina* and duckling densities, in July in the four study areas

	Cacouna	Trois-Pistoles	Cap-à-l'Orignal	Ste-Luce
Food density (*Littorina* in ml/m²)	27.136	26.112	29.104	36.864
Eider ducklings/km² of intertidal area				
July 1	57.0	36.9	123.2	161.5
July 15	42.8	33.9	111.4	93.3
Eider ducklings/metric ton of *Littorina*				
July 1	1.40	0.95	2.85	3.31
July 15	1.05	0.87	2.58	1.91

kilometer of beach (i.e., of intertidal area at low tide) as well as per metric ton of *Littorina* were calculated (Table 11). We selected 1 and 15 July since, at that time, most of the eggs had hatched and the ducklings were still easy to distinguish from adult females. Moreover, movements of the broods and creches (groups of broods) along the coast appeared to have stopped in early July.

The numbers of ducklings per unit area of intertidal shore during the early part of July showed a direct relationship with food densities over the four study areas (Table 11). However, the number of ducklings per unit weight of food is not constant from one area to another (varying from a low of 0.95 in Trois-Pistoles on July 1 to a high of 3.31 in Ste-Luce for that same date); we are therefore forced to conclude that there exists no simple relationship between food abundance and the importance of any one brood-rearing area. Other factors such as freedom from disturbance, presence of shelter and loafing areas, proximity to good nesting habitat, tradition, presence of predators etc. will certainly influence the number of ducklings to be reared in any one of the coastal areas.

Discussion

In the Ythan estuary, Scotland, Gorman and Milne (1972) consider that the female spends, on the average, a mere 3.5 days with her brood, only to leave it for feeding grounds where she has a better opportunity to recoup weight losses that occurred during incubation. In such a situation, broods amalgamate to form large creches in which survival of ducklings is very low. Although we do not have quantitative and comparative data, a good proportion of the females in the St. Lawrence estuary tends to stay much longer with the brood, often accompanying it well into the 8th or even the 10th week of life. Creches do exist in the St. Lawrence but they are much smaller in size than in the Ythan and perhaps involve no more than 50% of all the ducklings compared with about 95% of the ducklings in the Ythan. So that, throughout the rearing period, adult females of the St. Lawrence estuary feed in the intertidal zone upon *Littorina*, whose flesh/shell ratio is much lower than that of *Mytilus* and who may, therefore, be considered a less desirable food supply than the latter for a bird in poor physiological condition. Here, one can only conclude that this food supply is adequate and that the survival of postnesting females is not adversely affected by their habit of remaining with their ducklings. Perhaps also duckling survival is enhanced by the presence of the parent bird and we are currently exploring these relationships.

Pertsov and Flint (1963) have attempted to estimate the impact of feeding by ducklings and adult females on their food supplies in the Kandalaksha Reserve in the White Sea area of the Union of Soviet Socialist Republics; these early estimates suggested that consumption values by eiders were around 15% (94.7 metric tons (t)) of *Littorina* stocks, and 2.7% (123.3 t) of *Mytilus*. In the same locality, Gerasimova and Baranova (1960) have shown that gastropods formed 38% of the overall diet of ducklings, but may be as high as 80% of the diet up to 2 weeks of age. *Gammarus* only became an important food item after the ducklings were 10–12 days old.

In the latter study, gastropods formed only 17% of the diet of the adult females, while bivalves made up 56%, *Balanus* 17%, and *Gammarus* 18%.

These findings, although differing in detail from ours in the St. Lawrence are in general agreement with the diets we have described. They contrast markedly with observations made in Scotland where eider ducklings have been recorded feeding largely on *Corophium volutator*, *Hydrobia ulva*, *Mytilus edulis*, and *Littorina* spp. in the Ythan estuary (Milne 1963). Those ducklings which feed on exposed mud flats of the intertidal zone of necessity eat mud-dwelling invertebrates, whereas, in the estuary of the St. Lawrence, they seldom feed on the exposed shore, but remain in the shallow water feeding upon invertebrates attached to floating algae or rocks.

Estimates of the proportion of the food supplies eaten by eiders have been made for winter situations in the Ythan estuary (Milne 1968; Milne and Dunnet 1972) and in Balsfjord, Norway, by Brun (1971). In these latter studies, the depletion of the standing-crop biomass of food during the winter has been used as an estimate of the impact of bird predation on their food resources. This is reasonable over a time period when no production is taking place, but when applied to a summer situation, when production is likely to mask any predatory effect, the results obtained would be of little value. We have attempted to estimate consumption values by an independent method (not dependent upon a measured depletion of standing crop) and have then applied these values to the field situation. To express these calculated consumption values as a proportion of the summer standing-crop biomass is, at best, a crude method of estimating the importance of these secondary consumers in the littoral ecosystem. The production of *Littorina*, occurring simultaneously with predation, will tend to replace the losses, and our calculations will show underestimates of the proportion of the food resources eaten by the birds.

Brun (1971) found that, in depths less than 30 m, common eider predation (amounting to 25 g/m^2 per year) was sufficient to balance the annual production of *Chlamys islandica*; and Milne and Dunnet (1972) have also shown that all of the annual production by *Mytilus edulis* in the Ythan estuary may be accounted for in terms of predation, of which eiders represented some 30%. A study using this approach was undertaken at Cap-à-l'Orignal in 1972, and data are currently being analyzed.

The predation values of 15–30% of the July standing-crop biomass may be overestimates in the sense that production has not been considered; on the other hand, selection by the birds of food items of a restricted size range of food item and the availability of these organisms to the birds as food (e.g., many *Littorina* crowd into crevices in the rocks where they are not readily picked up by the birds) serve to reduce the actual food resource from which eiders may feed, and their impact on the available food may be even higher than we are suggesting. Further studies on these aspects are required.

The estimated values for consumption from captive birds raise the problem of the relevance of such data to the wild situation. From observations of feeding rates of wild birds in the Ythan estuary, Milne (unpublished) has estimated a daily consumption value of around 520 kcal/bird per day when feeding on *Mytilus*. Under semi-captive conditions, Swennen (1970) conducted feeding trials, using *Cardium edule* as food, and has estimated a consumption rate of about 720 kcal/bird per day. These independent studies and widely differing sets of observations lend credence to our estimated consumption values and hence, to our estimated measurements of impact upon the food resources.

We have confined our observations mainly to those eiders that feed in the intertidal zone. We estimate that about one-half of the 25 000 pairs of nesting birds do most of their feeding in this intertidal zone during May (males and females), an equal number (females and ducklings) during June, about 15 000 (females and ducklings) during July, and 10 000 in August (females and ducklings). For the most part, birds feeding in the intertidal zone make use of *Littorina*; the caloric content of this invertebrate was found to be 3.4 kcal/g dry-flesh weight. Converting to whole weight (using a 75% water content and a $\frac{1}{8}$ flesh/whole ratio), we can estimate the amount that is removed from the beach by the eiders. This amounts to 100 t/day during May and June, to 60 t/day during July, and to 40 t/day during August. Similar figures are obtained for the rest of the population that obtains its food (*Mytilus* for the most part) in the infralittoral zone. The role of such a consumer in the estuarine ecosystem in the recycling of nutrients and the turnover of inorganic material in littoral waters must be of considerable importance to the productivity of the estuary; especially since this occurs in a relatively narrow and shallow littoral corridor along the southern shore of the estuary at a time when biological productivity is peaking. It would seem important to measure how much of the rejecta are returned in an instantly usable form to the littoral waters.

Appendix 1

Organisms found in the gut of eiders; frequency of occurrence. Birds examined included 162 adults and 245 ducklings. Only those animals that occurred in at least 5% of either group are included. A 2% minimum level has been established for algae

	Adults	Ducklings
Mollusks		
Gastropods		
Acmaea testudinalis	27.2	1.6
Buccinum undatum	27.8	1.2
Hydrobia minuta	0.6	5.3
Lacuna vincta	6.2	7.3
Littorina saxatilis	44.4	47.4
Littorina obtusata	37.6	41.6
Littorina sp.	66.0	95.5
Pelecypods		
Mya arenaria	8.0	0.4
Mytilus edulis	29.6	9.0

Appendix 1 (*Concluded*)

	Adults	Ducklings
Crustaceans		
Amphipods		
Gammarus oceanicus	3.7	7.3
Unidentified	12.3	19.2
Echinoderms		
Strongylocentrotus droebachiensis	11.1	2.0
Annelids		
Nereis virens	24.7	8.6
Insects		
Diptera		
Bibionidae	2.4	6.1
Unidentified	0.6	15.9
Fishes		
Clupea harengus (eggs)	24.1	3.7
Phanerogams		
Unidentified	8.0	6.9
Algae		
Acrosiphonia arcta	3.1	
Diatoms	1.8	2.0
Fucus sp.	3.7	0.8
Monostroma sp.	3.1	0.4
Pilayella littoralis	2.5	1.2
Ulothrix	3.1	0.4
Unidentified	9.3	7.3

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