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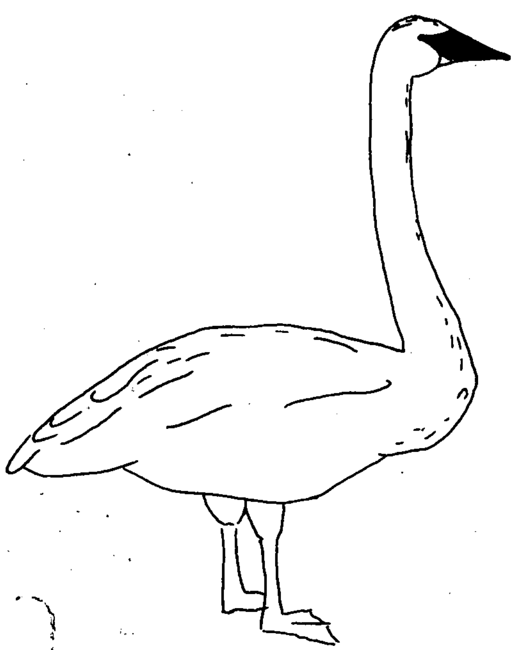
SOME ASPECTS OF THE WINTER FEEDING ECOLOGY OF TRUMPETER SWANS AT PORT ALBERNI AND COMOX HARBOUR BRITISH COLUMBIA

by

Richard W. McKelvey



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Frontispiece. Trumpeter Swans feeding on the emergent vegetation at Comox Harbour.

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SOME ASPECTS OF THE WINTER FEEDING ECOLOGY OF TRUMPETER SWANS AT PORT ALBERNI AND COMOX HARBOUR, BRITISH COLUMBIA

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ABSTRACT

The winter feeding ecology of the Trumpeter Swan (*Cygnus cygnus buccinator*) was studied between 1977 and 1980 at the Somass River estuary, Port Alberni, and Comox Harbour, British Columbia. Studies included an examination of habitat characteristics, habitat use, and food habits at Port Alberni and Comox Harbour; an analysis of behaviour patterns, particularly feeding behaviour, at Comox Harbour; and a measure of the amount of food consumed on the estuary and on an adjacent farm at Comox Harbour. Management recommendations are presented for the habitat and the swan populations at Comox Harbour.

Biomass, protein, carbohydrate, fat and fiber content, and gross energy levels of potential foods available are reported. In general, estuarine foods were low in protein (7.1% at Port Alberni; 7.0% at Comox) and high in fiber (47.8% at Port Alberni; 63.4% at Comox) while foods available on dairy pastures at Comox were high in protein (22.9%) and lower in fiber (32.2%). During the winter of 1977-78 Port Alberni received 6229 swan-days use, or 272.0 swan-days/ha, while Comox Harbour received 12671.5 swan-days use, or 1534.1 swan-days/ha. The attractiveness of the Comox Harbour area was thought to be due to the availability of nearby dairy pastures and the swans recent acquisition of the habit of grazing on those pastures.

The predominant food items, determined visually, were rhizomes of *Scirpus americanus* at Comox Harbour. Microscopic analysis of scats at Comox Harbour for food preferences revealed fronds of *Zostera marina* to be the most important food item (frequency of occurence = 33.8%) followed by *Scirpus* spp. rhizomes (30.8%), pasture grasses (18.5%) and *Carex* spp. rhizomes (13.8%).

Of eight categories of behaviour studied at Comox Harbour, feeding was the dominant activity in daylight periods (37.7% of the time), while sleeping predominated during the night (41.5%) and over the total 24h period (36.0%). Feeding on dairy pastures occured only during daylight and accounted for 74.6% of the time spent there. All types of behaviour were found to be reducible to two basic types: feeding and resting. On average 57.6% of a given daylight period and 47.2% of a night period was spent feeding on the estuary, while 86.1% of the time on dairy pastures was spent feeding. Feeding on the estuary was regulated by tidal conditions which in turn caused both diurnal and nocturnal feeding. No other environmental factor was seen to be important in regulating feeding behaviour, except perhaps temperature. There was a slight negative correlation (r= -.53) between number of swans feeding at night and temperature. When grazing on dairy pastures, feeding was more or less constant, with no daily peaks of intensity.

It was estimated that approximately 10% of the available standing stock of emergent vegetation was removed annually from the Comox Harbour study area. Based on estimates of regeneration time of emergent vegetation on the Fraser River estuary, the Comox Harbour habitat is thought to be capable of sustaining slightly higher levels of use. Swans grazing on pastures removed 1.2 kg (dry weight) of grass per swan per day; studies of the effect of that level of use on forage crop yields are continuing.

Management recommendations considered to be of prime importance in maintaining swan populations at Port Alberni and Comox include: protection of habitat at both locations; rehabilitation of habitat at Port Alberni polluted by wood chips and logging debris; completion of studies of the long term effects of grazing by swans on forage crop yields.

ACKNOWLEDGEMENTS

Many people have contributed to this study, in all its phases. I thank Dr. N. Verbeek for his advice and support throughout, and for editorial criticism of this report and related papers. Committee members Drs. R. Sadleir and R. Brooke provided helpful criticisms and direction also. The project was financed by the Canadian Wildlife Service, Pacific and Yukon Region, and thanks go to N. Perret and G. Kaiser for their assistance.

I thank the following people for assistance in the field, in the lab., with data analysis, manuscript review and general discussions: K. Simpson, L. Cullen, M. Wyborn, N. Dawe, M. Noble, D. Flook, P. E. Whitehead, P.M. Whitehead, E. McEwan, M. Mazalek, D. Boak and R. Rogers. Special thanks go to N. Holman for assistance with aerial photography, E. Smith for his friendly cooperation during the swan grazing study on his farm, L. Reid for typing and to P. Sanders for putting up with me during this study.

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FOREWORD

The idea for this project was first developed in the winter of 1974-75, when I was employed by the Canadian Wildlife Service to make weekly counts of birds wintering at Comox Harbour. I had many opportunities to observe Trumpeter Swans at Comox Harbour, and was intrigued by their feeding behaviour. Early in the winter, feeding was concentrated on the emergent vegetation of the Harbour, where large amounts of material was excavated as the swans grubbed for rhizomes. In late winter swans began to feed on adjacent agricultural fields, spending less time on the estuary. I hypothesized that overuse of the emergent vegetation as a food source was forcing the swans to make use of less desirable foods, such as waste agricultural crops.

In 1977-78 I embarked on a research project to determine if overuse of the estuarine food was forcing swans onto adjacent farm fields. Two things soon became evident: (1) there was almost nothing known of the winter ecology of Trumpeter Swans, including habitat preferences, food habits and feeding behavior; and (2) swans were being attracted to Comox Harbour because of the farm fields. The fields were not a second choice, to be used after the estuarine food resources were depleted, but rather the first choice, to be used in preference to the estuarine foods. The project was modified and expanded so that basic information on Trumpeter Swan winter ecology was collected. The emphasis was mainly on feeding ecology, with the impact of swans on their winter food resources, both estuarine and farm fields, also being investigated.

This report presents the results of that study. It consists of four sections, each more or less independent of the others. Each addresses one of the following objectives of the project: (1) describe what constitutes wintering Trumpeter Swan habitat, in terms of abiotic and biotic factors, and habitat use, and foods at two main wintering areas - Comox Harbour and the Somass River estuary at Port Alberni; (2) describe the behaviour of wintering Trumpeter Swans at Comox, particularly feeding behaviour, to determine how Trumpeter Swans interact with their environment; (3) determine what effect Trumpeter Swans have on the Comox area habitat; and (4) make recommendations that might be useful in formulating a Trumpeter Swan management plan and in directing further research efforts.

I. HABITAT CONDITIONS

INTRODUCTION

The current world population of Trumpeter Swans (Cygnus cygnus buccinator) is thought to number about 5500 birds, in two subpopulations. One subpopulation, about 500 birds, breeds in northwestern Alberta and in the tri-state area of Montana, Wyoming and Idaho and winters in the tri-state area. The larger subpopulation, about 5000 birds, breeds mainly in Alaska and winters along the Pacific coast from Alaska to northern California (McKelvey and Stroops in prep).

At least 50% (about 2500 birds) of the Alaska subpopulation winters in British Columbia (McKelvey in press). Preferred winter habitats are the estuaries of the many creeks and rivers along the coast, while smaller groups of swans are found on inland waterbodies which remain ice free. Until recently, information on the ecology of Trumpeter Swans wintering in British Columbia consisted only of winter surveys (Smith and Blood 1972; Davies in press; McKelvey 1979) and the casual observations of naturalists (Campbell et al. 1979: 145). The importance of estuaries to wintering swans has long been recognized (Brooks 1923; Smith and Blood 1972) but the intensive grazing of dairy pastures is a recent phenomenon (McKelvey 1979).

Data on the habitat characteristics, habitat use and food habits of Trumpeter Swans wintering on the Somass River estuary at Port Alberni, the Courtenay River estuary at Comox Harbour, and on dairy pastures adjacent to Comox Harbour are presented in this section.

The analysis of food habits of many animals has traditionally required the collection of a number of specimens, their dissection and an analysis of their gut contents. However, collecting is not always possible, particularly when the species of interest is rare or otherwise protected. An alternative method for the analysis of food habits of herbivores has been the identification of plant epidermal fragments in fecal material. Although this method has been used most extensively in ruminants (Stewart 1967), it has also been applied to waterfowl (Owen 1975). Gilham (1956) ascertained the seasonal food preferences of Mute Swans (Cygnus olor) on estuaries in South Devon, England by fecal analysis; Luther (1963) used the technique on Mute Swans in southern Sweden to confirm the findings of other studies relying on direct field observation and stomach content analysis; and Mathiasson (1973) studied food habits of moulting Mute Swans in Sweden by collecting fecal samples from swans caught for banding.

The selection of habitat by birds is thought to result from both ultimate and proximate factors (Hilden 1965). Of the three ultimate factors (food availability, structural and functional characteristics of the species, and protection from enemies and weather), food availability may have been the most important influence in the evolution of the migratory habit (Lack 1968). If swans wintering along the coast of British Columbia are doing so by tradition (sensu Hochbaum 1955) in response to food availability then the most important aspect of their wintering behaviour may be how they provide for themselves (MacFadyen 1963).

In this section I have assumed that the most important aspect of Trumpeter Swan habitat selection is the ecological relationship between the swans and their food resource. I measured habitat use by monitoring bird distribution (sensu Nilsson 1972, and Stott and Olson 1973) and I measured its quality through the collection of floristic data, and selected ecological data (sensu Patterson 1976, and Courcelles and Bedard 1979).

STUDY AREAS

COMOX HARBOUR

Comox Harbour is situated on the east coast of Vancouver Island (Fig. 1). It has a southeast exposure and is characterized by above freezing temperatures, frequent precipitation and moderate snowfall in winter (Table 1).

One major river and several smaller creeks flow into Comox Harbour. Most of the freshwater comes from the Courtenay River, which flows at a mean annual rate of 57.3 m^3/sec. (Morris et al. 1979). Tides are of the mixed semi-diurnal type (Canadian Hydrographic Service 1979); during the winter highest tides generally occur in the early morning and lowest tides at midnight (Fig. 2). Flood tides cause a counter-clockwise circulation of water, freshwater from the Courtenay River being deflected and mixed along the southeast side of the harbour.

Although Comox Harbour is relatively large (app. 900 ha) and the surrounding area well settled, the harbour and foreshore remain lightly developed (Figs. 3 and 4). Only about 86 ha of wetland are alienated (Ministry of Lands, Parks and Housing 1979) the rest remaining essentially untouched.

The surficial substrate of the Comox area has developed by the deposition of glacial debris at the end of the last ice-age (Fyles 1963), and by the continued transport of sediment by the Courtenay River (Clague 1976). The substrate in the vicinity of the estuarine emergent vegetation consists of fine sands and silts over gravel at the Courtenay River mouth, grading into gravel and then cobbles to the south-east.

Farms adjacent to Comox Harbour occur on relatively well drained, alluvial soils (Day et al. 1959), while those on the uplands lie on sandy loams (Keser and St. Pierre 1973).

Fig. 1. Location of the Comox Harbour study areas.

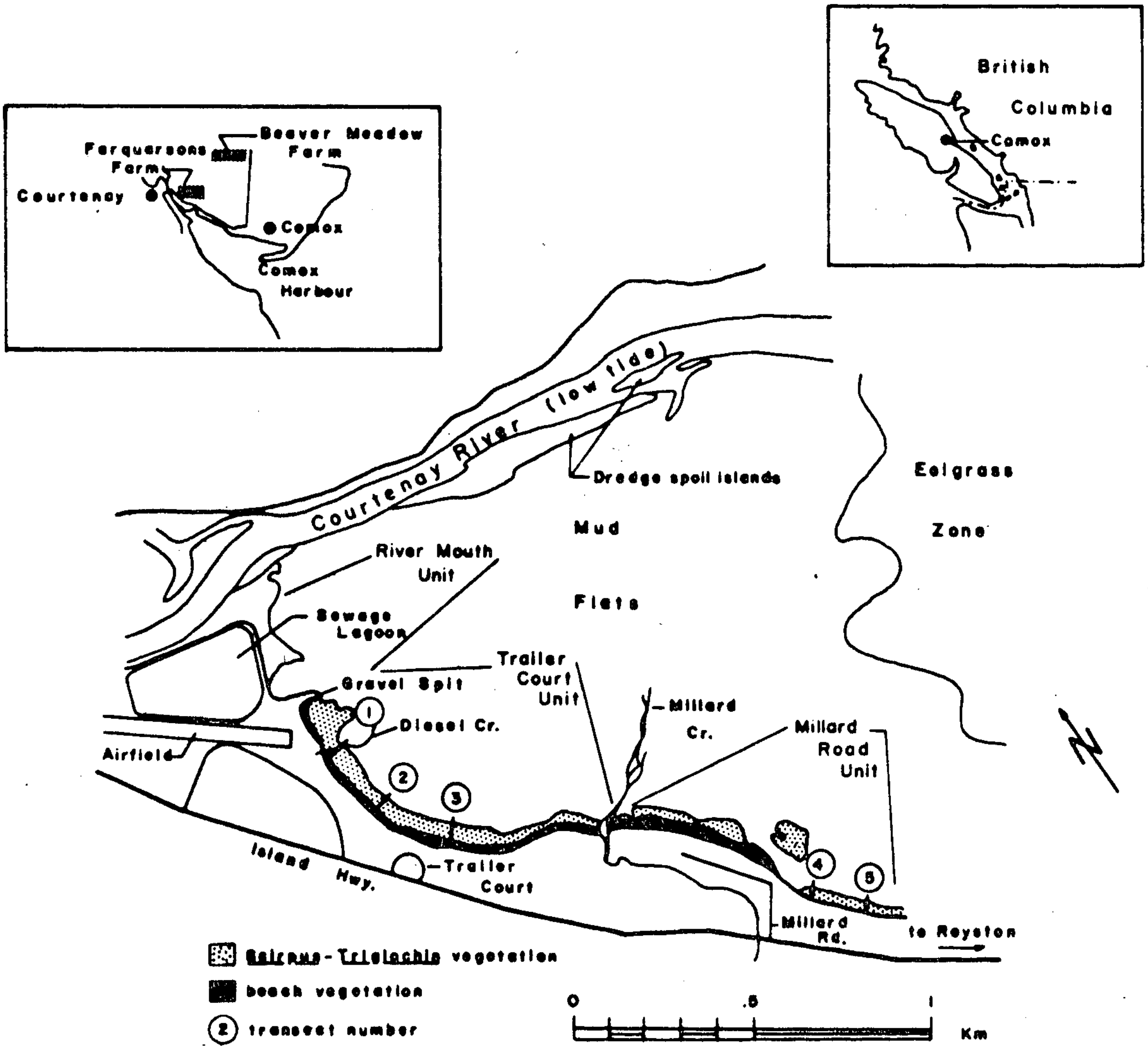
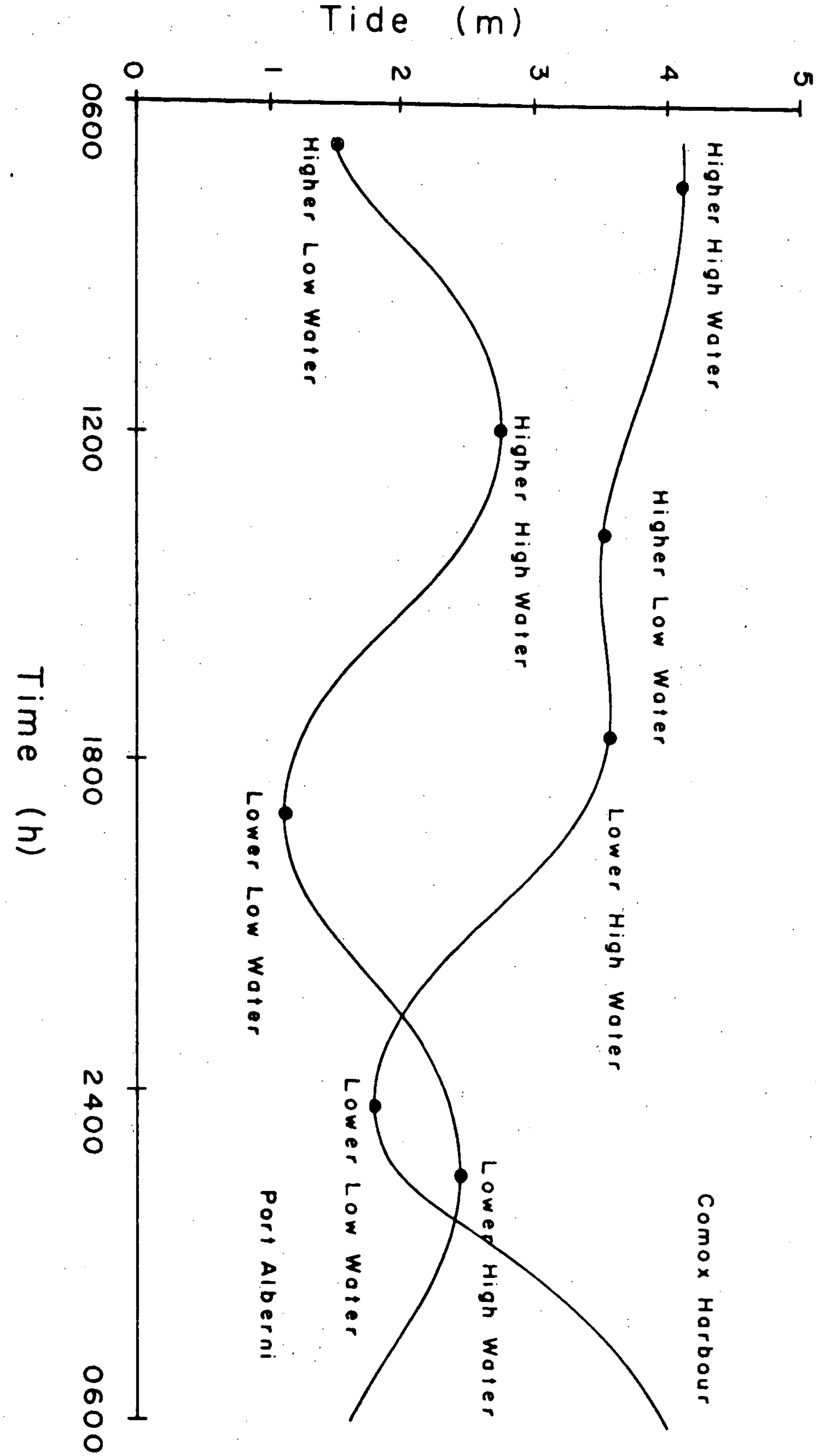

British
Columbia
Comox
Beaver Meadow
Farm
Ferquarsons
Farm
Courtenay
Comox
Comox
Harbour
Courtenay River (low tide)
Dredge spoil islands
Eelgrass
Zone
Mud
Flats
River Mouth
Unit
Sewage
Lagoon
Trailer
Court
Unit
Gravel Spit
Diesel Cr.
Millard
Cr.
Millard
Road
Unit
Airfield
Island Hwy.
Trailer
Court
Millard
Rd.
to Royston
Scirpus-Triglochin vegetation
beach vegetation
transect number
0
.5
1
Km

Table I. Long term summary of temperature (°C) and precipitation (cm) data for the winter months at Comox Harbour and Port Alberni. (Data taken from Canada Department of Environment 1971).

Comox Harbour	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Year
Mean daily temp.	5.4	3.6	2.1	3.9	4.9	7.9	9.3
Mean daily max.	8.5	6.3	4.9	7.2	8.8	12.3	13.4
Mean daily min.	2.3	.7	-.8	.6	1.1	3.4	5.2
Mean rainfall	18.0	18.2	15.3	10.9	9.9	5.5	110.1
Mean snowfall	6.9	30.2	43.2	15.7	8.9	1.3	106.2
Mean total ppt.	18.7	21.2	19.6	12.5	10.8	5.7	120.7

Port Alberni	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Year
Mean daily temp.	4.8	2.4	.6	2.6	4.7	8.0	9.1
Mean daily max.	7.7	4.6	3.0	5.9	9.4	13.8	14.1
Mean daily min.	1.9	.1	-1.8	-.8	-.1	2.1	4.1
Mean rainfall	30.6	31.3	26.7	20.1	20.2	14.0	191.6
Mean snowfall	8.1	22.1	22.6	19.6	7.9	.8	81.0
Mean total ppt.	31.4	33.5	29.0	22.0	21.0	14.1	199.7

Fig. 2. Composite tide cycles at Comox Harbour and Port Alberni from November to March 1979.


Tide (m)
0
1
2
3
4
5
Time (h)
0600
1200
1800
2400
0600
Higher High Water
Higher Low Water
Lower High Water
Lower Low Water
Comox Harbour
Higher Low Water
Higher High Water
Lower Low Water
Lower High Water
Port Alberni

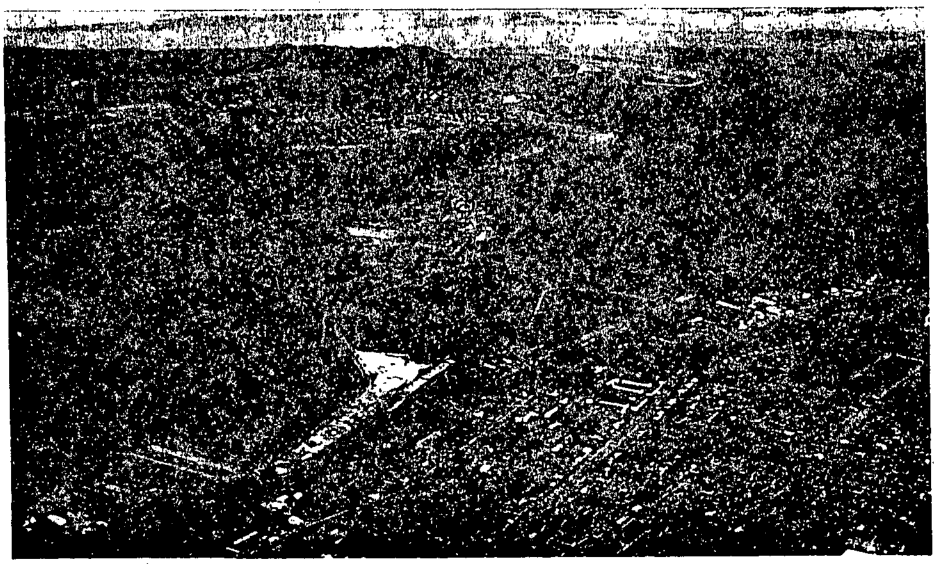


Fig. 3. Oblique aerial photograph of Comox Harbour showing the nature of the harbour and the Courtenay River estuary. Comox is at the top left and Courtenay is on the bottom right. Note the lack of development in the harbour.

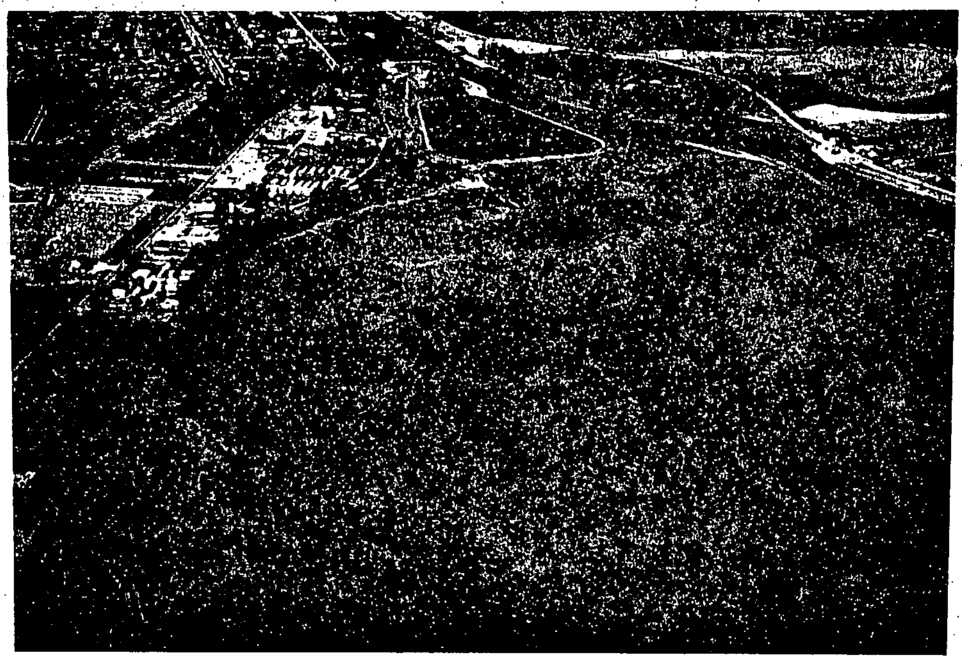


Fig. 4. Oblique aerial photograph of Comox Harbour showing the study area on the Courtenay River estuary. The emergent vegetation of importance to the swans is indicated by the arrow.

Fields grazed by swans are dairy pastures which become too wet during the winter to be used by cattle, or which are used only for the production of forage crops. Swans graze only on certain pastures, generally the most productive ones in the area. The soil is only moderately fertile, high yields of forage crops being obtained by heavy fertilization (R. DeMong, pers. comm.). The fields most frequently used by swans are dominated by rye grass (Lolium perenne)[1] and orchard grass (Dactylis glomerata).

PORT ALBERNI

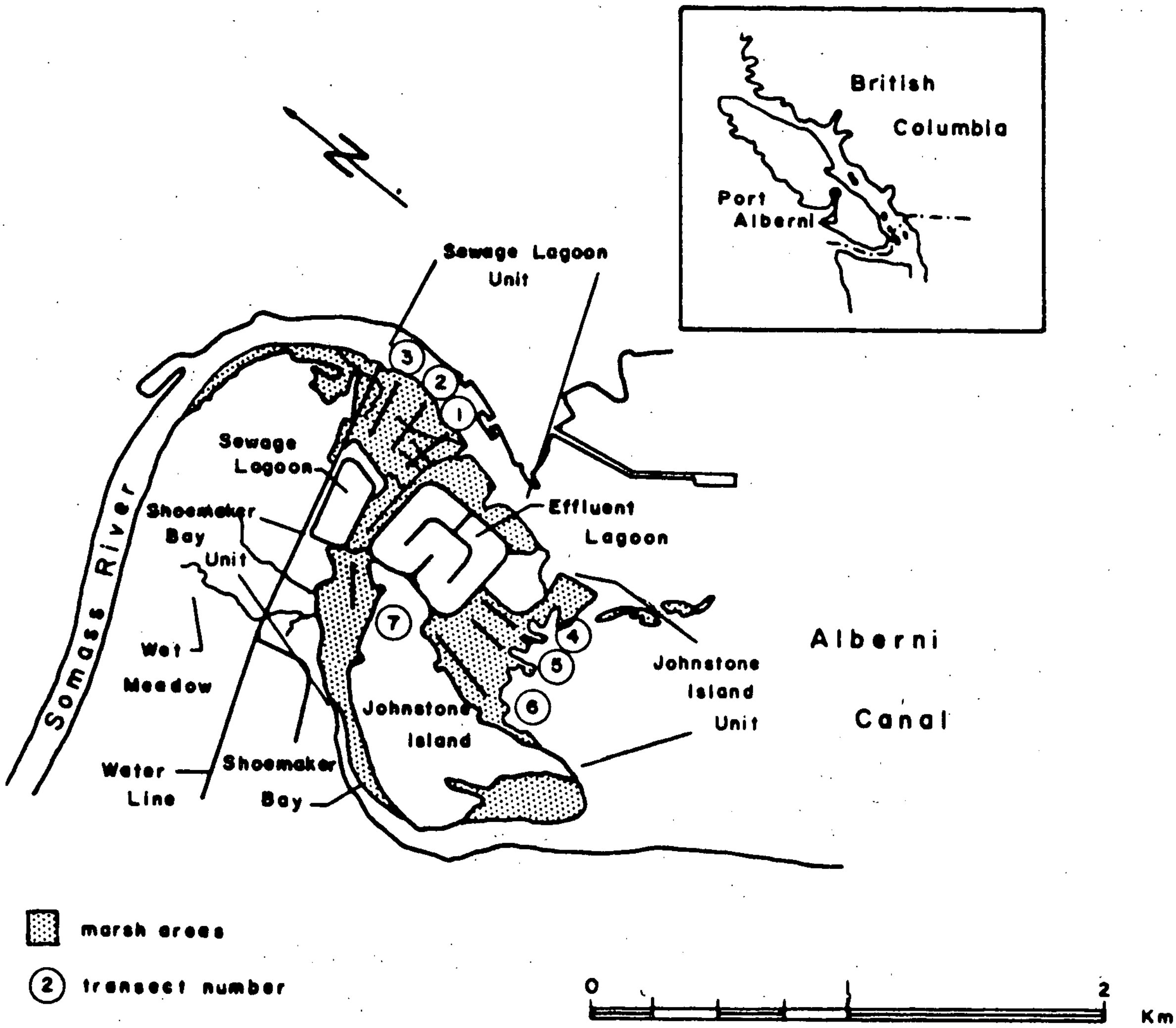
Port Alberni is located at the head of the Alberni Canal, a fjord-like inlet on the west coast of Vancouver Island (Fig. 5). The climate is similar to that of Comox Harbour but is slightly wetter and cooler in the winter (Table 1).

The Somass River is the only major source of freshwater at the head of the Alberni Canal. Its flow is regulated by a dam with a mean annual discharge of 84 m^3/sec. (Canada Dept. Fish. and Env. 1978). The tides during the winter tend to be lowest in the early evening with high tides of similar magnitude at mid-day and midnight (Fig. 2). Freshwater - saltwater mixing occurs near the foot of the delta of the Somass River (Tully 1949), the result being weak tidal currents and very little saltwater influence on the vegetation of the delta (J. Pojar, pers. comm.).

The substrate of the Somass River delta ranges from coarse sands near Shoemaker Bay, to gravel near the Somass River, overlaid by a gleysolic soil up to 1.2 m thick (Paish and Assoc. Ltd. 1973). The unconsolidated materials in the delta have been transported by the Somass River from adjacent glacial deposits (Fyles 1963), while the soil layer continues to develop from the desposition of decaying marsh vegetation (Paish and Assoc. Ltd. 1973).

[1] Plant nomenclature after Hitchcock and Cronquist (1973)

Fig. 5. Location of the Port Alberni study area.


British
Columbia
Port
Alberni
N
Sewage Lagoon
Unit
Sewage
Lagoon
Shoemaker
Bay
Unit
Effluent
Lagoon
Somass River
Wet
Meadow
Johnstone
Island
Johnstone
Island
Unit
Alberni
Canal
Water
Line
Shoemaker
Bay
marsh areas
2 transect number
0
1
2
Km

The estuary of the Somass River has been greatly affected by the settlement of the Port Alberni area. A sewage effluent pond and a pulpmill effluent treatment lagoon cover two large portions of the delta. They appear to have caused changes in the drainage pattern of the marsh (Figs. 6 and 7) in addition to removing about 16 ha of wetlands. The marsh soils are heavily polluted with wood chips from the handling facilities of the adjacent pulp mill and many parts of the marsh are covered by drift logs, bark and debris from log sorting below Johnstone Island.

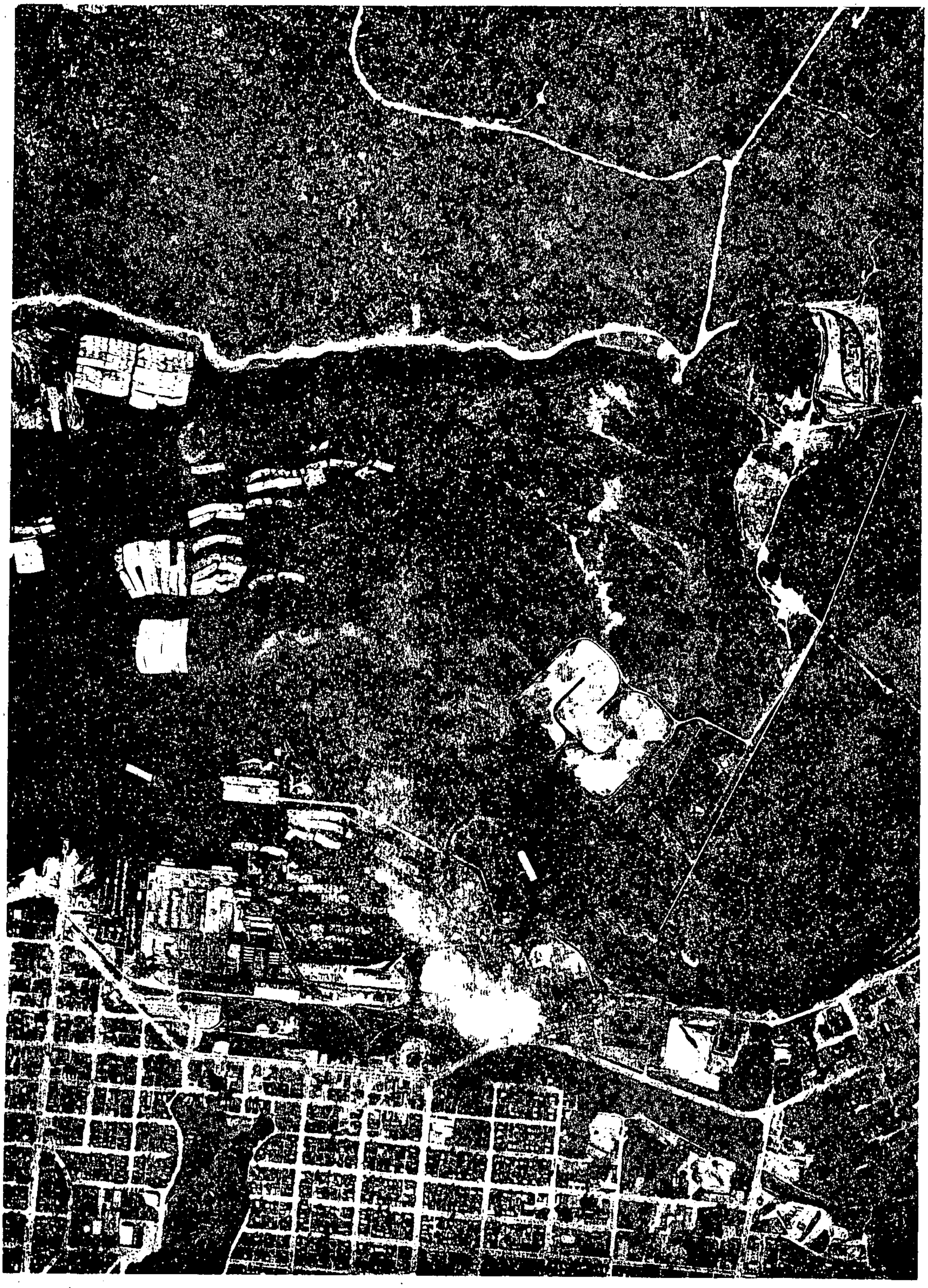
METHODS

Vegetation structure, (Mueller-Dombois and Ellenberg 1974:139) biomass and proximate analysis (Crompton and Lloyd 1959:13) of potential foods were assessed on both estuaries. A vegetation description was determined from the literature for the Somass River delta at Port Alberni (Paish and Assoc. Ltd. 1973) and by the Braun-Blanquet plant relevé technique (Mueller-Dombois and Ellenberg 1974) for the Courtenay River estuary at Comox Harbour. Vegetation composition of 327 relevés on 13 permanent transects was determined in August 1978. Methods of transect and relevé location are described in Section III. The relevé synthesis was accomplished using a computer program developed at the University of Victoria (Ceska and Roemer 1971).

Biomass of below ground plant material was measured by core sampling a volume of 2.75 l in stands of uniformly dense vegetation, in the late fall of 1977. The core diameter was arbitrarily chosen at 15.2 cm; the core depth was also 15.2 cm, that being deeper than any previously observed swan feeding craters. On the Somass River estuary 75 samples were taken from 20 stations located along seven transects. Forty-six samples from 13 stations on five transects were collected at

Fig. 6. Vertical aerial photograph of the Somass River delta, 1951.

Fig. 7. Vertical aerial photograph of the Somass River delta, 1971. Note changes in the delta from 1951 (Fig. 6).



Comox Harbour. Approximate positions of those transects are shown in Figs. 1 and 5. Transects and sample stations were located in a random fashion to cover as much of the habitat as possible. The cores were washed free of silt over a 1 mm fiberglass screen, using high pressure water and hand separation of the root mat. All material retained in the screen was dried at 100°C to constant weight and ground in a Wiley mill. Because variable amounts of sand and silt remained attached to the roots and rhizomes, final weights were expressed as g/m^2, on an ash-free dry weight basis.

Proximate analysis for fiber, fat, and gross energy levels followed the methods of Horowitz (1965) and were performed by the Department of Animal Sciences, University of British Columbia, and by the Canadian Wildlife Service. Protein and carbohydrate levels were assessed using a Perkin Elmer Elemental Analyzer, by the Department of Biological Sciences, Simon Fraser University. Tests were performed on subsamples of the core samples. No separation of plant material by species was possible because of extensive inter-growth of the plant roots.

Twenty-two samples of grasses from dairy pastures adjacent to Comox Harbour were collected in the winters of 1977-78 and 1978-79. They were analyzed for fat, fiber, protein and carbohydrate levels, using the same procedures as for the estuary plant samples.

Habitat use was measured by recording the number and location of swans on both estuaries and on pastures adjacent to Comox Harbour, and by calculating the number of swan-use days each area received. The estuaries were divided into units (Figs. 1 and 5) for those counts, based on easily recognizeable physical features, so that preferences for certain areas might be revealed. A swan-use day consisted of the use of the habitat by one bird for part or all of one day. Because the counts were made only once on any particular day, the underlying assumption was that the number of birds counted was representative of the level of use of the habitat. Counts were made at approximately weekly intervals from 1 November 1977 to 15 April 1978, usually about mid-day, to avoid incorrect estimation of habitat use by counting swans that had not yet settled down to their daily routine (see Section II, p 42). The total use was estimated by measuring the area under the curve of a plot of the number of swans counted against the date of each count. Relationships between habitat parameters and the degree of use of each marsh were investigated by linear regression procedures (Zar 1974). Parameters tested included protein, carbohydrate, fiber and fat content, and gross energy levels.

Food habits were assessed by visual observation at Port Alberni and Comox Harbour and by the microscopical analysis of scats at Comox Harbour. Visual methods consisted of collecting and identifying apparent food materials from areas in which swans were observed feeding. Microscopical methods were based on techniques reported by Baumgartner and Martin (1939), Stewart (1967) and Parker et al. (1976). Scats were collected during the day at intervals throughout the winters of 1977-78 and 1978-79. They were transported cold to the lab within 18 hours and stored frozen. Prior to analysis for epidermal fragments subsamples were extracted and stored in formalin at room temperature. For analysis several drops of the formalin-scat slurry were placed on a covered slide. Epidermal fragments were identified by comparisons with photomicrographs of root and rhizome preparations of the dominant plants growing in areas where swans fed regularly. Tissue preparation and staining techniques producing the best photomicrographs were based on those of Storr (1961). Material was boiled in chromic acid/nitric acid for 10 minutes, stained in gentian violet for 30 minutes, washed, and wet mounted on glass slides for photography. Photomicrographs were made with unfiltered white light, and blue filtered light, at 100X and 400X magnification using Kodak Kodachrome 400 ASA film. To verify identification of structural detail, mounted slides of cross sections and transverse sections of roots and rhizomes were prepared from the same plant species used to make the photomicrographs. Permanent mounts were prepared by the Department of Biological Sciences, Simon Fraser University, after the methods of Metcalfe (1971).

RESULTS

HABITAT CHARACTERISTICS

Vegetation

The vegetation of both estuaries reflected the differences in the degree of mixing of salt and freshwater. At Comox Harbour little or no delta formation occurs; the river is somewhat channelized and most of the original delta has been usurped for farmland. Much of the harbour consists of tidal flats, devoid of macrophytes above the eelgrass beds. Where the saltwater - freshwater mixing occurs, typical estuarine emergents have developed. They are confined to a narrow strip which tapers away from the Courtenay River mouth towards the southeast (Fig. 1). The vegetation was characterized by two plant communities composed of 16 species (Appendix 1). The communities are: (1) *Scirpus americanus* - *S. cernuus* - *Triglochin maritimum* community and (2) *Carex lyngbyei* - *Potentilla pacifica* - *Deschampsia cespitosa* community. The *Scirpus* community was the more widespread while the *Carex* community occurred between the *Scirpus* and the beach, and on elevated portions of the substrate within the *Scirpus* community.

The distribution and abundance of the species forming the *Scirpus* community varied somewhat, from the Courtenay River mouth towards Millard Road. From the river mouth to Millard Creek the substrate was predominantly fine grey sand overlaid by a thin layer of mud. There, the Scirpus community, when undisturbed, formed a root mat usually slightly raised above the surrounding substrate (Fig. 8). It was dominated by S.americanus and T. maritimum.

Between Millard Creek and Millard Road the substrate near the beach was coarser, ranging from sandy-gravel at Millard Creek to small cobbles near Millard Road, with few sandy areas. The vegetation was dominated by Spergularia canadensis near Millard Creek, and by D. cespitosa, T. maritimus and Juncus balticus in mats, and patches of Spergularia on the cobble near Millard Rd. One sandy area near Millard Rd. was covered by an almost pure stand of Scirpus americanus, growing much more robustly than any other stands of bulrush seen on the study area.

In areas where the S. americanus - T. maritimum dominated root mat had been disturbed, other species forming the Scirpus community were more common, and vegetative propagation of S. americanus was evident. S. cernuus and to a lesser extent Spergularia canadensis often grew much more profusely in areas where the root mat had been disturbed than in the undisturbed root mat. Shoots of S. americanus were seen growing in lines into some disturbed areas, presumably as rhizomes extended outward from the adjacent root mat. S. cernuus and Spergularia canadensis appeared to be successional species, more abundant prior to the formation of the Scirpus-Triglochin root mat.

The strong influence of salt water at Comox Harbour was also reflected in plant vigor. The dominant Scirpus americanus seldom grew taller than 50 cm, while on estuaries more influenced by freshwater (e.g. Fraser River) it reached a height of over 1 m (pers. obs.).

The Somass River estuary at Port Alberni is more typically deltaic. Although parts of it have been developed for industrial use, sedimentation and mixing

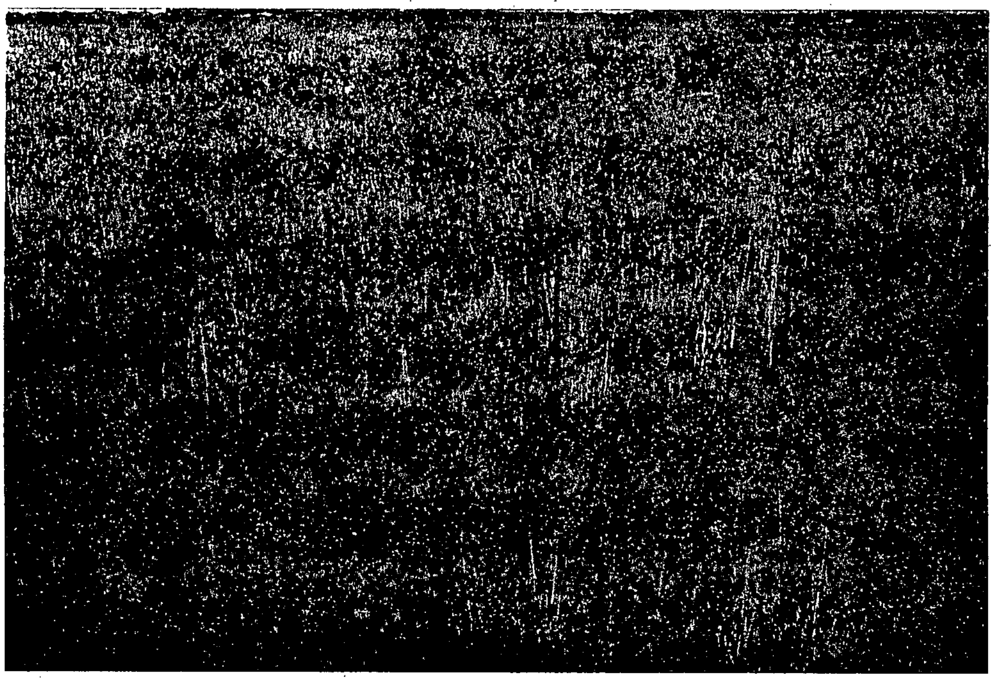


Fig. 8. The emergent vegetation at Comox Harbour. Note the nature of the root mat formed by the *Scirpus americanus* - *S. cernuus* - *Triglochin maritimum* community.

continue in their original patterns. The strong freshwater influence has resulted in a great diversity of vigorous plants (Fig. 9). Over 60 species of emergent plants have been catalogued, and 5 aquatic vegetation communities recognized (Paish and Assoc. Ltd. 1973): (1) Sidalcea canadensis - Fritillaria camschatcensis -Solidago canadensis; (2) Juncus balticus - Deschampsia cespitosa; (3) Carex lyngbyei; (4) Scirpus acutus variant of the Carex lyngbyei type; and (5) Myriophyllum spicatum - Potamogeton natans. The most frequently seen species are listed in Appendix I.

Plant growth on the Somass River delta was exceptionally luxuriant. On average, the Carex grew to a height of at least 1 m, and could be found in some locations over 2 m high. Similarly Scirpus acutus grew to heights above averages reported for the area (Hitchcock and Cronquist 1973).

Biomass and Proximate Analysis

There were some differences in biomass and proximate analysis of the vegetation between both estuaries and the dairy pastures (Table 2). The biomass per m^2 was significantly higher ($p < .05$) and there was a much larger standing crop of potential food available at Port Alberni, than at Comox Harbour. Fiber levels were significantly higher at Comox Harbour ($p < .05$), while protein, fat, carbohydrate and gross energy levels were not significantly different. Pasture grasses were similar to both estuaries in fat levels, but were significantly higher in protein ($p < .01$), and lower in carbohydrate levels ($p < .05$) and in fiber ($p < .01$). Gross energy determinations were not made on pasture grasses.

No significant differences were found between transects at Comox Harbour in any of the factors assessed (Table 3). Some differences were found, however, between transects at Port Alberni, in protein content only. Newman-Keuls multiple range tests (Zar 1974:151) showed significant differences ($p < .05$) between transects 1,2,3,7 and 4,5,6 (Table 4). A lack of material precluded between transect analysis for significant differences in fiber levels.

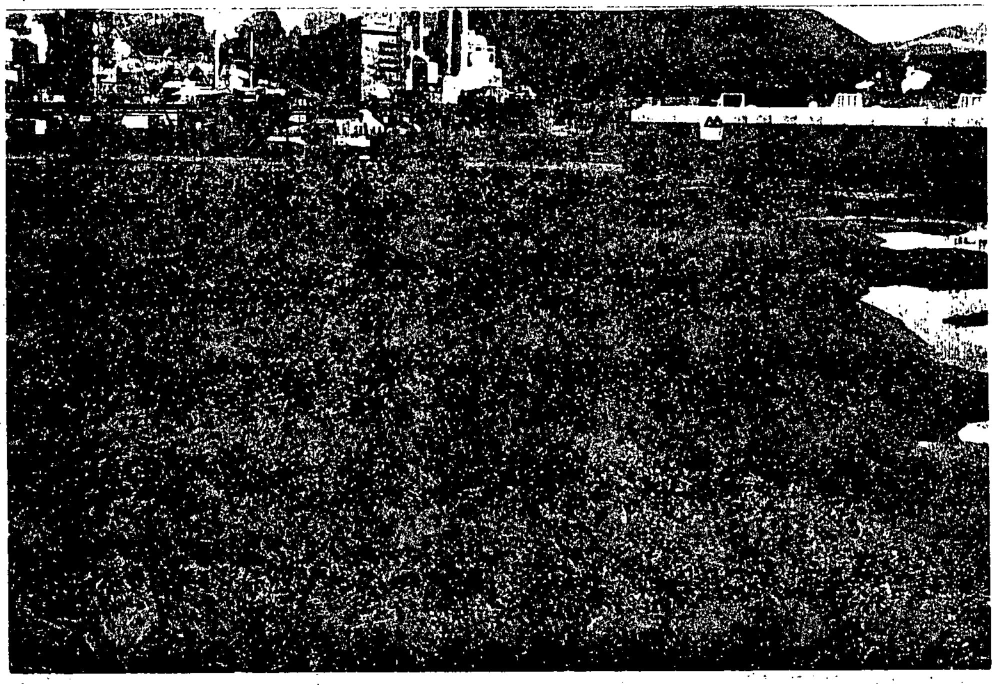


Fig. 9. The emergent vegetation at Port Alberni.

Table 2. Mean biomass estimate and proximate analysis of potential wintering swan foods at Comox Harbour and Port Alberni, and proximate analysis of pasture grasses near Comox Harbour. Values are ± one standard error; numbers in ( ) are sample sizes

Factor	Comox Harbour	Port Alberni	Pastures
mean biomass (g/m^2)	1452.2±113.5(45)[1]	1755.7±95.4(49)[2]	NA
surface area (ha)	8.3	22.9	80
food potentially available (metric tonnes)	115.6	401.4	NA
protein (%)	7.0 ± 0.3 (45)[5]	7.1 ± 0.3 (48)[5]	22.9 ± 1.2 (14)[6]
fat (%)	1.2 ± 0.1 (39)	1.0 ± 2.6 (30)	0.4 ± 0.1 (4)
carbohydrate (%)	46.8 ± 1.0 (46)[7]	48.0 ± 0.3 (48)[7]	44.0 ± 0.5 (14)[8]
fiber (%)	63.4 ± 1.2 (39)[3]	47.8 ± 1.7 (7)[4]	32.2 ± 1.4 (27)[9]
gross energy (Kcal/g)	4.76 ± 0.27(9)	4.82 ± 0.16 (49)	NA

2<1, $p<.05$
3<4, $p<.05$
6<5, $p<.01$
7<8, $p<.05$
4<9, $p<.01$

Table 3. Analysis by transect of mean biomass and proximate factors assessed at Comox Harbour. Values are means ± one standard error; number in ( ) are sample sizes.

Transect Number	1	2	3	4	5
Mean biomass (g/m^2)	1221.4±144.9 (12)	1631.2±153.0 (12)	1188.5±369.0 (8)	1213.1±136.4 (8)	2019.5±523.1 (6)
Protein (%)	7.7±14.4 (12)	8.0±0.8 (12)	6.1±0.4 (8)	6.1±0.3 (8)	6.1 ±1.0 (6)
Fiber (%)	67.4 ± 2.8 (7)	66.7 ± 2.2 (8)	65.3 ± 2.4 (8)	61.6 ± 2.9 (8)	56.7 ± 2.2 (8)
Carbohydrate (%)	48.1 ± 2.7 (12)	48.6 ± 2.1 (12)	48.1 ± 1.1 (8)	46.4 ± 0.9 (8)	42.3 ± 3.1 (8)
Fat (%)	.6 ±0.1 (8)	1.2 ±0.3 (8)	1.8 ±0.4 (8)	1.4 ±0.1 (8)	1.3 ±0.1 (7)

Table 4. Analysis by transect of mean biomass and proximate factors* assessed at Port Alberni. Values are means $\pm$ one standard error; numbers in ( ) are sample sizes. Superscripts denote means that are not significantly different, $p < .05$.

Transect number	1	2	3	4	5	6	7
Biomass	1567.3 $\pm$ 118.8	1859.2 $\pm$ 265.5	2395.5 $\pm$ 121.0	1593.8 $\pm$ 286.1	1823.8 $\pm$ 457.1	1566.4 $\pm$ 435.0	1231.5 $\pm$ 118.5
(g/m^2)	(16)	(7)	(8)	(8)	(4)	(4)	(2)
Protein	8.6 $\pm$ 0.5^1	9.6 $\pm$ 0.4^1	7.4 $\pm$ 0.4^1	3.5 $\pm$ 0.3^2	5.5 $\pm$ 0.3^2	5.1 $\pm$ 2.4^2	7.5 $\pm$ 0.7^1
(%)	(16)	(6)	(8)	(8)	(16)	(14)	(12)
Carbohydrate	48.8 $\pm$ 0.5	45.8 $\pm$ 0.8	49.4 $\pm$ 0.3	46.8 $\pm$ 0.6	48.1 $\pm$ 0.6	47.5 $\pm$ 0.8	47.4 $\pm$ 0.8
(%)	(16)	(6)	(8)	(8)	(4)	(4)	(2)
Fat	.83 $\pm$ 0.04	.78 $\pm$ 0.2	.89 $\pm$ .01	1.36 $\pm$ 0.5	1.18 $\pm$ 0.3	.85 $\pm$ 0.1	1.24 $\pm$ 0.1
(%)	(8)	(2)	(2)	(2)	(4)	(6)	(6)

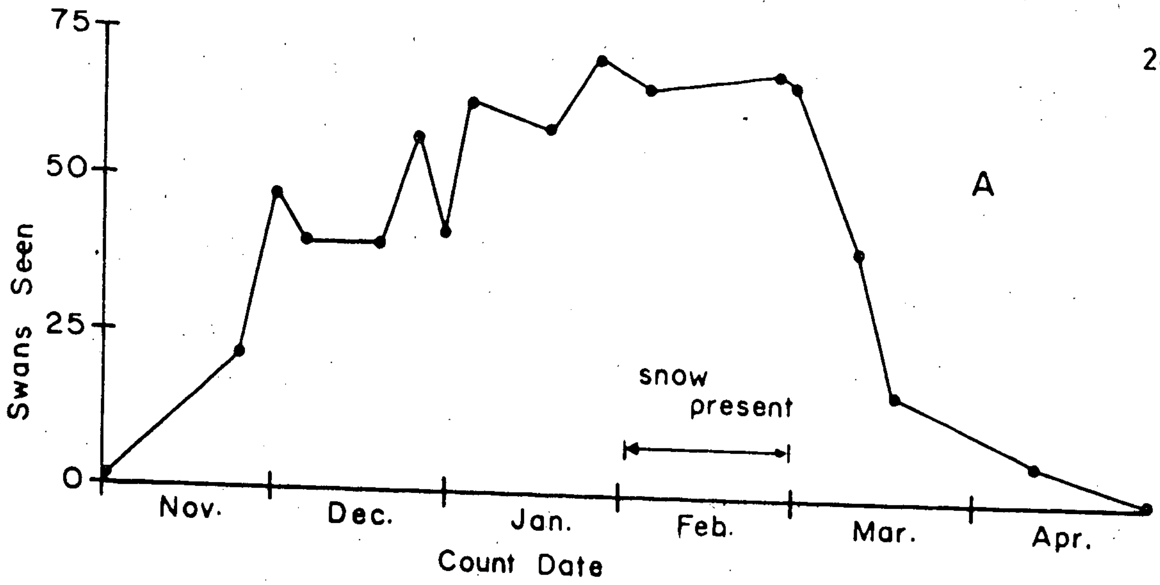
*Analysis for between transect differences in fiber levels was precluded by inadequate samples of material.

In the winter of 1977-78 the estuary at Port Alberni received 6200 swan days use, or 270 bird-days/ha (Fig. 10A; Table 5). The actual dates of arrival and departure of the swans were not observed, but were estimated as 1 November and 15 April, respectively, based on observations at Port Alberni, other parts of the coast and discussions with local residents. Peak swan use of the estuary corresponded to the coldest part of the winter, presumably as smaller inland wintering areas became frozen (Smith and Blood 1972). Heaviest swan use was seen on the Sewage Lagoon marsh unit with lighter use at the Shoemaker Bay unit and the Johnstone Island Marsh unit. Juvenile swans were seen most frequently at the Sewage Lagoon marsh and were never seen in the Johnstone Island Marsh. The average protein content of each marsh unit had a relationship similar to that of swan use (Table 6) but the other proximate factors did not.

Comox Harbour received approximately 12700 swan-use days in the winter of 1977-78, or 1540 bird-days/ha (Fig. 10B; Table 5). Estimated dates of arrival and departure from the area were 1 November and 15 March, respectively, although departure dates normally may be later. In the winters of 1978-79 and 1979-80 departure dates were 22 and 26 March, respectively. Peak use of the Comox Harbour habitat also occurred in the coldest part of the winter. Heaviest use of the habitat occurred in the Trailer Court marsh unit. Habitat use in the Millard Road marsh unit was moderate and use of the River Mouth unit was light. Juvenile swans were seen most frequently near Millard Road while the Trailer Court area was favoured slightly less; the River Mouth was of little importance to juvenile swans. There were no correlations between the number of swan-use days and any of the habitat parameters measured on individual parts of the marsh.

Dairy pastures included in the 1977-78 counts received 4500 days of swan-use

Fig. 10. Total swan use of the study areas in 1977-78. (A) Somass River estuary; (B) Courtenay River estuary; (C) Farm Fields.


75
50
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snow present
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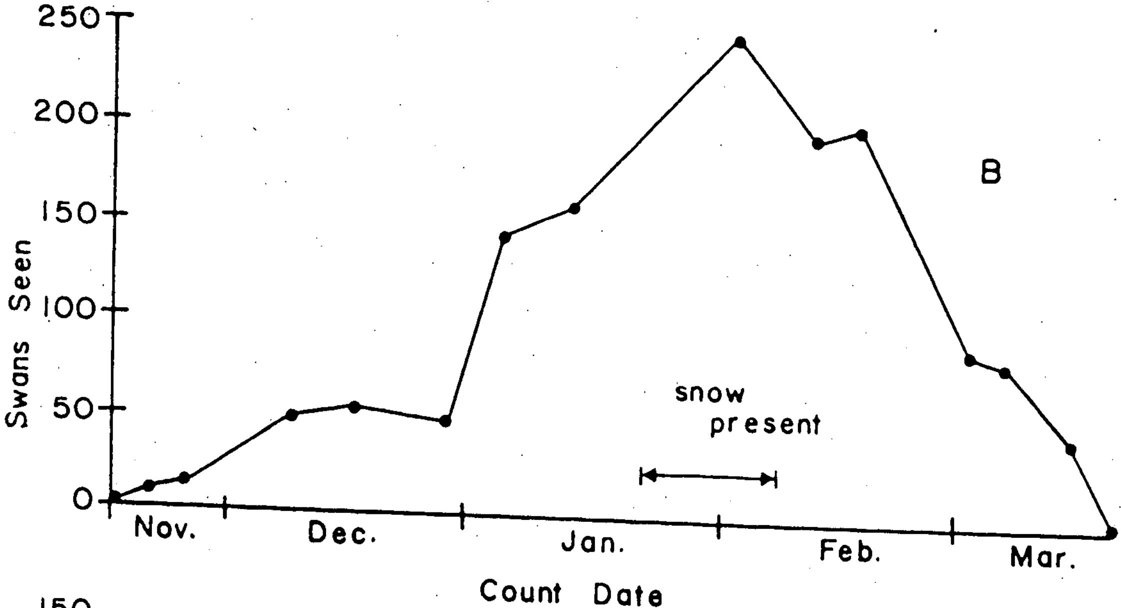
250
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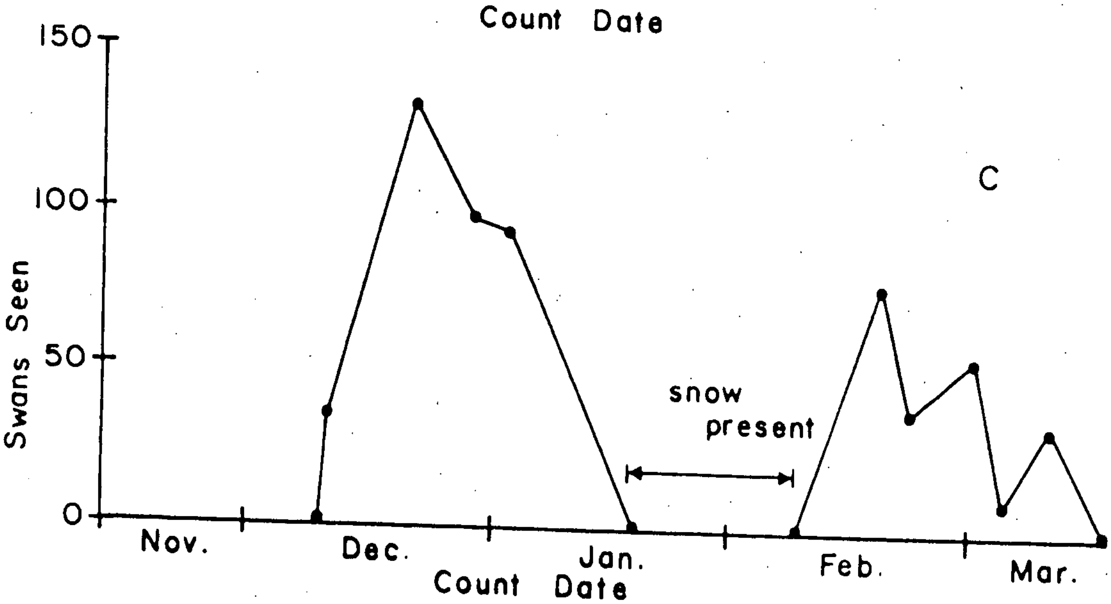
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snow present
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Table 5. Rates of swan-use for each study area and study area unit.

Area	Surface area (ha)	Swan-use days/ha (adult/juvenile)
Somass River	22.9	249.0/23.4
Sewage Lagoon	8.5	422.0/44.0
Shoemaker Bay	5.9	233.6/27.5
Johnston Island	8.5	82.2/0
Courtenay River	8.3	1284.0/250.1
Trailer Court	3.4	1718.1/253.4
Millard Road	3.4	1121.8/279.5
River Mouth	1.4	678.8/181.0
Farm Fields	80	3617.1/914.4
Farquarson's Farms	40	53.1/7.2
Beaver Meadow Farms	40	37.3/15.6

Table 6. Number of swan-use days per hectare and average protein content of each marsh unit at Port Alberni in 1977-78.

Marsh unit	Area (ha)	Swan-use days/ha	Protein content (%)
Sewage Lagoon	8.5	466.1	8.5
Shoemaker Bay	5.9	260.0	7.2
Johnstone Island	8.5	87.3	4.6

(Fig. 10C). Heaviest total use occurred on Farquarsons Farms (Table 5) but more use was made of the Beaver Meadow Farm by juveniles. Use of the fields apparently did not commence until early December 1977. Feeding in fields was not possible between 18 January and 15 February because the fields were snow covered. Field use continued later in the spring than did use of the estuary; no swans were seen on the estuary after 1 March but swans were present on fields until 15 March 1978.

Counts of swans using the fields tended to fluctuate widely, particularly after the snow disappeared. Swans which spent the night on Comox Harbour were probably flying to fields outside the study area on occasion, and not using the same fields consistently.

FOOD HABITS

Visual Analysis

Trumpeter Swans were observed feeding by extracting the roots and rhizomes of the dominant emergent plants at both estuaries. At Port Alberni most feeding took place on *Carex* beds but also occurred in beds of *Scirpus acutus*. On one occasion, a crater, characteristic of swan feeding activity as described in Section II, was found along the edge of a bed of *Typha latifolia* though there were no actual observations of the use of that species as food. At Comox Harbour, the swans fed mainly on the *Scirpus* - *Triglochin* community. Smaller numbers of birds fed on *Carex* beds, and occasionally a swan was seen picking up a frond of eelgrass (*Zostera marina*) drifted in by the tide. At night, feeding activity was observed on *Zostera* beds when these were exposed by low tides.

Animal matter appeared to contribute very little to the winter diet of Trumpeter Swans. The dense growth of the plant rhizomes provides habitat only for microscopic forms. However, one source of animal protein which may be used occasionally is the carcasses of spawned salmon (Oncorhynchus sp.). Butler (1973) recorded a Trumpeter Swan picking at a dead salmon at the mouth of the Big Qualicum River, 80 km south of Comox Harbour and I have seen similar activity at the same river by a single family of swans every winter since 1974-75. In January, 1979 similar behaviour was observed in a single juvenile swan at Comox Harbour. No observations of swans feeding on fish carcasses have yet been made at Port Alberni.

Fecal Analysis

The results of the microscopical analysis of scats for food preferences are summarized in Table 7. Differences in root and rhizome epidermal tissues of the plant species studied were found to be very slight. As a result only four dominant plant types could be recognized. The importance of, or a preference for, the less common plant species could not be ascertained.

DISCUSSION

HABITAT CHARACTERISTICS

Vegetation

Studies of the vegetation of the numerous estuaries along the British Columbia coast have been confined to the larger and more accessible areas near Vancouver (Lim and Levings 1973; Yamanaka 1975; Dawe 1976). Plant species and associations seem to be similar from one estuary to another, the extent of mixing of saltwater and freshwater being most important in determining final vegetation structure. The estuaries at Comox Harbour and Port Alberni differ in physio-

Table 7. The frequency of occurrence of major food items in Trumpeter Swan droppings collected at Comox Harbour, 1978-80 (n = 65).

Item	Number of scats containing item	Frequency of Occurrence (%)
Zostera	22	33.8
Scirpus	20	30.8
Grass	12	18.5
Carex	9	13.8
unidentified	2	3.1

graphy and in freshwater influence, which has resulted in differences in species diversity and the extent of their emergent vegetation. Freshwater tends to remain over the Somass River vegetation (Tully 1949), while tidal circulation causes better mixing at Comox Harbour and a resultant stronger saltwater influence.

Vegetation patterns observed during aerial surveys of swans wintering on Vancouver Island (McKelvey 1979) appeared to be similar to those seen at Comox Harbour and Port Alberni, and to those reported by Lim and Levings (1973), Yamanaka (1975) and Dawe (1976). The most abundant plant species in most estuaries, including estuaries used by swans, are Carex sp. and Scirpus sp. Their importance to swans is undoubtedly as a food source.

Biomass and Proximate Analysis

Estimates of below-ground biomass of emergent plants will vary depending on the depth to which the plants are sampled. Estimates from this study fall within the range of below-ground estimates of Carex lyngbyei (Kistritz and Yesaki 1979) from a 20 cm deep sample, and from below-ground estimates of Scirpus validus and S. maritimus using a 40 cm deep sample (K. Hall, pers. comm.) on the Fraser River estuary. However, they are far above the estimates given by Burton (1977) for below-ground biomass of S. americanus, using a 25 cm deep sample, on the Fraser River estuary. I believe my estimates are accurate and realistic when compared to those given by Kistritz and Yesaki (1979) and Hall (pers. comm.), and that Burton's estimates are inaccurate. Burton's reported analytical techniques are poor and his unreported field techniques for stand identification and sampling may therefore also be suspect.

Crude protein levels found in this study (Table 2) were also similar to those reported elsewhere. Burton (1977) measured protein levels of 7% to 14% in rhizomes of Scirpus spp. consumed by Lesser Snow Geese (Anser c. caerulescens) in the Fraser River estuary. De la Cruz and Hackney (1977) reported crude protein levels in below ground parts of Juncus sp. of between 4.0% and 5.4%. Similar ranges of crude protein have been reported for above ground emergent plant parts by Boyd (1970a and 1970b) and Auclair (1979). Thus swans wintering on the estuaries at Comox Harbour and Port Alberni have available to them crude protein levels similar to those in many other emergent plant communities.

It is difficult to say whether those levels of protein suffice nutritionally. Studies of the nutritional requirements of wintering waterfowl, and its long term effect on productivity, are lacking. If some Trumpeter Swans have traditionally wintered on estuaries (sensu Hochbaum 1955), it must be concluded that those protein levels are adequate.

The importance of the high levels of fiber found is more difficult to assess. High fiber content may reflect a low quality diet, or it may be an artifact of the sampling procedure. Cellulose, the major component of fiber, is not digested by geese (Mattocks, 1972) and there is no evidence that swans digest it either. In mammals capable of cellulose digestion, winter diets high in fiber were thought to result in a negative energy balance (Gasaway and Coady 1974). Ingestion of high fiber foods by birds may similarly lower the efficiency of digestion, but quite high levels (30%) are reported to be tolerated by chickens (Bolton 1962).

Swans are probably more selective in their food habits than was the core sampling procedure of this study. Core samples often contained large quantities of roots, attached to the rhizomes, which appeared to be dead. If so they would be highly fibrous. Swans may be able to extract rhizomes only, leaving much of the root material behind, in which case the fiber levels of the actual diet would be lower than those suggested by this analysis.

The higher biomass and potential value of the food available at Port Alberni may also be related to the influence of saltwater and freshwater mixing. Plant nutrient content is thought to reflect the quality of the habitat (Boyd 1969): better habitat may produce a more nutritious food. The heavier freshwater influence at Port Alberni, due to the hydrography of the estuary (Tully 1949), has probably made the Somass River delta a higher quality habitat than that at Comox Harbour.

Another factor related to tidal mixing, that may be contributing to the higher protein content of plants at Port Alberni, is the outflow of the Sewage Lagoon. There is evidence that some wetlands may be useful as water purifiers, because of the tendency of emergent plants to incorporate large proportions of the available essential minerals (Auclair 1979). More nutrients may be available from the Sewage Lagoon outflow at Port Alberni than at Comox Harbour because of the different nature of tidal mixing.

Trends in the protein content (or their lack) in both estuaries, may also be due to tidal circulations. Tide mixing at Port Alberni may cause enrichment with sewage effluent near the Sewage Lagoon and in Shoemaker Bay, but prevent such enrichment in the Johnstone Island marsh. At Comox Harbour, however, strong tidal mixing together with entrainment of sewage effluent by the Courtenay River may have precluded nutrient enrichment of the emergent vegetation.

Differences in potential food quality between both estuaries and the dairy pastures reflects the management of the pastures for high levels of nutrients for dairy cattle. Heavy applications of nitrogenous fertilizers and the frequent mowing of the grass has resulted in a feed high in protein and relatively low in fiber.

Although there are many factors to consider when discussing the nutritive value of a diet, the critical component may be protein content. A continuous source of protein is essential to animals throughout their lives because it is the principal constituent of all organs and soft structures (Maynard and Loosli 1969). Protein content may also be the most important aspect of the relationship between an animal and its selection of habitat. Recently, White (1978) has proposed that the abundance of all animals is ultimately controlled by the availability of nitrogenous foods. If that is so, selectivity for nutritional value of food, particularly protein, would be expected.

The distribution of swans at both estuaries and the dairy pastures seems to reflect the variable protein content of the foods available. Differences in the protein content between marsh units at Port Alberni seemed to result in greater use by swans of those areas with higher protein levels.

Studies of waterfowl food selection in relation to nutritional value have not been extensive and are completely lacking in swans. Some species select food on the basis of quantity, or availability (Owen 1972a; Stott and Olson 1973; Fruzinski 1977); others are affected by factors such as disturbance (Ranwell and Downing 1959; Owen 1972b; Fruzinski 1977); and some select food in response to quality, or nutritional value (Ranwell and Downing 1959; Owen 1971). The results of this study indicate that Trumpeter Swans are not concerned with the quantity of food available, at least on the estuaries. The quantity of food potentially available at Port Alberni far exceeds that at Comox yet the use of the Comox Harbour area increases yearly (McKelvey 1979). Disturbance may also be discounted as a factor because the levels of disturbance may be higher at Comox Harbour than at Port Alberni, the human population being much closer to the habitat at Comox Harbour.

Nutritional value of the food resource seems to explain both within habitat variation in amount of use (eg. Port Alberni), and between habitat variation in use. I believe that wintering Trumpeter Swans are attracted to the Comox Harbour area by the availability of the highly nutritious pasture grasses. They are dependent on the estuary at night and in times when snow cover precludes feeding on fields, but their preference is for high nutrient foods. The apparent decline in numbers of swans using certain estuaries may be a relocation of swans into more desirable areas, like Comox Harbour (McKelvey 1979), where those high nutrient foods are available.

The manner in which Trumpeter Swans acquired the habit of grazing on pastures is unknown. Because swans are forced onto unfrozen coastal areas in severe weather and off pastures and fresh water bodies, it cannot have occurred in response to weather as reported for other species of swans (Owen and Kear 1972). The taste for high nutrient grasses may have been acquired by chance. Birds landing on rain flooded fields and remaining to feed would have decoyed other swans and thus alerted them to the presence of this new food source. The result of the acquisition of that habit seems to have been a rapid increase in the number of swans wintering at Comox Harbour, the area now supporting 5-7% of the world population of Trumpeter Swans in the winter.

The effect of pasture grazing on the swan population is as yet unknown. Reed (1976) speculated that species of geese which have adapted to using agricultural crops may have lowered their reproductive output, and shifted the age distribution through increased winter survival. There have been no studies yet of the reproductive success of swans feeding on pasture grass compared to those feeding only on natural foods, but yearly observations on the productivity of swans wintering at Comox Harbour would be useful. Here is an opportunity to look for the changes in population structure Reed (1976) postulated for geese, in a waterfowl population that is still adapting to the agricultural habit.

FOOD HABITS

Winter food habits of Trumpeter Swans in this study are unlike those reported for other species of swans (Owen and Kear 1972; Owen and Cadbury 1975). They also differ from those reported for Trumpeter Swans on breeding areas in Montana (Banko 1960; Page 1976; Shea 1979). Other wintering species of swans and Trumpeter Swans breeding in Montana seem to prefer above ground plant parts, on wetlands and/or fields, and rooted aquatics. Trumpeter Swans wintering on estuaries in coastal British Columbia prefer the roots and rhizomes of emergent plants .

Visual Analysis

Food of a similar nature to that used at Comox Harbour and Port Alberni is readily available in British Columbia. Emergent vegetation is found in all the estuaries of the numerous creeks and rivers along the coast. Because of the tidal influence on estuaries, that food source remains available even in the coldest parts of the winter. However, the extent of the use of eelgrass by Trumpeter Swans in British Columbia is speculative because eelgrass does not occur at every Trumpeter Swan wintering location. It has been recorded in other northern species of swans (Owen and Kear 1972), and it probably is used by Trumpeter Swans wherever it is available.

This study showed that eelgrass is a major food item of swans wintering at Comox Harbour, a finding which has some interesting implications. Either eelgrass is consumed in very large quantitites, and is even more important than these results show, or the passage rate of food in the Trumpeter Swan gut is much slower than in other waterfowl. If the passage rate is similar to that of other waterfowl, time of passage may be about 4.5 hr based on gut lengths in MacGillivary (1852), and passage rates for lesser Snow Geese reported by Burton (1977). However, I believe passage rates in Trumpeter Swans may be much slower for two reasons. First, droppings for this study were collected throughout the daylight period, when eelgrass was not available to the swans because of tidal conditions. If the passage rate was about 4.5 hr., one would expect most of the eelgrass consumed at night to have passed through the gut by early morning, resulting in a lower number of droppings containing eelgrass. However, if Trumpeter Swans had a slower passage rate than other waterfowl or if eelgrass was consumed in very large quantities, more eelgrass would be present in droppings collected later in the day.

The second piece of evidence for a slow passage rate is based on observations made while conducting behavioural studies reported in Section II. I frequently observed that individual swans spend most of the daylight period out of the water, feeding on emergent plants, or resting. The only time I saw them defecate was towards dusk, when they would begin to move towards the receding tide. That was up to 8 hrs after the tide had receded below the emergent plants, and after the time of peak feeding, indicating a proportionately much longer time of passage than in other waterfowl.

The other alternative, that eelgrass is consumed in very large quantities, does not seem likely. The amount of time spent feeding at night (Section II) does not seem great enough to cause a large amount of eelgrass to appear in droppings collected during the day, if the passage rate was proportional to that of other waterfowl.

Fecal analysis

The technique of food habits analysis by fecal examination has severe limitations when relatively undifferentiated materials such as rhizomes are involved. Microscopical identification of rhizomes of Cyperaceae is based on vascular bundle characteristics (Plowman 1906). Whole mounts may readily reveal those characteristics but in preparations of fecal materials, those characteristics are obscured by tangling of the bundles, and the presence of other plant debris.

II. BEHAVIOUR

INTRODUCTION

Waterfowl activity consists of a more or less regular pattern of feeding and resting interspersed with less frequent flight, maintenance and alert behaviour (Burton and Hudson 1978). Feeding may be the most important activity because it supplies the energy necessary for all other activities (Lack 1970).

Many factors may affect the patterning of waterfowl behaviour and therefore the regimen of energy uptake and expenditure. Some waterfowl feed during the day (Brackenridge 1953; Ranwell and Downing 1959; Linsell 1969; Gorman 1970; Raveling et al. 1972; Folk 1973; Owen 1973); while others feed at night (Ranwell and Downing 1959; Raveling et al. 1972; Zwarts 1972; Swanson and Sargeant 1972; Owens 1977). Factors known to affect the feeding behaviour of waterfowl include: temperature and weather conditions (Nilsson 1972; Bryant and Leng 1975), tidal conditions (Ranwell and Downing 1959; Pounder 1976; Bryant and Leng 1975), and disturbance (Owen 1972a, 1972b; Owens 1977).

There have been few studies of the behaviour of waterfowl during the winter (Tamisier 1976; Burton and Hudson 1978) and none concerned specifically with species of swans. Few behaviour studies have attempted diel observations. During the winters of 1977-78 and 1978-79 I recorded the diel behaviour of Trumpeter Swans wintering on the estuary at Comox Harbour and on adjacent dairy pastures. My objectives were to determine how the swans budgeted their time in those two habitats, particularly the time used for feeding, and to determine what factors might have affected that budgeting.

METHODS

FIELD PROCEDURES

Observations were made during 11 daylight periods and six night periods on the estuary at Comox Harbour and seven daylight periods on adjacent dairy pastures for a total of 202.25 hours. During each observation interval the flock of swans visible from the vantage points was scanned from side to side with a 20X telescope in daylight or with a Starton night vision scope at night. The behavior of each bird was recorded on tape, as one of the following: feeding, swimming, walking, preening, sleeping, alert, flying or agonistic. Descriptions of what constituted each type of behaviour are given in Table 8. The dates of each observation period are shown in Table 9. Observations were made at the estuary from vantage points close to the flock, at 60 min, 30 min, or 15 min intervals. In 1977-78 the swans were using the Millard Road area and the Trailer Court area (Fig. 1) equally. That year observations were made at 60 min or 30 min intervals from both locations; one observation from both locations took about 20 min. In 1978-79, the majority of the flock were most visible from the Sewage Lagoon (Fig. 1). It was possible to remain at that location most of the day, making observations at 15 min intervals. Observations were made on the fields at Farquarsons Farms in late 1978, and at the Beaver Meadow Farms from Anderton Road, January to March 1979. (Fig. 1). Observation intervals on the fields varied depending on the amount of activity being studied on the estuary. That is, when there were no swans on the estuary observation intervals on the fields were 15 min. When swans were being observed on both the fields and the estuary, observation intervals were 60 min, to allow me to change location.

Environmental factors that may have affected the behaviour of the swans

Table 8. Descriptions of the types of behaviour recognized in Trumpeter Swans wintering at Comox Harbour.

Behaviour	Description
feeding	any feeding act including excavating rhizomes, up-ending, drinking, loosening rhizomes, by foot agitation or picking up pieces of floating vegetation.
swimming	movement through the water with no other obvious activity occurring at the time.
walking	purposeful movement between feeding sites or from a resting area to the water's edge.
preening	cleaning and arranging feathers, scratching, stretching (especially the wings).
sleeping	diagnosed anytime a bird was seen with head and neck stretched over its' back, eyes open or closed.
alert	observing surroundings; looking in one direction for some time.
flying	movement of the wings resulting in the bird becoming completely airborne, free of the ground or water.
agonistic	any encounter between two or more birds resulting in a visual or vocal display.

Table 9. Percentage of total time of each observation period spent feeding and mean time feeding on Comox Harbour and adjacent fields.

Location and Date	Total hours of observation	Period of observation	Time spent feeding(%)	Snow present on fields
Estuary daylight				
12-1-78	9.0	0830-1730	50.0	+
19-1-78	10.5	0730-1800	62.0	+
1-2-78	4.0	1300-1700	37.3	+
2-2-78	9.0	0800-1700	65.3	+
15-2-78	10.0	0700-1700	74.8	-
5-11-78	9.0	0730-1630	80.6	-
21-12-78	10.0	0630-1630	43.3	-
4-1-79	9.5	0730-1700	48.0	-
17-1-79	2.0	1500-1700	56.5	-
18-1-79	10.75	0630-1715	41.5	-
7-2-79	2.5	0715-0945	84.9	-
Mean time spent feeding			57.6	
Estuary night				
18/19-1-78	12.0	1830-0630	32.2	+
3/4-1-79*	7.5		-	+
4/5-1-79	13.75	1800-0745	68.6	+
17/18-1-79*	4.5		-	-
6/7-2-79	13.25	1745-0700	40.8	-
7/8-2-79	15.5	1615-0745	45.0	-
Mean time spent feeding				
Estuary night			47.2	
Estuary night and daylight combined			54.6	
Fields				
25-11-78	7.5	0830-1600	79.7	-
21-12-78	7.5	0800-1530	74.3	-
17- 1-79	6.75	0945-1630	86.8	-
6- 2-79	2.5	1430-1700	97.9	-
7- 2-79	5.5	1015-1545	95.7	-
25- 2-79	9.0	0930-1830	81.7	-
26- 2-79	10.75	0730-1815	93.6	-
Mean time spent feeding on fields		86.1		

* Because of weather caused interruptions in observations on these nights no data are available.

were also recorded. Tide heights were calculated from Canadian Hydrographic Service Tide and Current Tables, temperature and wind speed were obtained from Atmospheric Environment Service records for Comox Airport, and snow was noted as present or absent on adjacent pastures. Miscellaneous factors noted included: loud noises, changing weather conditions, low flying aircraft, and the presence of potential predators such as eagles, dogs and humans.

DATA ANALYSIS

The number of birds observed in each category of behaviour was expressed as a percentage of the total number of birds visible. For regression analyses of the various types of behaviour observed versus factors that might potentially regulate those behaviours, percentages were transformed to arcsine values (Zar 1974).

The mean time spent in each type of behaviour was calculated to provide an average time budget. Time was calculated by measuring the area under the curve of the ethogram produced for each day or night of observation.

As data collection progressed it became evident that the eight behaviour categories I recognized (Table 8) were actually parts of only two major types: feeding and resting. Feeding involved what appeared to be swimming and walking while searching for food, alertness during feeding, and flying, when the flight was into an area where feeding was occurring. Sleeping, preening, alertness following sleeping or preening, and flying into an area to rest or sleep were non-feeding activities, or resting. Agonistic encounters formed a special case, most likely but not clearly related to feeding, through maintenance of individual distance.

Because I had assumed feeding to be the most important winter activity (see

Introduction, Section I) I reduced the eight types of behaviour to two for final analysis. Swimming and walking were combined with feeding, to form feeding, and preening was combined with sleeping, to form resting. Alertness was assigned to feeding when feeding was the predominant activity, and to resting when sleep predominated. Flying and agonistic encounters were not used because they were so rarely observed.

The data were analyzed for factors potentially capable of regulating feeding behaviour. Linear and non-linear regression analysis (Zar 1974) was used to look for correlations between numbers of swans feeding and tide height, and numbers of swans feeding and time of day. Those regression methods were employed on those factors only after triangular regression procedures (Le and Tenisci 1978), used to test for correlations between all behaviour types and all environmental factors measured, produced ambiguous results.

RESULTS

TIME BUDGET

Feeding Behaviour

Feeding occurred on various parts of the estuary both day and night, and on adjacent dairy pastures during the day in the winter of 1978-79. Birds feeding on fields that year returned each night to the estuary. However, in the late winter of 1979-80, some swans were reported to have remained throughout the night on fields at the Beaver Meadow Farm (E. Smith, pers. comm.).

Feeding on emergent vegetation was accomplished by pulling up plant rhizomes with the bill, leaving a depression or crater in the substrate (Fig 11). During low tides the birds stood or sat, extracting rhizomes from the edge of a crater. When the vegetation was covered by water during high tides the rhizomes

Fig. 11. A typical swan feeding crater in the emergent vegetation at Comox Harbour.

were reached by submerging the head while swimming, or by up-ending when the vegetation was deeply covered.

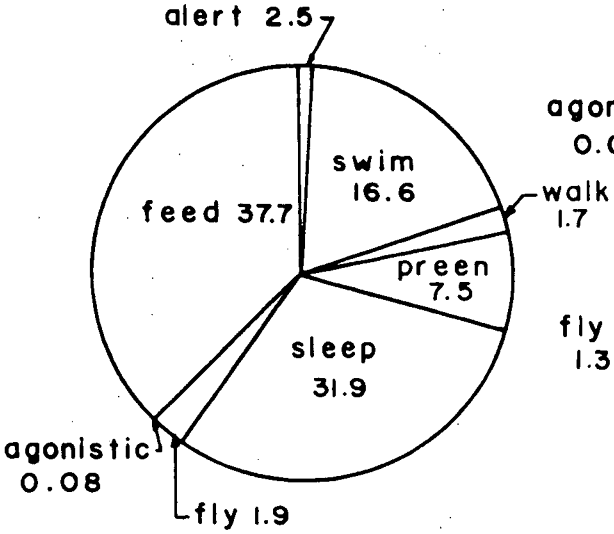
When the vegetation was covered with shallow water, swans used their feet to loosen the substrate from the rhizomes. Water was forced through the silt by alternately pumping the legs, an action similar to that termed paddling in gulls (King 1974). After several seconds of paddling the swan settled back onto the water, submerged its' head and continued grubbing. If a rhizome was not soon extracted, paddling was repeated. Scratching or clawing the substrate, reported by Owen and Kear (1972) and Shea (1979), was never observed.

Close observation of eelgrass (Zostera marina) consumption was not possible because of the distance of the eelgrass beds from the observation points. However, because of the heavy occurrence of eelgrass fronds in scats analyzed for food habits (Section I), it was presumed to be mostly obtained by grazing, with little or no grubbing for rhizomes. Swans were also occasionally observed picking up eelgrass fronds drifted close to shore on rising tides, perhaps further indicating a preference for eelgrass leaves.

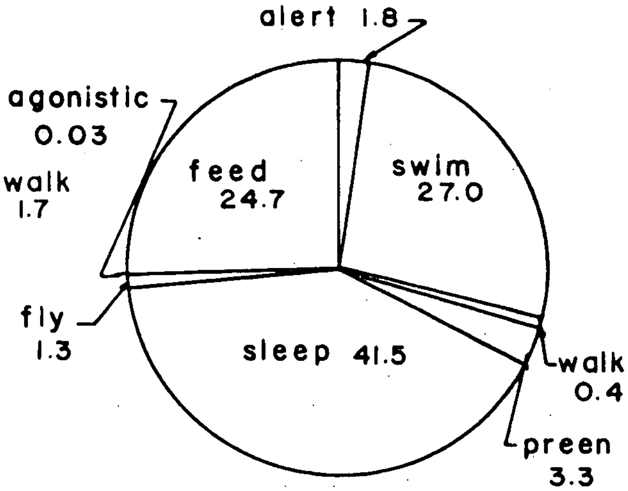
Feeding on pastures was almost always by grazing, although occasionally, when there was much standing water on the fields, grubbing for grass roots did occur.

The amount of time spent feeding varied between daylight and night periods on the estuary, and between the estuary and the fields (Fig. 12). The average percentage of time devoted solely to feeding over a 24 hour period on the estuary was 32.1%. On the fields, where feeding only occurred during daylight, 74.6% of the time was used for feeding.

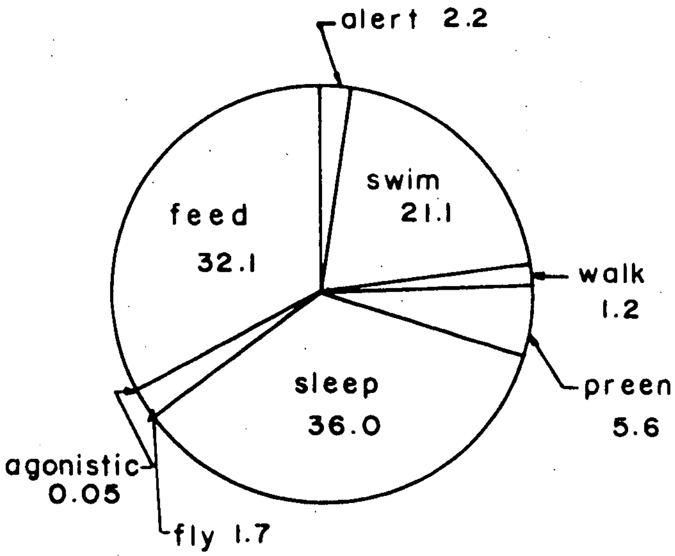
Fig. 12. Mean time spent in each category of behaviour by Trumpeter Swans wintering at the Comox study areas, 1978-79. (A) Daylight observation periods on the estuary; (B) night observation periods on the estuary; (C) day and night observation periods on the estuary combined; and (D) daylight observation periods on the farm fields. Numbers in ( ) are the number of sample periods.



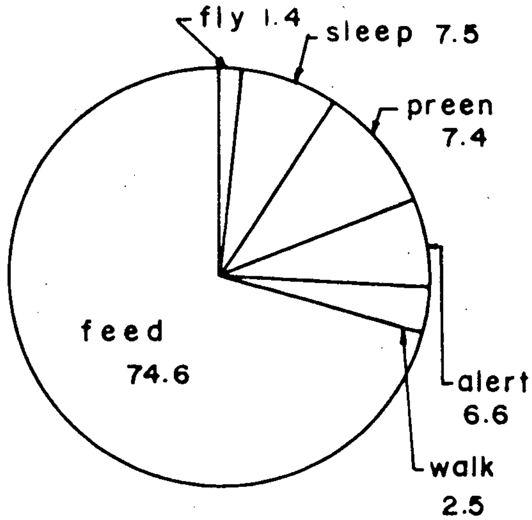
Daylight (11)



Night (4)



24 hr (15)



Fields (7)

Alert Behaviour

Alert behaviour constituted a relatively small proportion of the swans' daily activity budgets but was more important on the fields than on the estuary (Fig. 12). Slightly more time was spent alert during daylight periods (2.5%) than during night periods (1.8%).

Alertness was recognized when a single bird, or a group of birds, looked intensively in one direction, usually with the neck fully extended. If the perceived danger was real, the next action usually consisted of some vocalizing, followed by either walking, or flying away.

I was unable to determine how knowledge of the presence of potential danger was transmitted through the flock. Often a single bird would stare in one direction, with no apparent response from the flock. In contrast, when actual danger was present the whole flock seemed to become alert simultaneously. Some form of vocal signal may have been involved but I was unable to discover it; considerable vocalization was common at most times, although more sporadic when the birds were sleeping.

The only things observed to cause alertness on the estuary were the presence of people or dogs. The appearance of Bald Eagles (Haliaeetus leucocephalus) had no effect, except to cause the swans to lower their heads, to avoid collisions with ducks flushing to deeper water. Similarly, the occasional low flying aircraft, landing or taking off from the runway adjacent to the Sewage Lagoon (Fig. 1) did not cause any alarm either.

The only causes of alertness observed on the fields were people or their vehicles. Cars stopping to view the swans caused an increase in the vigilance of the flock as a whole when the birds had been feeding close to the roadway. Regular movements of farm equipment, however, were soon recognized as non-threatening, causing little or no disturbance.

Swimming and Walking

Swimming was a major activity on the estuary, while walking on both the fields and the estuary was a relatively infrequent action (Fig. 12). Swimming was associated with both feeding and resting. It seldom occurred by itself, but when it did it was only over short distances. Longer distance movements, e.g. across the harbour, or from Millard Road to the Sewage Lagoon, usually involved flights.

Walking on the estuary was most commonly seen near dusk when birds that had been sleeping near the shore moved down to the water's edge to join the rest of the flock. Occasionally distances of nearly 2 km were covered if the tide had receded to the eelgrass beds (Fig. 1).

Walking on the fields was almost always associated with feeding, the birds walking as they fed, or involved only short walks to more choice feeding areas. Movement on the fields often involved a circular or more commonly a spiral pattern. Birds flying into the fields tended to land near the middle, walking in expanding circles towards the edges of the field as the day progressed.

Sleeping and Preening

Preening and sleeping were closely associated, a preening session usually ended with the swan taking up a resting or sleeping position. These two types of behaviour, when combined, were the dominant activities of swans on the estuary but of minor importance to those on the fields (Fig. 12). Preening and sleeping on the estuary occurred at many locations but were seen most consistently on gravel bars near the Sewage Lagoon, at the mouth of Millard Creek, and at the water's edge in the early evening (preening only). During the night, sleeping occurred on the water; tidal currents drifted the birds as far south as Royston or into the centre of the Harbour. No preferred locations were evident for sleeping or preening when the birds were using the fields.

A number of different attitudes were assumed while sleeping. The head and neck were always laid back across the body but the head was only tucked under the scapular feathers in colder weather. The swans slept while standing, usually on one leg, or sitting when on the fields or on the estuary, or while floating when on the water. A resting position was seen occasionally, in which the head was laid across the back, but the eyes remained open.

Feather preening did not seem to follow any particular pattern, except that the wing feathers received the most attention. Most wing preening was accomplished by extending the wing and preening the feathers from the underside, rather than the top, of the wing. The head and neck feathers were preened by rubbing the head across the top of the back. Coloured neck collars, seen on some swans in 1979-80, did not cause noticeably higher levels of neck feather preening, nor any other types of behaviour.

Flying and Agonistic Behaviour

Little time was devoted to flying or to agonistic displays (Fig. 12). Flights to and from adjacent dairy pastures, when feeding in the fields was possible, occurred near dawn and dusk. The birds usually moved in small groups, either pairs, families or groups of apparently mature but unpaired birds. I occasionally saw flights into the estuary well after dark, presumably as birds returned from fields some distance away. Generally, flights were of short duration due to the proximity of the fields to the estuary.

Occasionally birds were seen to take flight from the estuary at odd times throughout the night. Single birds or small groups would fly off the water, circle the harbour, and settle at some distance from the flock. Reasons for those flights are speculative because the birds involved were usually beyond the useful range of the night scope but agonistic encounters seem probable. On one occasion many flights followed a general disturbance of the flock, and were probably caused by something other than disagreements. Harbour seals (Phoca vitulina) were seen regularly in the harbour during the day, and were likely present at night also. Although it seems unlikely seals would attempt to capture swans they will take scaup (Athya sp.) (Lee 1976); their presence among the flock of swans at night may well have been cause for a general alarm.

As mentioned, flights usually involved only small groups of birds at any one time. Flights of the entire flock from the fields or the estuary only occurred after the sudden appearance of a predator, usually a dog. In non-predator induced flights head bobbing and vocalizing preceded the flight of the group from the land or the water. Head bobbing and vocalizing would be initiated by one or more members of the flock; flight would ensue shortly after all members of the group bobbed and vocalized, in a manner similar to that reported in Canada Geese (Branta canadensis) (Raveling 1969). Occasionally, wing stretching and flexing was also associated with head bobbing and vocalizing. If, after initiating bobbing and vocalizing, the group did not take flight, the initiator would stop bobbing, flex the wings, and settle back onto the water.

Agonistic encounters, although rarely seen (Fig. 12), were of three main types that varied in degree of aggressiveness. The most overt encounters involved vocal threats and wing displays. These were the rarest encounters but also the most noticeable because of the accompanying sound. The common, single-note trumpet call, that formed the background "conversation" in most groupings or flocks, was broken in those encounters by a staccato series of trumpets by one or both antagonists. The two or sometimes three birds involved would be seen facing each other, necks stretched upwards and bills open, trumpeting. Wing displays usually followed, with a short chase on land, or pecking at each others wings when on the water. Most encounters were very brief and were never seen to develop into more serious conflicts involving wing strikes. One of the combatants usually swam or walked quickly away, shook its tail and adjusted its feathers.

The other two types of encounters were much more subtle, and may have gone unnoticed on many occasions. The more aggressive of these encounters involved a peck on the back or wing of an interloper, usually by the larger bird of a family group. The interloper usually moved off by itself or approached the group from another side. The least aggressive encounter involved the simple displacement of one feeding bird by another. The approaching bird was usually larger, and the feeding bird usually moved to another area with no resistance.

Combined Activities

The amount of time devoted to the combined activity of feeding on each date of observation varied considerably on the estuary, but was relatively constant on the fields (Table 9). On average, 57.6% of a given daylight period and 47.2% of a night period on the estuary was spent feeding. Feeding on the fields accounted for 86.1% of the time spent there.

REGULATION OF FEEDING BEHAVIOUR

When the eight behaviour categories originally recognized (Table 8) were reduced to feeding and resting, correlations were found between the numbers of swans feeding and tide height, and between numbers feeding and time of day. None of the other environmental factors recorded had any apparent relationship with numbers of swans feeding, with one exception presented below. Of the 11 daylight periods when swans were observed on the estuary, six showed strong positive correlations with tide height, four showed weak positive tide correlations, and one showed a negative correlation with tide height.

In attempting to explain why there should be three different types of relationship between tide height and numbers of swans feeding I found that the tides were classifiable into two general types (Fig. 13). Certain tides were highest in the early morning (Type A tides, Fig. 13A) and tended to drop throughout the day, while other tides peaked near 1200 h (Type B tides, Fig. 13) and were moderately high all day.

On days of Type A tides the numbers of swans feeding were well correlated with tide height (r = 0.79, Fig. 14A) when the data from the day on which there was a negative correlation between tide height and numbers feeding were excluded. Although the tide on the day of that negative tide height feeding correlation was of the Type A class (Fig. 13C), the feeding data obviously were not related to the other feeding data for that type of tide (Fig. 14B). The tide conditions on that day were also slightly different with a higher peak tide and slower drop in height during the day, than the average for Type A tides (Fig. 13C). Because the tide was an extreme of the Type A tides, and the feeding data were so much different than the data for other days of Type A tides I felt it was justifiable to treat that data separately.

On the days of Type B tides the number of swans feeding was poorly correlated with tide height (r = 0.37, Fig. 14C).

The relationship between time of day and numbers feeding on days of Type A tides was the opposite of that seen with tide height. Numbers feeding were negatively correlated with time of day (r = -0.67, Fig. 15A), with the exception of one day, when there was a positive correlation (r = 0.81, Fig. 15A). On days of Type B tides numbers of swans feeding was also negatively correlated with time of day (r = -0.54, Fig. 15B). Time of day was used because no relationships could

Fig. 13. Average tide conditions during daylight observation periods of Trumpeter Swan behaviour at Comox Harbour. (A) Type A tides; (B) Type B tides; (C) extreme Type A tides.

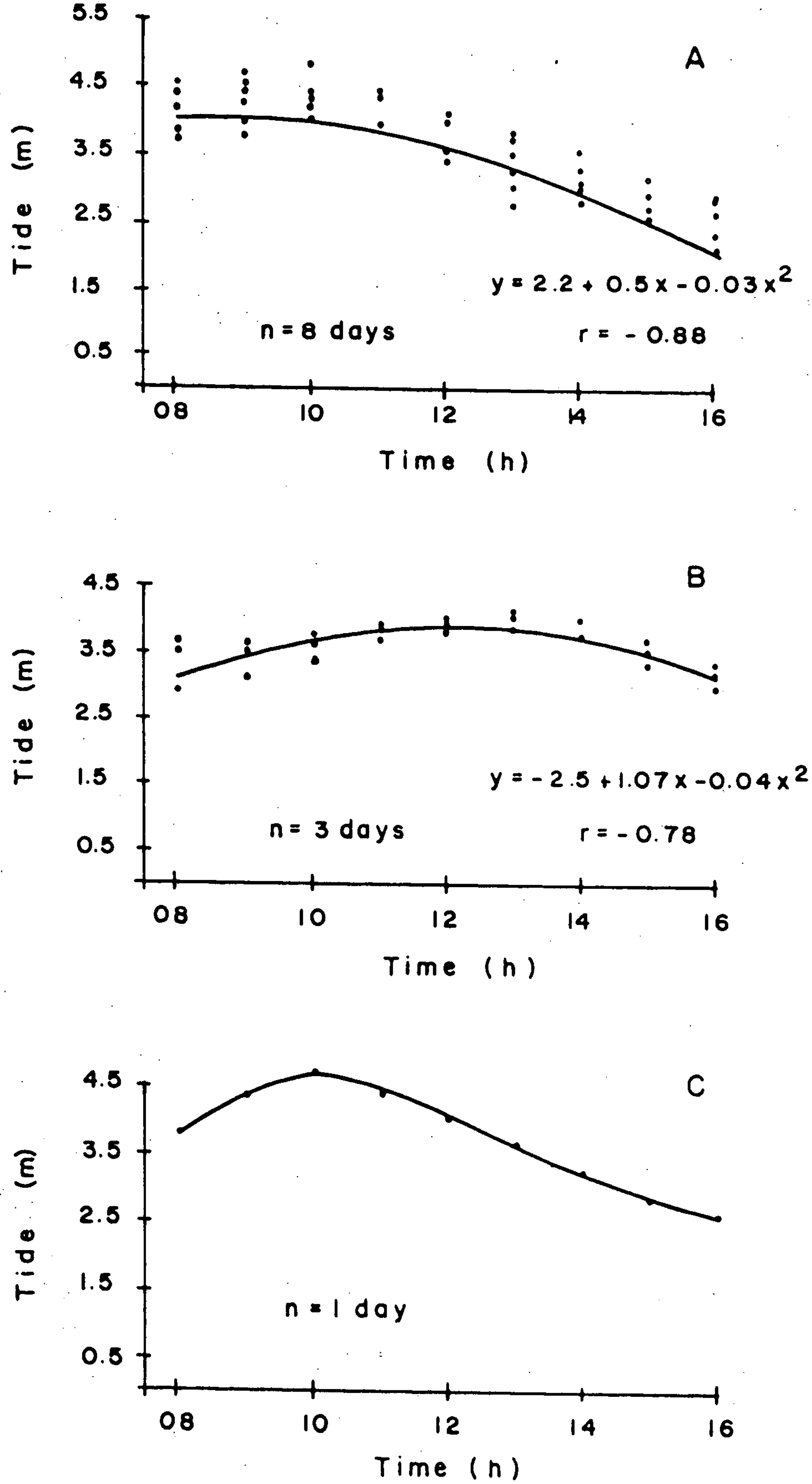

A
Tide (m)
5.5
4.5
3.5
2.5
1.5
0.5
y = 2.2 + 0.5x - 0.03x²
n = 8 days
r = - 0.88
08
10
12
14
16
Time (h)
B
Tide (m)
4.5
3.5
2.5
1.5
0.5
y = -2.5 + 1.07x - 0.04x²
n = 3 days
r = - 0.78
08
10
12
14
16
Time (h)
C
Tide (m)
4.5
3.5
2.5
1.5
0.5
n = 1 day
08
10
12
14
16
Time (h)

Fig. 14. Relationships between numbers of Trumpeter Swans feeding and tide height at Comox Harbour. (A) feeding versus tide on days of Type A tides; (B) feeding versus tide on one day of negative correlation with Type A tides; (C) feeding versus tide on days of Type B tides. Numbers feeding are arcsine transformed percentage values (Zar 1974).

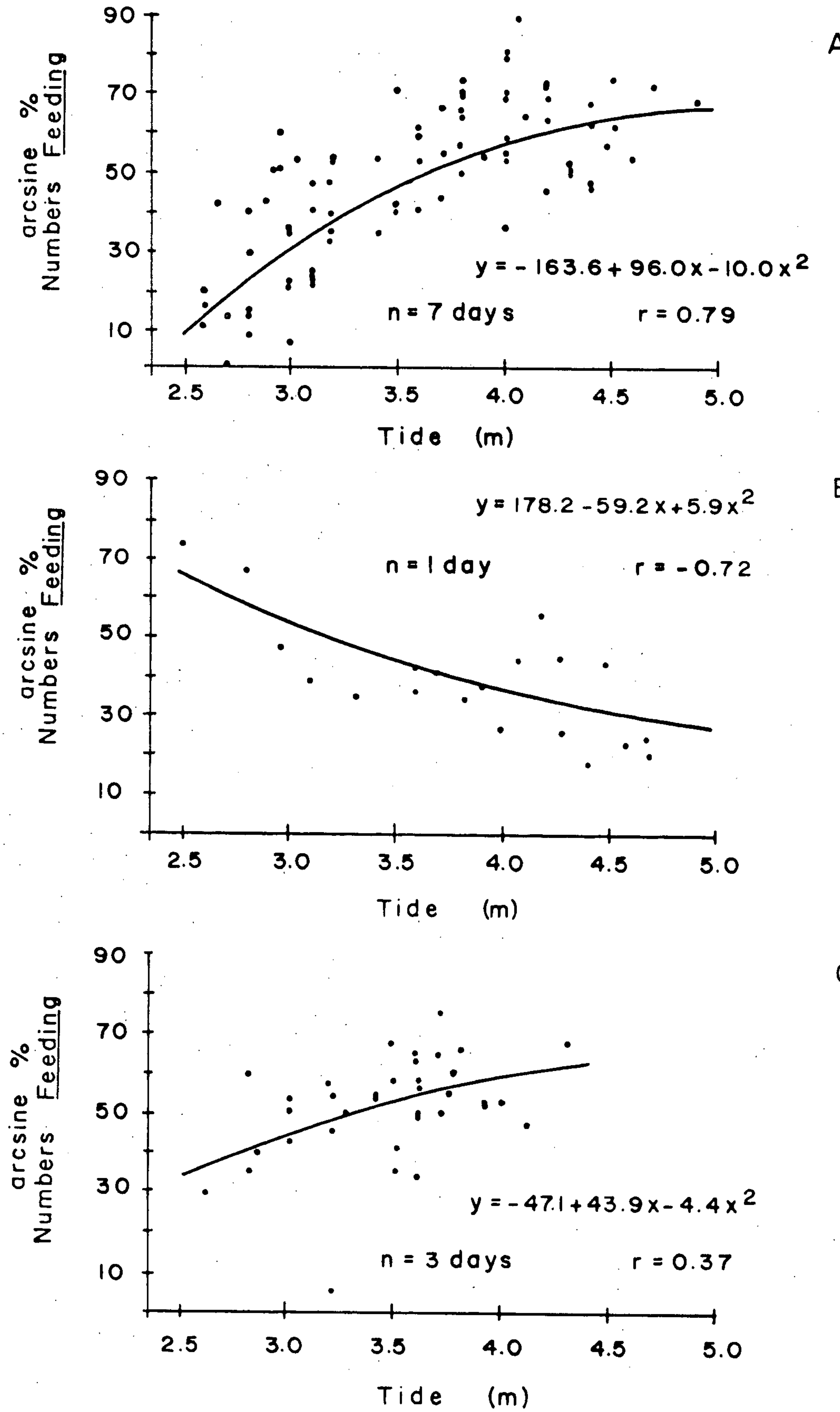
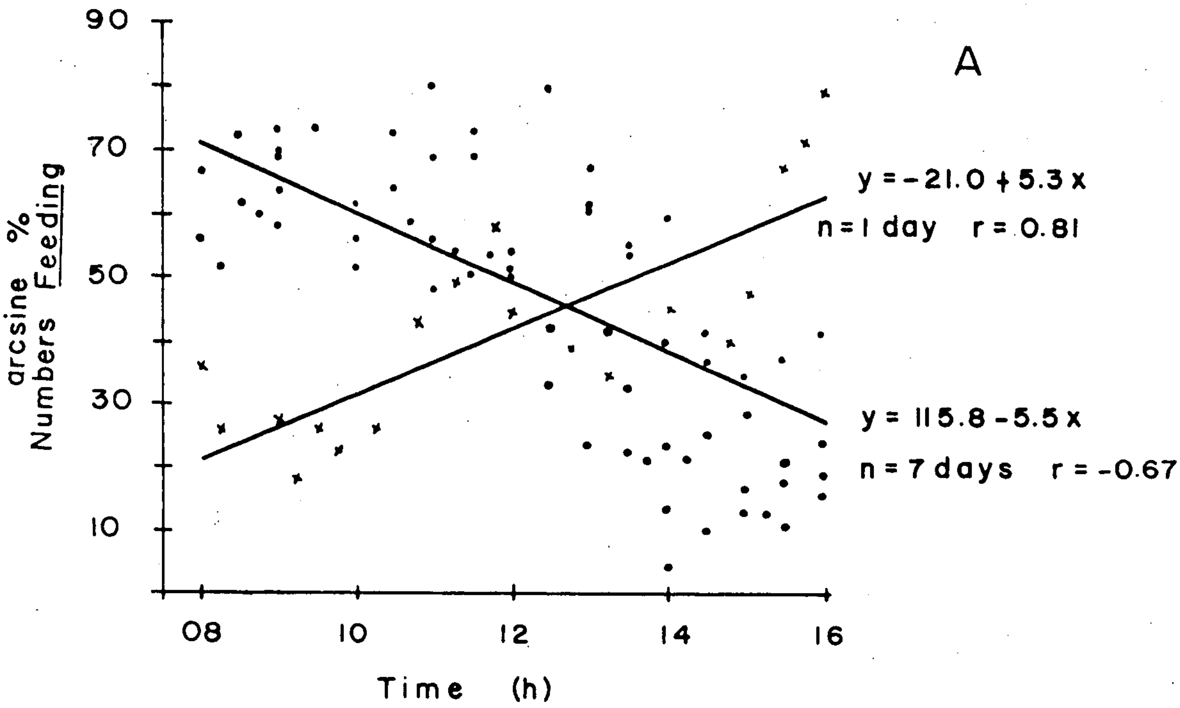
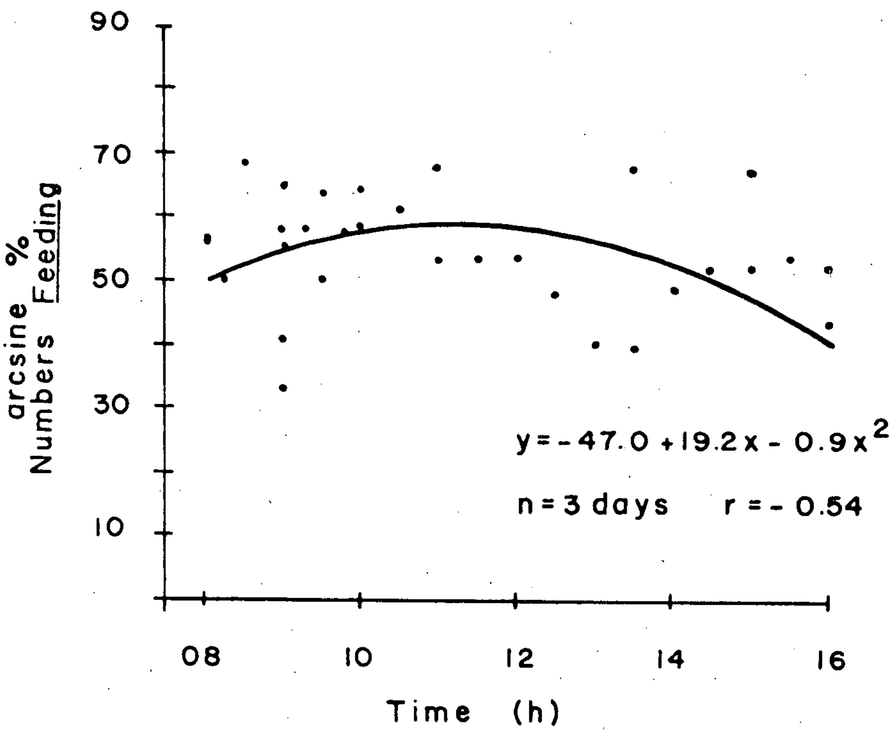

A
arcsine % Numbers Feeding
90
70
50
30
10
$y = -163.6 + 96.0x - 10.0x^2$
n = 7 days
r = 0.79
2.5
3.0
3.5
4.0
4.5
5.0
Tide (m)
B
$y = 178.2 - 59.2x + 5.9x^2$
n = 1 day
r = -0.72
arcsine % Numbers Feeding
Tide (m)
C
arcsine % Numbers Feeding
$y = -47.1 + 43.9x - 4.4x^2$
n = 3 days
r = 0.37
Tide (m)

Fig. 15. Relationships between number of Trumpeter Swans feeding and time of day at Comox Harbour. (A) feeding versus time of day on days of Type A tide; (B) feeding versus time of day on days of Type B tide. Numbers feeding are arcsine transformed percentage values (Zar 1974).


A
90
70
50
30
10
arcsine %
Numbers Feeding
y = -21.0 + 5.3 x
n = 1 day r = 0.81
y = 115.8 - 5.5 x
n = 7 days r = -0.67
08
10
12
14
16
Time (h)


B
90
70
50
30
10
arcsine %
Numbers Feeding
y = - 47.0 + 19.2 x - 0.9 x²
n = 3 days r = - 0.54
08
10
12
14
16
Time (h)

be found between feeding rates and times of sunrise and sunset in preliminary data analysis.

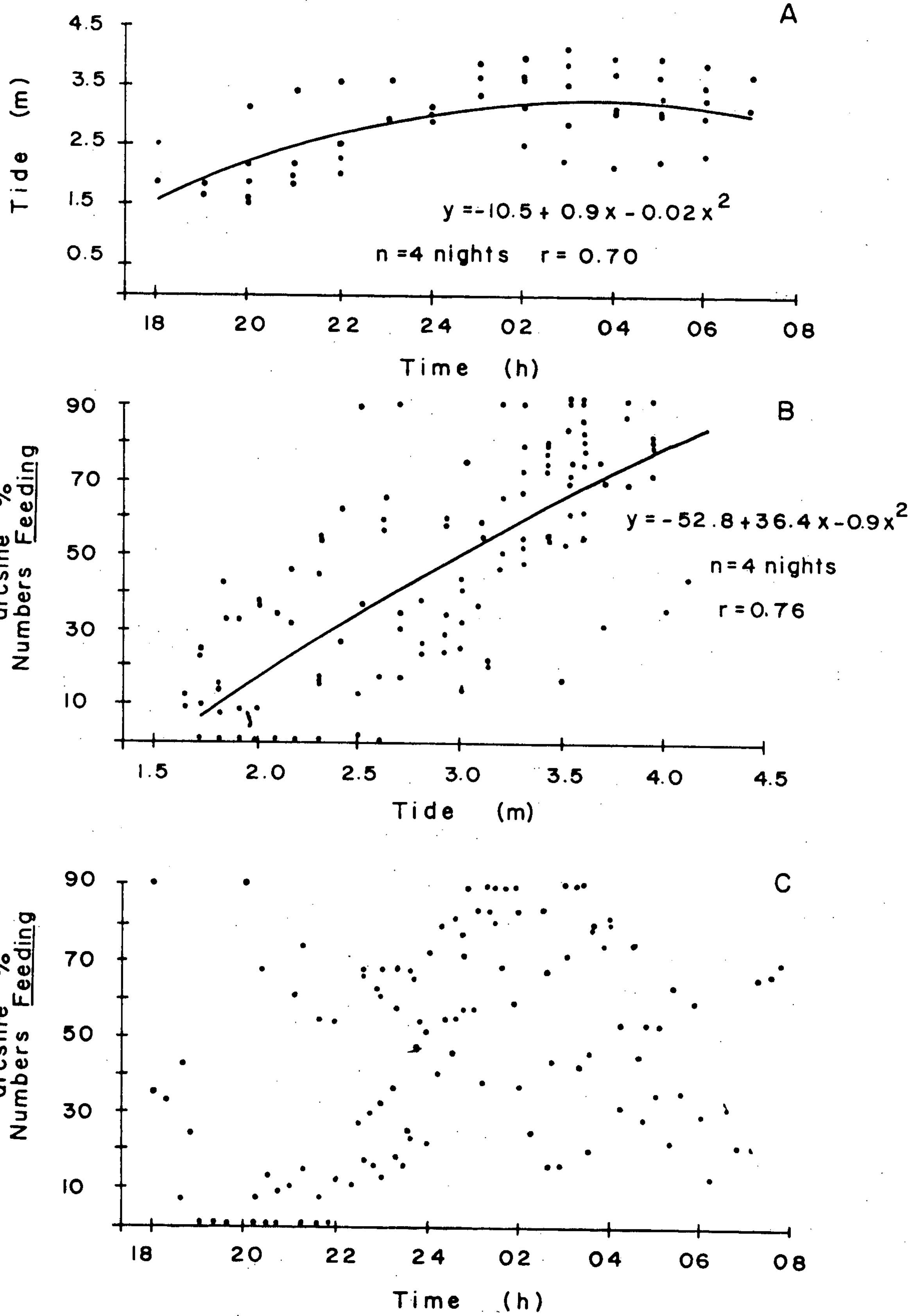
Swans were observed during six night periods, but because of weather-caused interruptions in data collection, only four nights of observations were available for analysis. Tide actions were approximately the same on all four nights (r=0.70, Fig. 16A), rising from the daily lowest tide in the early evening to the lower high tide around 0300 h. The number of swans feeding was positively correlated with tide height (r = 0.76, Fig. 16B), but was not correlated with time of day (Fig. 16C).

As mentioned, no strong correlations could be found with percentages feeding and air temperature, wind speed, or the presence or absence of snow on the fields, with one exception. There was a slight negative correlation (r = -0.53, Fig. 17) between numbers feeding during the four complete night observations, and temperature.

Temperatures during the study period ranged from -7° C to +7° C. Wind was usually light (under 10 kmh), reaching a high of 20 kmh only once. Snow was present on the fields for half of the observation periods. Snow falls were infrequent but were heavy when they occurred, the snow remaining for some time. Snow on the fields prevented feeding there, but its absence had little effect on the proportion of time spent feeding on the estuary (Table 9).

On only one occasion was the effect of adverse weather apparent on the feeding routine of swans on the estuary. During the observation period 5-7 February 1979, a south-east wind came up ca 0600h. The tide was beginning to cover the root mat and the majority of swans were feeding. As the water depth increased over the root mat, wave activity increased also. The numbers of birds feeding declined rapidly as a result of the interference of the waves with the swans' up-ending and underwater grubbing.

Fig. 16. (A) Tide height versus time of day, (B) numbers of Trumpeter Swans feeding versus tide height, and (C) numbers of Trumpeter Swans feeding versus time of day for 4 nights of complete observations at Comox Harbour. Numbers feeding are arcsine transformed percentage values (Zar 1974).


A
4.5
3.5
2.5
1.5
0.5
Tide (m)
y =-10.5 + 0.9 x - 0.02 x^2
n =4 nights r= 0.70
18 20 22 24 02 04 06 08
Time (h)
B
90
70
50
30
10
arcsine % Numbers Feeding
y = -52.8 + 36.4 x - 0.9 x^2
n = 4 nights
r = 0.76
1.5 2.0 2.5 3.0 3.5 4.0 4.5
Tide (m)
C
90
70
50
30
10
arcsine % Numbers Feeding
18 20 22 24 02 04 06 08
Time (h)

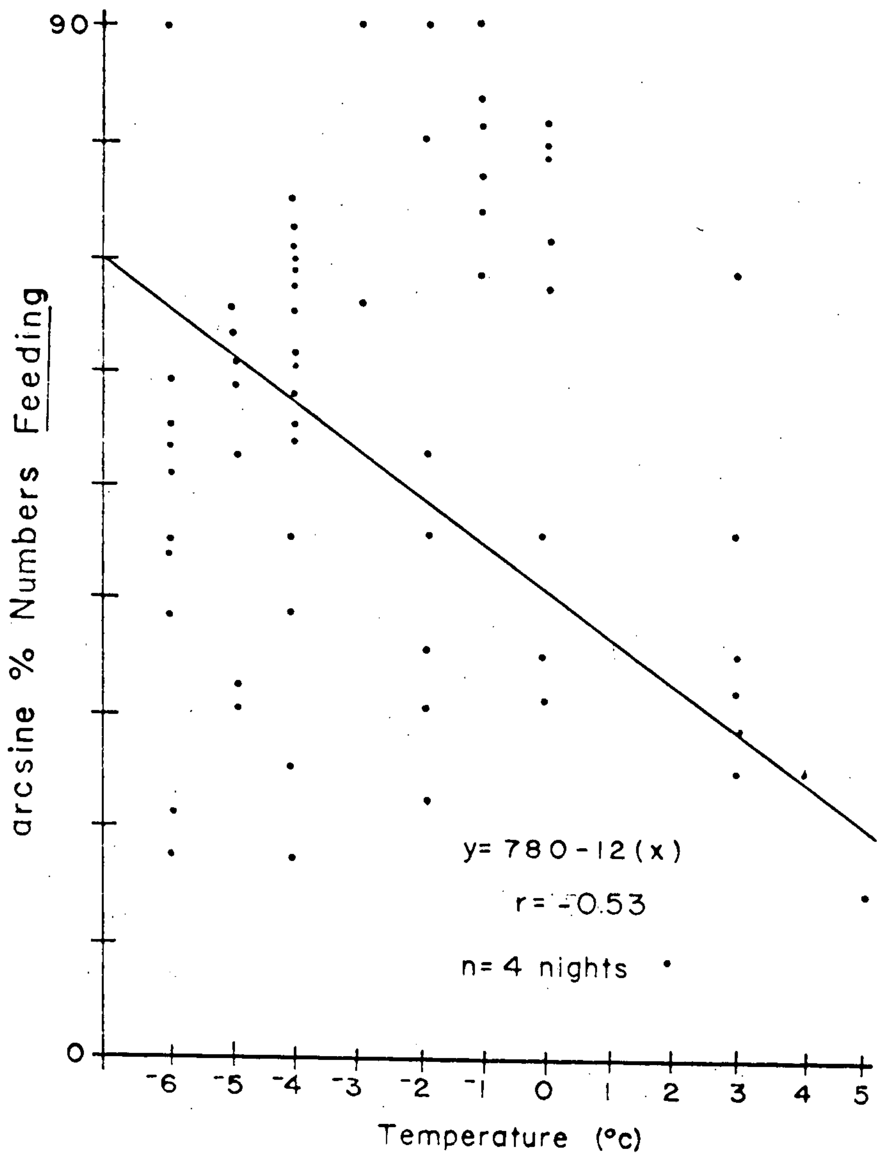


Fig. 17. Percentage of Trumpeter Swans feeding at night versus temperature for 4 nights of complete observations. Percentage values have been arcsine transformed (Zar 1974).

Birds feeding on fields were only observed to do so during daylight. They returned to the estuary at night, except in the late winter of 1979-80 when they began to stay at the Beaver Meadow Farm all night. I was unable, however, to determine if any night feeding occurred then. Feeding on the fields during the day was more or less continuous, with no significant correlation with time (Fig. 18).

DISCUSSION

TIME BUDGET

Feeding Behaviour

The results of this study show that Trumpeter Swans wintering at Comox Harbour spent a relatively small proportion of their time in feeding, at least while on the estuary. Although the estuarine diet is low in protein and high in fiber (Section I) it must be adequate nutritionally and metabolic demands must not be too great, for such a small amount of time to be budgeted for feeding. Studies of other species of birds have shown that a relatively greater proportion of time must be devoted to feeding during the winter (Murton et al. 1963; Verbeek 1964), even though the foods available to them were probably more nutritious than those available to the swans.

Feeding on the estuary occurred both day and night throughout the study. Night feeding by waterfowl has been reported (Ranwell and Downing 1959; Raveling et al. 1972; Zwarts 1972; Swanson and Sargeant 1972; Owens 1977), and is probably a widespread phenomenon. Many other species were active at night with the swans, particularly American Wigeon (*Anas americana*). Most estuarine feeding seems to involve the tactile sense because the rhizomes were covered with silt or silty-water and thus not visible. Thus night feeding by Trumpeter

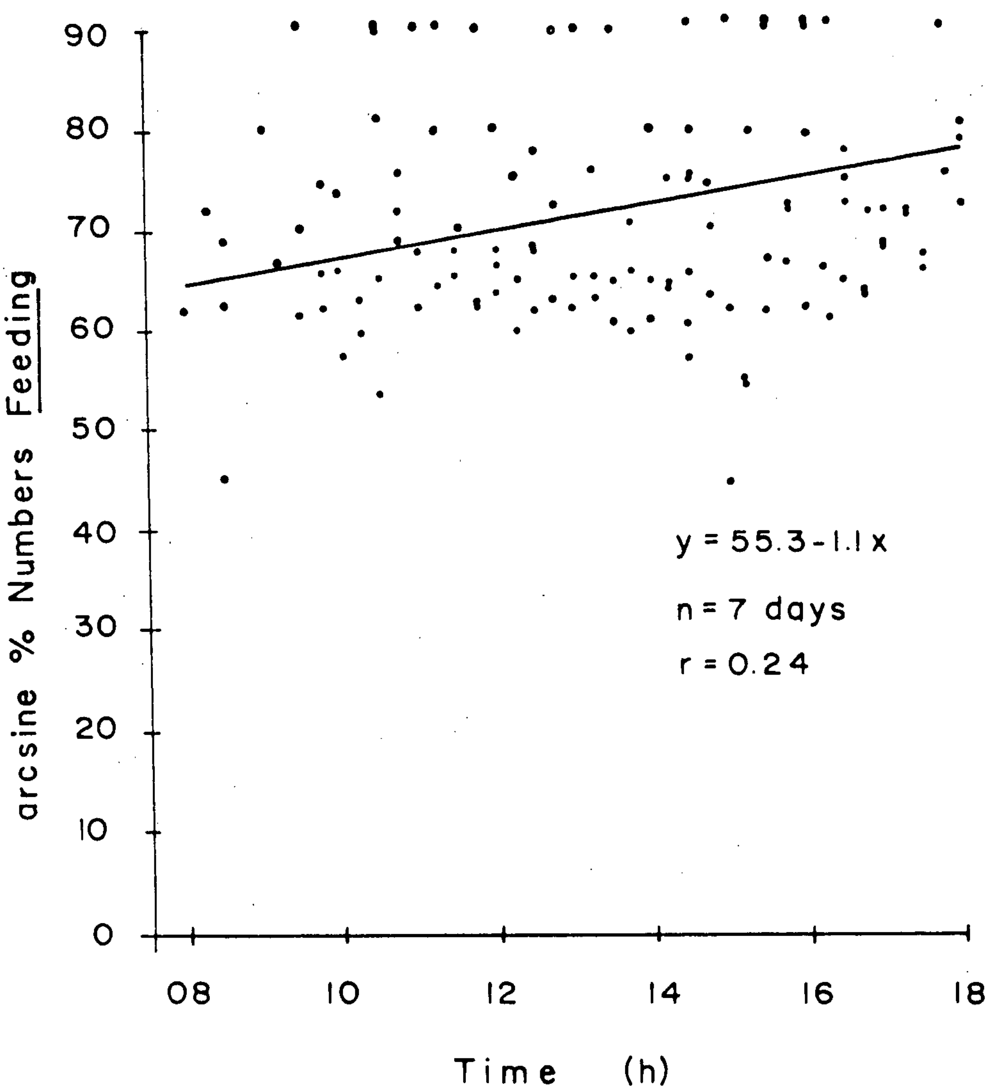


Fig. 18. Percentage of Trumpeter Swans feeding on fields versus time of day for 7 days of observations. Percentage values have been arcsine transformed (Zar 1974).

Swans and other species of waterfowl may be common wherever food can be found without actually seeing it.

Time spent feeding on the fields was similar to amounts reported in other species of waterfowl. Ebbinge et al. (1975) reported 82.5% of the day was spent feeding by Barnacle Geese (Branta leucopsis) and Owen (1971) found that White-fronted Geese (Anser albifrons scopoli) spent over 90% of their day feeding.

Unfortunately, there was no way to tell how much swans grazing on pastures fed after returning to the estuary at night, because there were no marked birds in the flock at that point of the study. There is evidence that Trumpeter Swans wintering at Comox Harbour have two feeding strategies, because not all the birds leave the estuary to feed in the fields until later in the winter. Those strategies are: (1) acquire enough nutrients by feeding on the fields during the day so that there is no need to feed at night; and (2) feed on the fields as much as possible during the day and supplement the diet with feeding on the estuary at night. Birds which feed on the fields during the day throughout winter, then, may not need to feed at night on the estuary, because they acquire enough nutrients from the grass alone. However, because they return each night to the estuary until late in the winter, night feeding may still be necessary. This later view is supported by the observation of birds at night on the fields in late winter, when the longer daylight period allows more time for feeding.

If grazing in fields is restricted to daylight periods, the visual sense, as opposed to the tactile sense used while feeding on the estuary, may be the most important sense for grazing. Visual selection may occur on two levels: for specific parts of the grass plant, and thus the requirement for daylight while grazing; and for initially locating the most desirable fields for grazing. Highly productive pasture remains a lush green throughout the winter while less productive areas turn yellow, probably indicating a high proportion of fiber.

Large open fields with yellow coloured grass within 2 km of the Beaver Meadow Farms were not used by the swans, even though there was less probability of disturbance on them, because of the distance of those fields from the road.

The craters that wintering Trumpeter Swans made while feeding on the estuary are typical of the excavations of other species of swans, but the manner in which they are made may have been misinterpreted by other researchers. Some workers have concluded that feeding craters were produced by the action of the swans' feet through a scratching and clawing motion (Owen and Kear 1972; Shea 1979). The feet are used in feeding, as my results show, but not in the fashion reported by others. Swans, and most waterfowl, are quite capable of walking but are not particularly agile. Swans are clumsy enough on land to lead me to believe they lack the co-ordination to use their feet for anything in the horizontal plane but walking. Swans are not as well adapted morphologically either for scratching and clawing as are birds like pheasants. Although waterfowl have sharp claws, as many bird banders will attest, the webbing of their feet does not allow the claws to penetrate the substrate more than a few millimeters. However, the size of the swans webbed foot makes it very useful as a "suction pump", forcing water over the substrate to loosen the rhizomes, thus freeing them of silt.

The fact that Trumpeter Swans grazed when feeding on eelgrass and pasture grasses, and grubbed only for the rhizomes of emergent plants has some interesting implications. If Trumpeter Swans have wintered traditionally along the British Columbia coast they must have fed on estuaries, because pastures have only recently become available. The swans must therefore be adapted to grubbing. The reported food habits of Trumpeter Swans in the summer also seems to indicate a preference for grubbing (see Section I). However, Trumpeter Swans at Comox Harbour were able to switch between grubbing and grazing with apparent ease. Bolen and Rylander (1978) have postulated that the grubbing habit is reflected in certain morphological characteristics, notably stouter maxillary and mandibular serrations. Studies of the feeding apparatus of Trumpeter Swans are now in progress to see if Bolen's and Rylander's hypothesis applies to Trumpeter Swans also.

Alert Behaviour

The difference in the amount of time spent in alert behaviour between the estuary and the fields undoubtedly reflects the relative safety of those two areas. The spiral pattern of feeding in fields may also be related to safety. Full grown Trumpeter Swans seem to have no avian predators, probably because of their size. Natural enemies on estuarine wintering areas may consist only of members of the canine family, which would be only able to threaten sick or injured birds. On fields, however, the swans' vulnerability would be higher. The opportunities for a predator to closely approach a swan would be greater from bush or grass cover, and the chances of the swan escaping would be lessened by the lack of water nearby, and the need to escape by becoming completely airborne. The swans would tend to be more vigilant in higher vulnerability areas, such as fields, thus devoting more time to alert behaviour.

Swimming and Walking

Little need be said of the behaviour categories of swimming and walking except to note that they can probably best be considered as subgroups of other types of behaviour. They appeared never to occur for their own sake but were the products or the means of some other behaviour type, primarily feeding.

The only peculiarity needing discussion in these types of behaviour is the circular or spiral pattern of walking on the fields. Spiralling outwards from the field centre may have been a response to the crowding of birds landing in the centre, or a response to dangers potentially present at the edges of the fields. By moving close to the edges gradually, more time would be available to detect potential predators, and thus to escape.

Sleeping and Preening

The large amount of time spent sleeping and preening on the estuary is a corroborative piece of evidence for the apparently high value of the swans' estuarine diet. The small amount of time spent feeding allowed more time for other activities such as resting. Similarly, the small amount of time devoted to comfort behaviour and resting on the fields attests to the importance of the fields as a source of food. Most of the time there was spent feeding, so little time was left for sleeping. Also, sleeping on the fields may have been too dangerous a use of time compared to the safety afforded by the estuary.

The areas most heavily used on the estuary for sleeping and preening were those which were best protected from approach by land, at least at night. The apparent lack of aerial or aquatic predators is evidenced by the observed dispersion of many swans into the centre of Comox Harbour while sleeping at night. Presumably, if predation were a potential problem, the birds might tend to remain together more as a flock than to drift so passively with the tides.

Flying and Agonistic Behaviour

The flight behaviour of Trumpeter Swans at Comox Harbour, and their known pattern of winter distribution in B.C. (McKelvey in press) suggests that they do not readily form flocks. Johnsgard (1965:33) states that all northern swans are similar in general behaviour, often occurring in large, well-organized flocks. However, surveys of the winter distribution of swans along the B.C. coast show that many Trumpeter Swans winter in small groups (Smith and Blood 1972;

McKelvey 1979). When they do occur in large groups, such as at Comox Harbour, they do not exhibit the starting line behaviour at flight time as reported in the strongly flock-oriented Canada Goose (Raveling 1969).

None of the northern swans, as compared to geese, have the distinctive body or wing markings which are thought to be important in maintaining flock unity (Raveling 1969). Similarly, immature swans (in their grey plumage) differ more in colour from the adults than young geese do, when compared to adult ones. Either plumage characteristics in swans are not important in maintaining following and flock unity, or northern swans, particularly Trumpeter Swans, are not truly flock birds.

There appears to be no advantage to Trumpeter Swans to live in flocks either. Flocking is thought to be an anti-predator response (Goss-Custard 1970) or to result in increased feeding efficiency (Wilson 1975:53). However, Trumpeter Swans appear to have few natural enemies, probably because of their large size. Increased feeding efficiency through flocking also seems unlikely because of the relative abundance of what might be considered the natural food source of swans along the British Columbia coast, estuarine emergent plants and eelgrass (Section I).

The nature of the agonistic encounters observed agrees generally with those reported for Trumpeter Swans by others (Banko 1960; Johnsgard 1965; Cooper 1979). What is interesting, however, is the relative infrequency of such encounters. Banko (1960) noted that aggressive displays became more common in late-winter flocks, presumably as the birds began to come into breeding condition but the general levels of aggression reported seemed to be higher than noted in this study.

There is a possible explanation for the apparent difference in the levels of overt aggression reported by Banko (1960) and those noted in this study. It is based on food availability and perhaps nutritional value. The tri-state population of Trumpeter Swans, and the Grande Prairie swans that winter in the tri-state area may be limited by winter habitat (B. Turner, pers. com.) through ice cover and a shortage of food. Higher levels of aggression might be expected when food is scarce because at Comox Harbour, where food is abundant and apparently nutritionally adequate (Section I and this Section), aggressiveness is infrequent. Further evidence comes from personal observations of Bewick's Swans (Cygnus columbianus bewickii) feeding on rhizomes of wild rice (Zizania sp.) in Japan. Aggressive levels there were very high, causing interference among those birds that were feeding. The plant rhizomes were also very thick (+ 6 cm app.), growing in great profusion and requiring a great deal of effort to extract. It is possible that such high levels of aggression were caused by the lack of good feeding spots and a resultant struggle to make use of those that were available.

Combined Activities

The reduction of the various categories of behaviour to only two main types, feeding and resting, also indicated that a considerable proportion of the day remained available for other activities. The procedure of combining behaviour into two main categories is acceptable I think, and can be argued on logical grounds.

Fitness can be measured in terms of reproductive output, i.e. the more viable offspring an individual produces, the more fitness it has (Lewontin 1979). Animals adapted to seasonal exploitation of environments, such as Trumpeter Swans, can only maintain their fitness by surviving the winter or non-breeding period. To do that requires energy, which can only be obtained by feeding. Feeding must obviously also occur during the breeding season, to fuel the breeding process, but in the winter, it is only fueling self-maintenance (broadly speaking). Lack (1970) determined that feeding and associated concepts were the most important components of the ecology of a species, while Peek (1975), in reviewing food habits studies of moose (Alces alces) maintained that fundamental relationships between animals and their environments are expressed by feeding studies. Thus, the most important activity of Trumpeter Swans during the winter, and probably at other times of the year, is feeding. Other activities are possible only after energy is available, which can only be obtained by feeding.

REGULATION OF FEEDING BEHAVIOUR

The influence of the tides on the feeding behaviour of waterfowl wintering on estuaries has been observed in Sheldducks (Tadorna tadorna) (Bryant and Leng 1975; Buxton 1976), Brent Geese (Branta b. bernicla) (Ranwell and Downing 1959), Snow Geese (Burton and Hudson 1978), and Common Eiders (Somateria mollissima) (Campbell 1978). In most cases the food source was unavailable at certain tides because it was too deeply covered (Ranwell and Downing 1959; Burton and Hudson 1978) or because it was not possible to remove adhering silt (Burton and Hudson 1978) at low tides.

Few studies have reported on the winter feeding behaviour of swans, however Mathiasson (1973) recorded food habits of Mute Swans moulting in Sweden but gave no indication of feeding behaviour in relation to food availability. Berglund (1963) similarly reported on Mute Swans breeding and wintering in Sweden, but again gave no details of feeding behaviour.

The results of this study show that winter feeding by Trumpeter Swans was regulated by tidal conditions, which in turn caused both diurnal and nocturnal feeding (Figs. 13-16). Other factors likely to affect feeding seemed to be of little importance.

Swans wintering at Comox Harbour were apparently affected by both too little and too much water over the food source. Highest levels of feeding occurred on days of Type A tides near the peak of the tide, (Figs. 13A and 14A) with one exception. What may have happened on that day of negative correlation with tide height is that the peak tide was higher than usual for that tide pattern, the result being the unavailability of the food source at high tide (Figs. 13C and 14B). Because the food was unavailable until later in the day, feeding activity reached its peak later in the day on the falling tide. More extensive observations on days with tide above the average for Type A tides might even reveal a third tide type, when feeding rates would appear to be negatively correlated with tide height, because high tides would be above the level preferred for most intensive feeding.

The low correlation between numbers of swans feeding and tide height on days of Type B tides reflects the conservative fluctuations of the tides on those days (Figs. 13B and 14C). The emergent vegetation was covered or partially covered most of the time on days of Type B tides and feeding was possible for most of the day.

When the relationships between numbers of swans feeding and time of day (Fig. 15B) are compared with the graph of tide types, these relationships are clearer. Higher average rates of feeding occurred at the time of day at which the tide was highest, for Type A and Type B tides, and when the extreme Type A tide (Fig. 14B) fell within the range of the average Type A tide. Time of day rather than time in relation to sunrise and sunset was considered adequate in this analysis because preliminary analysis showed there was relatively little variation in day length between all observation dates. Relationships between numbers feeding and tide height were much more evident on a daily basis than were relationships with sunrise and sunset.

Night feeding on the estuary was most visible over the emergent vegetation. Feeding over the eelgrass beds appeared to account for a relatively small proportion of the night, but the limited range of the night scope precluded accurate observations. However, the occurrence of eelgrass in the fecal samples indicated eelgrass to be one of the most important foods consumed on the estuary (Section I). It is possible that, given the shallow nature of Comox Harbour, feeding on eelgrass could have occurred on average over a larger portion of the night than detected in the sample reported here. Night feeding on emergent vegetation, however, was well correlated with tide. The importance of some water cover to assist in extraction of rhizomes was the most probable reason for that relationship.

Extracting and cleaning roots and rhizomes was facilitated by the water covering. Although there may have been a preferred depth of water for feeding excessive depths of water likely never occurred over the root mats of emergent plants. The long neck of the Trumpeter Swan allows it to feed to depths of at least 1 m or more if the bird tips up, so if necessary, feeding could occur in relatively deep water.

Evidence for the dependence of feeding activity on tide levels is further gained by analysis of the relationship between activity and time of day. Campbell (1978) considers diurnal routines to be the rule for most waterfowl, day or night feeding being influenced by factors such as disturbance, predation, and food type. Trumpeter Swans fed at Comox in response to tides, relationships between time of day and feeding being a result of the timing of ideal tide conditions. Correlations between feeding and time of day were usually opposite to those between feeding and tide height because of the constantly changing nature of the tide cycle. The time of occurrence of preferred tides affected peak feeding, the time of day being incidental. Time regulated feeding would probably have exhibited a daily rhythm on all observation days, similar to those reported for other species of waterfowl that feed predominantly in fields (Raveling et al. 1972; Owen 1972a, 1972b, 1973; Ebinge et al. 1975).

Nocturnal feeding apparently occurs naturally in waterfowl (Tamisier 1976) or in response to disturbance and food availability (Ranwell and Downing 1959; Owen 1971; Swanson and Sargeant 1972). Nocturnal feeding in Trumpeter Swans at Comox probably occurred in response to food availability and possibly energy demand. Though the highest concentrations of feeding birds were seen when water covered the root mat, individuals were observed on occasion to feed all day on the exposed emergent root mat. Feeding in those instances may have been in response to metabolic demand, rather than to the ease of root and rhizome extraction when water covered the root mat.

A positive relationship between the amount of time spent foraging and temperature has been demonstrated in many species of birds (Verbeek 1964, 1972; Nilsson 1972). Geese appear to cope with lowered temperatures by migrating, changing feeding habits, and becoming less wary (Philippona 1966), or by becoming inactive (Raveling et al. 1972; Markgren 1963). Data from this study were inconclusive because of the narrow range of temperature and small sample size, but Trumpeter Swans appear to respond to colder temperatures by feeding more.

Trumpeter Swans however generally seem to be relatively cold tolerant, perhaps because of their large size and thick down insulation. Many species of highly migratory birds exhibit an inverse relationship between size, and distance between wintering and breeding areas. Small arctic breeding species of waterfowl winter in southern areas such as the Gulf of Mexico (LeFebvre and Raveling 1967) and southern California. But Trumpeter Swans, breeding within the boreal forest, seem to migrate only as far as necessary (Hansen et al. 1971; McKelvey in press), as does the similar sized Mute Swan (Olsson 1963:270). The smaller Whistling Swan (C. columbianus columbianus) breeds farther north and winters farther south (Sladen 1973).

A more pronounced feeding/temperature dependence may occur in colder inland portions of the Trumpeter Swan's range, than in coastal areas. Given the moderate range of winter temperatures experienced at Comox Harbour, the much harsher conditions found in parts of the Trumpeter Swans winter range, and the well-feathered nature of the bird, lack of temperature dependence does not seem improbable. The narrow range of temperatures and the strong influence of tide conditions on feeding behaviour may also have worked to obscure even the slight temperature dependence such large birds would exhibit on the coast.

Wind conditions have been observed to affect feeding behaviour of geese (Philippona 1966) and of some ducks (Nilsson 1972). Swans are also influenced by wave action caused by storm winds, as shown in this study. However, wind conditions may combine with temperature to produce a wind chill factor. Again, the moderate temperatures and winds experienced at Comox Harbour appear unlikely to adversely affect Trumpeter Swans wintering there.

Little needs to be said about the regulation of activity of swans feeding on fields. Their activity patterns resemble those of other grazing waterfowl such as geese (Raveling et al. 1972; Owen 1972a, 1972b, 1973; Ebinge et al. 1975) in that feeding occurs during most of the day. Waterfowl are generally known to have a rapid through-put of food when grazing. The swans probably grazed all day to obtain as much of the high nutrient grass as possible.

Unfortunately, no swans were marked or banded during this part of the study; it was therefore not possible to determine how much, if any, feeding occurred on the estuary following the field grazing periods. High levels of feeding in the fields during the day and again on the estuary at night might reflect an increasing demand for food prior to the spring migration (Reed 1976).

Disturbance levels at Comox Harbour were low and did not seem to affect the swans to any extent. The shallow, muddy nature of the harbour has limited industrial developments and recreational pursuits in areas used by swans (Section I). Although there are some residential developments on the south shore of the estuary, a border of trees and shrubs provides a barrier, preventing human presence from disturbing the swans.

Disturbance has been shown to be an important factor in the feeding behaviour of other species of waterfowl (Owen 1972b, 1973; Owens 1977; Nilsson 1972; Campbell and Milne 1977). The most important form of disturbance to those species appears to be shooting. Swans are occasionally shot on their wintering grounds but hunting pressure in general is low at Comox Harbour. However, the wariness of the swans at Comox Harbour may be caused by the swan's association of humans with being shot at.

Disturbance of geese by aircraft has been reported (Owen 1972; Burton 1977) and is common in ducks (pers. obs.). Trumpeter Swans, however, seem little bothered by low flying aircraft. Fortunately, air traffic into the Courtenay Municipal Air Field is light and seldom even disturbs the ducks. Swans were never observed to react to the presence of Bald Eagles, nor were they ever harassed by them. Because there are no aerial predators of swans, aircraft, despite being noisy, may not be seen as a potential predator by the swans.

III. FOOD USE

INTRODUCTION

Trumpeter Swans wintering on the British Columbia coast are dependent on the numerous estuaries found there, for part or all of the winter (McKelvey 1979, in press, and Section I). Certain estuaries, however, appear to be more attractive to wintering swans than others. At Comox Harbour, the numbers of swans over-wintering has increased from year to year at a faster rate than the total population of swans has grown (J. King, pers. comm.). The attractiveness of the Comox Harbor area is believed to be the availability of highly nutritious pasture grasses on nearby dairy farms (Section I).

As the numbers of swans wintering in the Comox Harbor area increases greater pressures result on both the newly acquired food source (pasture grasses) and on the traditional diet of estuarine emergent plants. This section presents an estimation of the amount of food removed by swans from the Courtenay River estuary over the winters of 1978-79 and 1979-80, and from dairy pastures on the Beaver Meadow Farm over the winter of 1979-80.

There have been only a few attempts to estimate the amount of food consumed by waterfowl by sampling the food resource (Anderson and Low 1976; Cornelius 1977). Generally those attempts have been concerned with the use made of submerged aquatic plants, rather than emergents, and have involved the use of extensive clipping or core sampling procedures to estimate biomass and its rate of removal.

Because of the feeding methods of swans wintering at Comox Harbour and the nature of the emergent plant food resource, random sampling of plant biomass likely will not detect real changes in the quantity of food available. When feeding occurs on the Scirpus-Triglochin root mat, the root mat disappears; random sampling of root mat biomass would never detect changes in mean biomass unless a large number of areas with no root mat were also sampled. A measure of the areal extent of the emergent plants (i.e. plant cover) may provide an alternative method of estimating the use made of that food resource. By extrapolation from the known biomass of the area expected to be fed on, a crude estimate of the amount of food removed can be obtained.

More traditional methods can be used to estimate the amount of food consumed by swans grazing on pastures during the winter. Grazing does not involve a complete disappearance of biomass from the grazed area because the grass is not usually destroyed in the process, and often continues to grow throughout the winter period. Thus standing crop and rate of biomass removal estimates can be easily made with grazing exclosures and clipping methods.

METHODS

ESTUARY

Three methods were used to measure the impact of swans feeding on the emergent plants at Comox Harbor: aerial photography, strip transect mapping of the vegetation, and point sampling of the root mat.

Aerial Photography

Photographs used in this study were obtained during three flights by a De Havilland Beaver equipped with a Hasselblad 500 EL and a Zeiss Distigon 50 mm f5.7 lens. All flights were made at a height of 610 m, resulting in a nominal air photo scale of 1:12000. On each flight the habitat was photographed twice: once using Kodak 2443 Aerocolour true colour negative film; and once using Kodak 2445 Aerochrome IR false colour reversal film. Flights were made in August 1978, May 1979 and May 1980 to photograph the habitat before the swans arrived and after they had fed on it for one and two winters.

The interpretation of the air photos was accomplished using 20 cm x 20 cm enlargements of stereo pairs of IR film and 70 mm contact prints of true colour film. The working scale of the enlargements was 1:3048 or 1 cm=30.5 m. Trace maps of portions of the habitat were made directly from the enlargements and the areas of those tracings determined with a digitizer. The total area of habitat within the study area was determined simply by adding the areas measured from each portion of the habitat traced. A paired t-test (Zar 1974) was used to ascertain whether the total areas measured in 1979 and 1980 were significantly different. Each identifiable portion of habitat from the airphotos of one year was treated as a sample and its area was compared with that measured in the following year. If the paired t-test showed the samples from the two years to be from different populations, the total areas of habitat measured in each year were assumed to be significantly different. Paired t-tests were not applied to samples from 1978 and 1979 because the total areas measured were radically different.

Strip Transect Mapping

A strip transect mapping procedure was employed to provide ground truth data, through a ground based sampling of the root mat area and a classification of the plant communities in the emergent vegetation zone. The area of the vegetation was measured in the fall of 1978 before the swans arrived and again in the spring of 1979 after they left from 1:40 scale sketch maps made from thirteen 2 m wide strip transects on the emergent vegetation. Plant communities were classified by the Braun-Blanquet plant relevé technique (Mueller-Dombois and

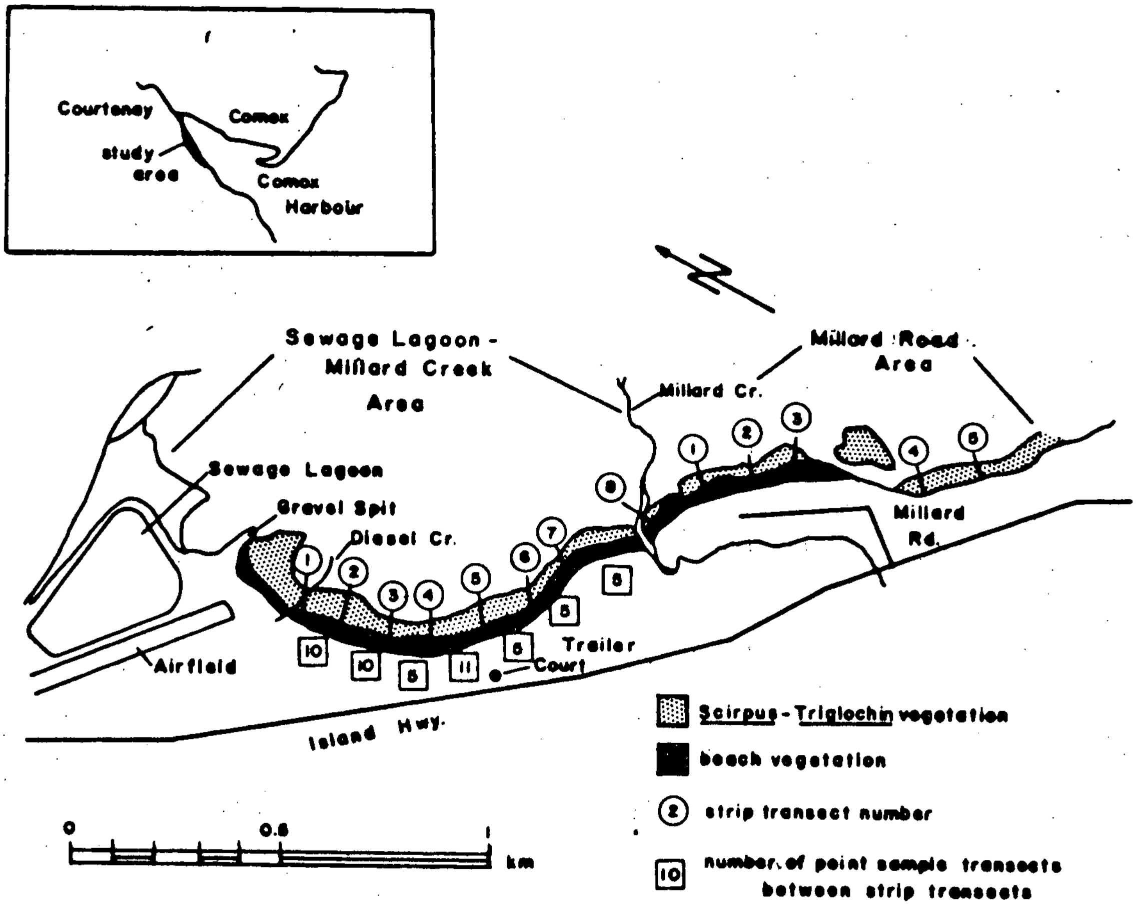
Ellenberg 1974:45) by computer (Cesca and Roemer 1971), from data collected during the mapping.

In August 1978, 13 permanent transects were located in a random fashion across the emergent vegetation, at specified distances from a corner stake on the gravel spit at the Sewage Lagoon (Fig. 19). Specified distances were chosen from a random number table between 0 m and 2000 m, the calculated length of the study area. In August 1978 and June 1979, a 2 m strip was mapped at each transect (Fig. 20). The length of each transect varied, as the width of the emergent vegetation varied between the beach and the rest of the harbour. Geometrically discernible plant communities or groups within each strip were sketched, the frequency of each plant species recorded (Mueller-Dombois and Ellenberg 1974:59), the height of Scirpus americanus and Triglochin maritimum measured, and the nature of the substrate noted. The substrate was characterized as either root mat, or some combination of silt, sand or gravel, variously oxidized or reduced.

The area of each piece of habitat recognized as geometrically distinct from its neighbour was measured from the sketch maps with a digitizer. It was then classified as root mat, sparse growth, or devoid of vegetation, based on plant species present, percent cover and substrate characteristics. Areas of sparse growth were characterized mainly by new growth of Scirpus americanus, with shoots at such a density that no root mat had yet formed (Fig. 21). Areas devoid of vegetation were those not capable of supplying any potential food for swans in the winter because no plants grew there, or only annuals were present.

For between-year comparisons of the total area of root mat measured, each transect was treated as a sample of the emergent vegetation, and paired t-tests employed. No assessment of real changes in the area of sparse growth or areas devoid of vegetation could be made because in May, plant phenology was such that areas of sparse growth and no growth were not always distinguishable.

Fig. 19. Approximate location of transects and intertidal vegetation mapped using the strip transect mapping procedure, and the point sampling procedure.



Courtenay
Comox
study area
Comox Harbour
Sewage Lagoon - Millard Creek Area
Millard Road Area
Millard Cr.
Sewage Lagoon
Gravel Spit
Diesel Cr.
Millard Rd.
Trailer Court
Airfield
Island Hwy.
Scirpus - Triglochin vegetation
beach vegetation
strip transect number
number of point sample transects between strip transects
0
0.5
1
km

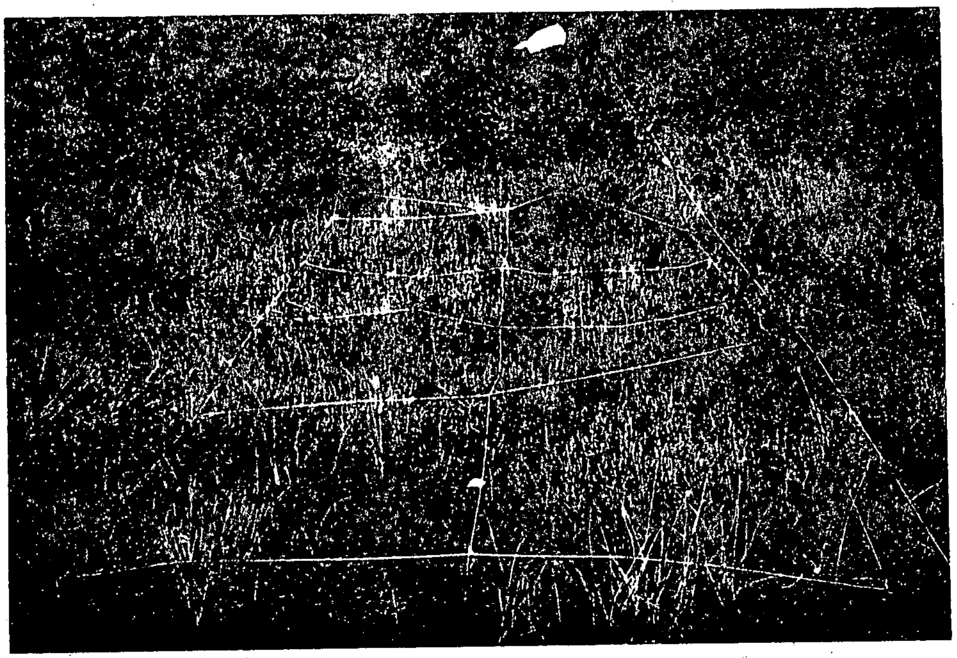


Fig. 20. Strip transect sampling of the vegetation at Comox Harbour. The 2X5 m rope grid was placed over the vegetation.

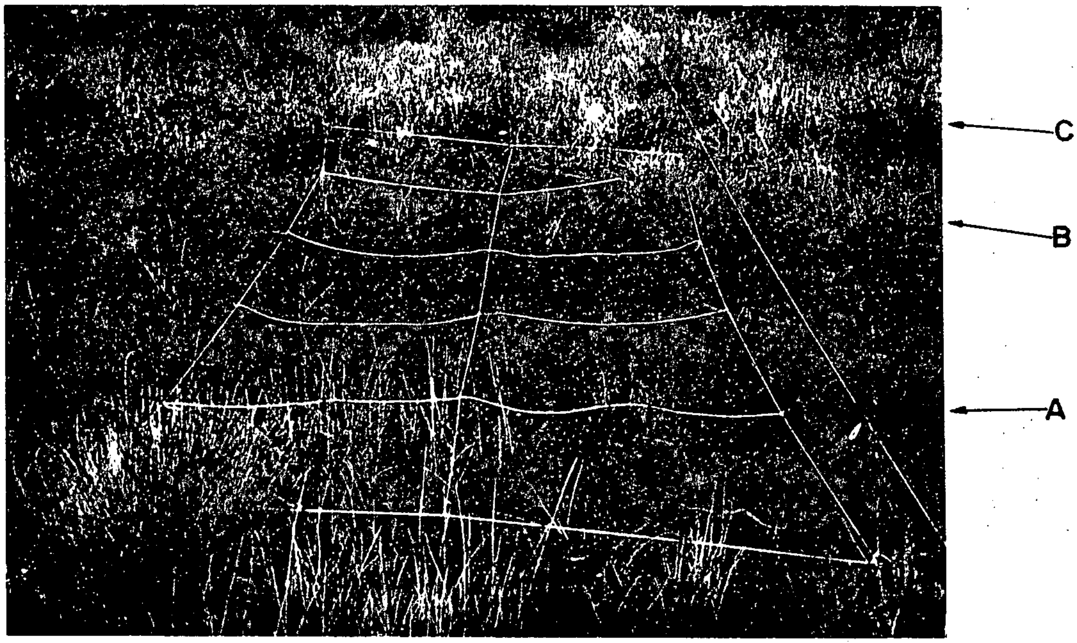


Fig. 21. The three types of emergent vegetation recognizable at Comox Harbour. (A) areas devoid of vegetation; (B) areas of sparse vegetation; and (C) areas of intact root mat. Scirpus americanus shoots formed most of the sparse vegetation, while the root mat resulted from the dominant Scirpus americanus - S. cernuus - Triglochin maratimus community.

Point Sampling

During the winter of 1979-80 a third method of measuring changes in the habitat was employed. The presence or absence of vegetation was determined at a large number of points on the estuary before the arrival of the swans in the fall and after their departure in the spring. The change in the number of vegetated points was taken as a measure of the amount of food removed by the swans. The point sampling technique actually measures plant cover, which can be related to total plant biomass if a biomass estimate is available (Mueller-Dombois and Ellenberg 1974:86).

The point sampling procedure was employed only on the habitat between the Sewage Lagoon and Millard Creek. It was confined to that area because the results of the strip transect mapping, and the behavioural observations reported in Section II, showed that little or no feeding occurred between Millard Creek and Millard Road.

Fifty-two transects were marked with stakes, each transect crossing the emergent vegetation at right angles to the shore. Transects positioned for the strip transect mapping procedure were used for the point sampling as well, with additional transects being located at random between the strip transects (Fig. 19). At 1 m intervals along a 50 m chain positioned on each transect, ground cover (i.e. emergent plant cover) was assessed as either present or absent. If the sample point fell on the root mat, or in an area of sparse growth of Scirpus americanus, the vegetation was classified as present. If the sample point fell on bare substrate, or in a successional community that did not contribute to the root mat (e.g. annual plants, or plants of very small ground cover), the vegetation was classified as absent. This procedure was repeated in April 1980, using the same transect stakes and 50 m measuring chain.

FIELDS

To measure the amount of food removed by swans grazing on pastures, 34 exclosures (0.25 m^2 each) were placed on a 40 ha field at the Beaver Meadow Farm, Comox, in November 1979 (Figs. 1 and 22). The exclosures were positioned by an "over-the-shoulder" randomization technique. Following the placement of each exclosure a second 0.25 m^2 plot was chosen by "over-the-shoulder" randomization a short distance from that exclosure. The vegetation at each exclosure was clipped approximately 5 cm above the ground to estimate biomass of grass available before the arrival of the swans in the fall. In the spring, after the swans had left, 17 exclosures and 17 random plots near those exclosures were clipped to measure the biomass of grass removed. The remaining 17 exclosures were left unclipped, to be used in an ongoing study of the effect of grazing by swans on the productivity of the pasture grass.

SWAN-USE

During the winters of 1978-79 and 1979-80 periodic counts were made of the number of Trumpeter Swans using the Comox area. A measure of swan-use was calculated by plotting the count obtained versus the date of the count, and measuring the area under the resulting curve, as the number of swan-use days. In 1978-79 daily peak counts, obtained during behavioural observations (Section II) were used, while in 1979-80 counts were made near dawn once every 2 weeks, when peak numbers of birds were present on the estuary.

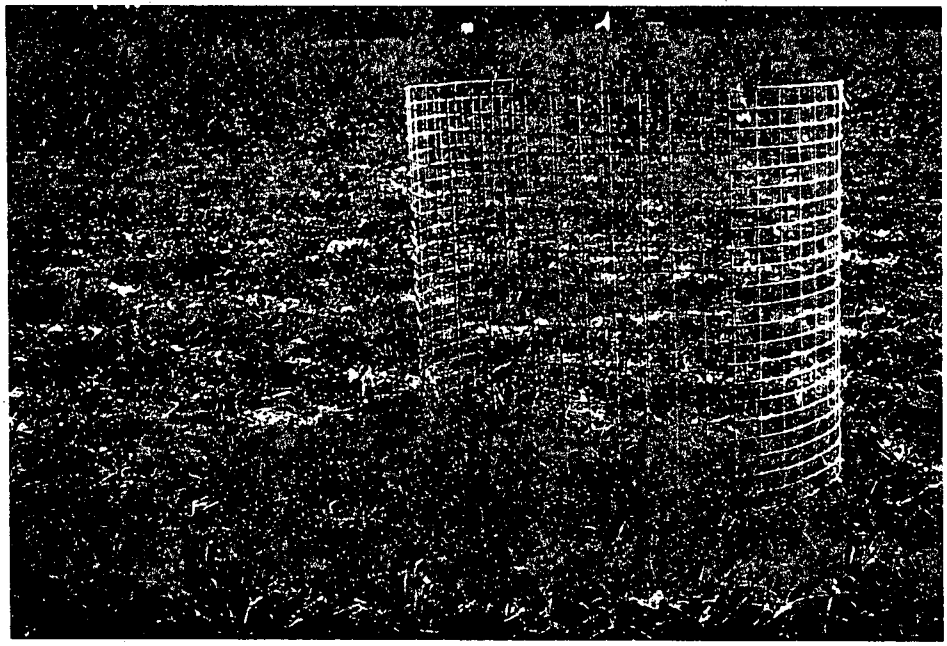


Fig. 22. An exclosure (0.25 m^2) used to study the effects of grazing by Trumpeter Swans at the Beaver Meadow Farm, Comox, 1979-80.

RESULTS

HABITAT CHANGES ON THE ESTUARY

Aerial Photograph Interpretation

The air photo technique showed an apparently gross change in the emergent vegetation at Comox Harbour between 1978 and 1979, but it was unable to detect changes between 1979 and 1980 (Table 10). However, the change noted between 1978 and 1979 seemed to be a result of emergent plant phenology rather than an actual decrease in the amount of vegetation present. It was not possible to differentiate consistently between the Scirpus-Triglochin root mat and areas vegetated by emergent annuals, such as Spergularia canadensis, using visual interpretation methods. The airphotos of May 1979, however, were taken before the development of those annuals, resulting in the measurement of a much smaller area of emergent plants.

No statistically significant differences were detected in the area of root mat between 1979 and 1980 ($p<.05$). Although the small format air photography employed in this study could not be used to distinguish between plant community differences, between-community differences and areas devoid of vegetation were clearly visible, though not always measureable because of their close proximity. Table 11 lists photograph characteristics used for plant community identification and interpretation on the airphotos.

The area between the Sewage Lagoon and Millard Creek received between 8135.3 and 9926.3 swan-days of use during the 1978-79 winter (Fig. 23A). The latter figure seems more probable, there being no good explanation for the low count of swans recorded on 21 December. Swans were numerous elsewhere on Comox Harbor that day; the low number recorded on the area between the Sewage

Table 10. The area of vegetation measured from air photos taken at Comox Harbour between 1978 and 1980.

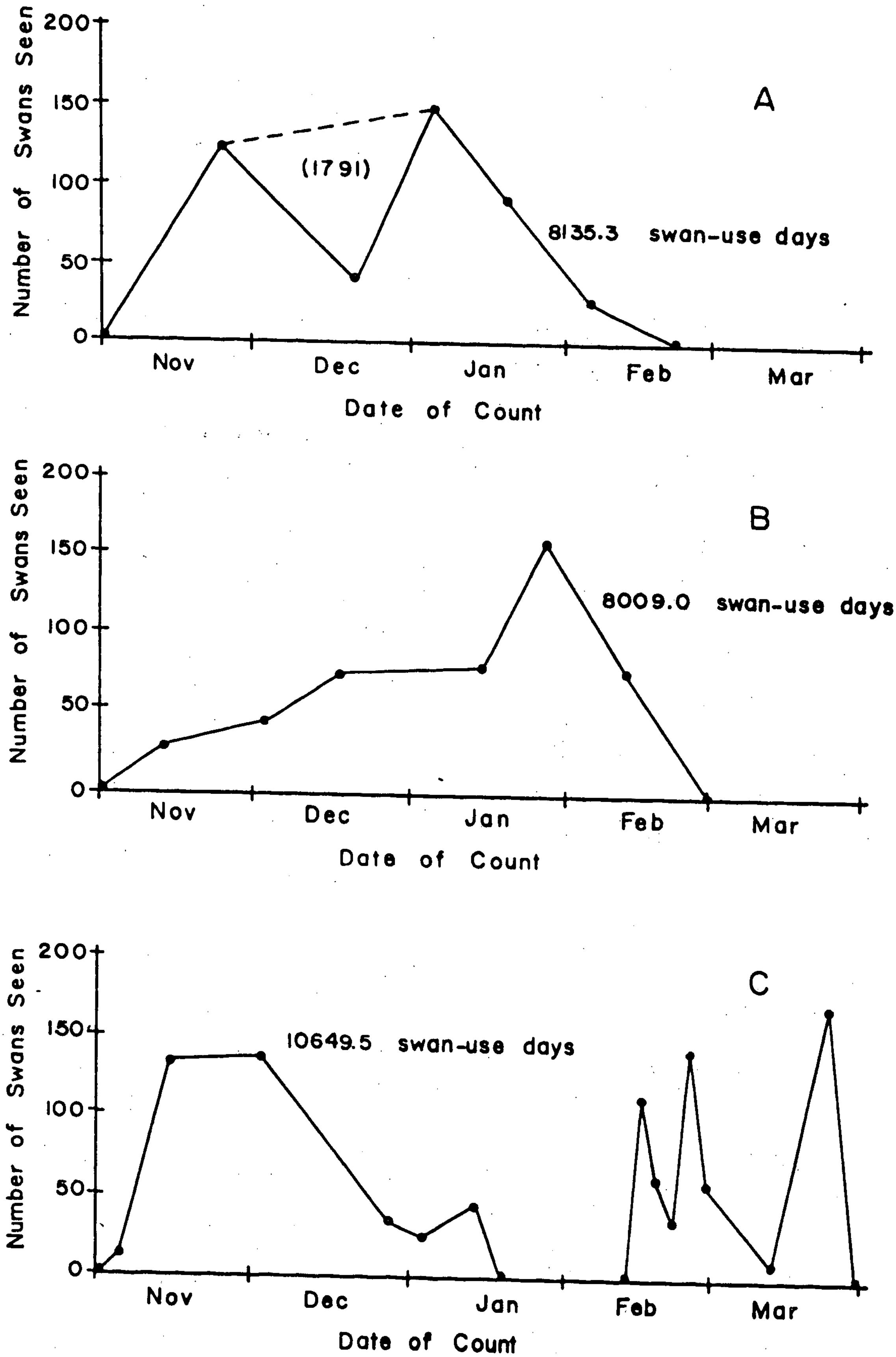
	Area (m^2)		
Marsh segment	1978	1979	1980
Sewage Lagoon	12,837	9,645	9,174
Diesel Creek Trailer Court	6,738	3,438	3,103
Trailer Court-Meadow	8,964	5,972	6,254
Meadow-Millard Creek	3,602	2,696	2,872
Foot of Millard Road	9,201	7,910	5,450
Total	41,342	29,661[1]	26,853[1]

[1] no statistically significant difference, $p < .05$

Table 11 Interpretation Key for identification of estuary plant features at Comox Harbour in the spring and late summer. (IR - infrared false colour film; AC - aerocolour true colour film; sp - spring; ls - late summer).

Feature	200 mm IR	70 mm IR	70 MM AC	Notes
Root mat (sp) (ls)	dark mauve to purple; rough mauve to purple; rough to ragged	dark mauve; mottled mauve	olive green; patchy olive; rough	mottled due to patchy distribution
Grass zone (sp) (ls)	mauve, smooth lt. blue or white; patchy	mauve, smooth light blue	dark green yellow-green	elev. change from root mat alwyas visible as as white line
Beach zone (sp) (ls)	mauve to lt. blue mauve; mottled	mauve	dark green green	elev. change from grass always visible as white line
Eelgrass (sp) (ls)	mauve; spongy	mauve; spongy mauve; spongy	purple; mottled or wavy purple	
Algae (sp) (ls)	lt. mauve to lt. purple	lt. mauve	lt. green; bright	usually absent in late summer.
Substrate (sp)	blue; dark when wet blue & smooth; darker when wet	blue blue	tan; bluish when wet tan	
Debris (sp) (ls)	absent white or lt. blue	absent white	absent white	vegetation too short to strand material in spring

Fig. 23. Counts of Trumpeter Swans using the habitat between the Sewage Lagoon Millard Creek during the winters of (A) 1978-79 and (B) 1979-80; and (C) swans using the Beaver Meadow Farm pastures in 1979-80. Areas under the graph represent the calculated number of swan-use days.



Number of Swans Seen
200
150
100
50
0
A
(1791)
8135.3 swan-use days
Nov
Dec
Jan
Feb
Mar
Date of Count
B
8009.0 swan-use days
C
10649.5 swan-use days

Lagoon and Millard Creek was probably just a chance occurrence.

Strip Transect Mapping

An area of 1640 m^2, in 13 transects (Fig. 19), was mapped in August 1978 and an area of 1392 m^2, in 11 transects, was remapped in May 1979. Two transects near Millard Road could not be remapped because the stakes marking those transects were lost. Between August 1978 and May 1979 there was a decrease of 5.2% in the total area of root mat, on the 11 transects present in both samples (Table 12). That decrease was significant at the $p < .05$ level; it occurred only in the area between the Sewage Lagoon and Millard Creek.

Changes in the area of sparse growth and those devoid of vegetation could not be assessed because of differences in plant phenology between August 1978 and May 1979. Some areas classified as sparse growth in August were apparently bare in May because the plants in those areas had not yet begun to grow. Areas where the root mat had been disturbed, however, were most obvious in May, before any regrowth had occurred.

Growth characteristics of the vegetation in the area between the Sewage Lagoon and Millard Creek differed from that between Millard Creek and Millard Road. The former was characterized by large areas of sparse growth (49.0%) and non-vegetated areas (21.5%), while the latter had a much larger area of root mat (67.2%) and small areas of sparse growth or no growth. The substrate of the Millard Creek-Millard Road area was predominantly gravel or cobble, while that of the Sewage Lagoon - Millard Creek area was silt or mud over sand.

Point Sampling

The study area consisted of between 41.5% and 44.3% root mat before the swans arrived in 1979, and 31.8% after they left in 1980 (Table 13). Eight of the

Table 12. Areas of root mat recorded by strip transect mapping in August 1978 and May 1979, and percentage changes in root mat area at Comox Harbour.

Transect number	Total area (m^2)	Area of root mat (Aug.1978/ May 1979)	Area of sparse growth Aug.1978	Area of no vegetation Aug.1978
<u>Sewage Lagoon Millard Creek area</u>				
1	270	42.0/38.4	190.8	37.1
2	180	24.6/17.4	111.8	44.3
3	160	29.7/11.8	111.8	18.4
4	120	54.7/53.4	8.0	57.3
5	100	39.3/35.3	42.2	18.6
6	140	38.3/35.6	86.2	15.6
7	90	69.6/61.2	0.0	21.7
8	62	33.8/ 9.9	0.0	28.2
Total	1122	332.0/263.0	550.8	241.2
% Total area in root mat		29.6/24.4		
% Change in area of root mat		-5.2		
<u>Millard Road area</u>				
1	138	74.0/*	0.0	64.0
2	80	58.5/58.4	0.0	21.7
3	110	59.9/*	19.2	30.7
4	120	104.4/104.4	1.0	13.8
5	70	51.5/51.1	0.0	18.9
Total	518	347.9/213.9	20.2	149.1
%Total area in root mat		67.2/*		
%Change in area of root mat		0*		

*Royston transects 1 and 3 could not be relocated because of the loss of marking pegs. Change in area of root mat was calculated using data from transects 2, 4 and 5.

Table 13. Areas of root mat recorded by point sampling in November 1979 and April 1980, and percentage changes in root mat area, at Comox Harbour.

	Sample dates	
	November 1979	April 1980
Number of transects	50	42
Number of points sampled	2653	2154
Number of points vegetated	1175	686
% cover of root mat	44.3 (41.5)*	31.8
% change in root mat cover	-9.7*	

*Change in vegetation was calculated using only those transects that were present in both the November 1979 and April 1980 sample periods.

original transect markers (499 sample points) disappeared during the winter. Using data only from those transects that were relocated in April 1980, 9.7% of the root mat was removed during the winter of 1979-80 (Table 13). That decrease was significant at $p < .001$. By graphing the percentage of each transect that was determined to be vegetated versus the transect number, a representation of both the sparseness of the vegetation, and the areas of greatest use by the swans, was produced (Fig. 24). From Fig. 24 it can be seen that the most intensive feeding occurred between the Sewage Lagoon and the Trailer Court area.

The study area on which I used the point sampling technique received 8009.0 swan-days use during the winter of 1979-80 (Fig. 23B). Bird use was assumed to start with the arrival of the first Trumpeter Swans, approximately 31 October (pers. obs. and pers. comm. with locals). No use was recorded after 28 February even though large numbers of swans remained in the Comox area, making extensive use of dairy pastures. The weather at Comox Harbor in the winter of 1979-80 was mild and without snow, and spring began early.

Estimation of Food Removed

The amount of food removed from the estuary during the winters of 1978-79 and 1979-80 was calculated using data from this section, and biomass estimates reported in Section I (Table 2). The results are shown in Table 14.

GRAZING PRESSURE ON PASTURES

Pastures at the Beaver Meadow Farms were replanted in the fall of 1979 and attempts were made to limit their use by swans to allow the new grass to establish properly (E. Smith pers. comm.). In spite of limited grazing a considerable amount of vegetation was removed by the swans during that winter. The pasture received

Fig. 24. A plot of the percentage of the area between the Sewage Lagoon and Millard Creek covered in root mat versus the transect number, showing the percent area of root mat (hatched area) that disappeared over the 1979-80 winter. Position of transects are relative, not to scale.

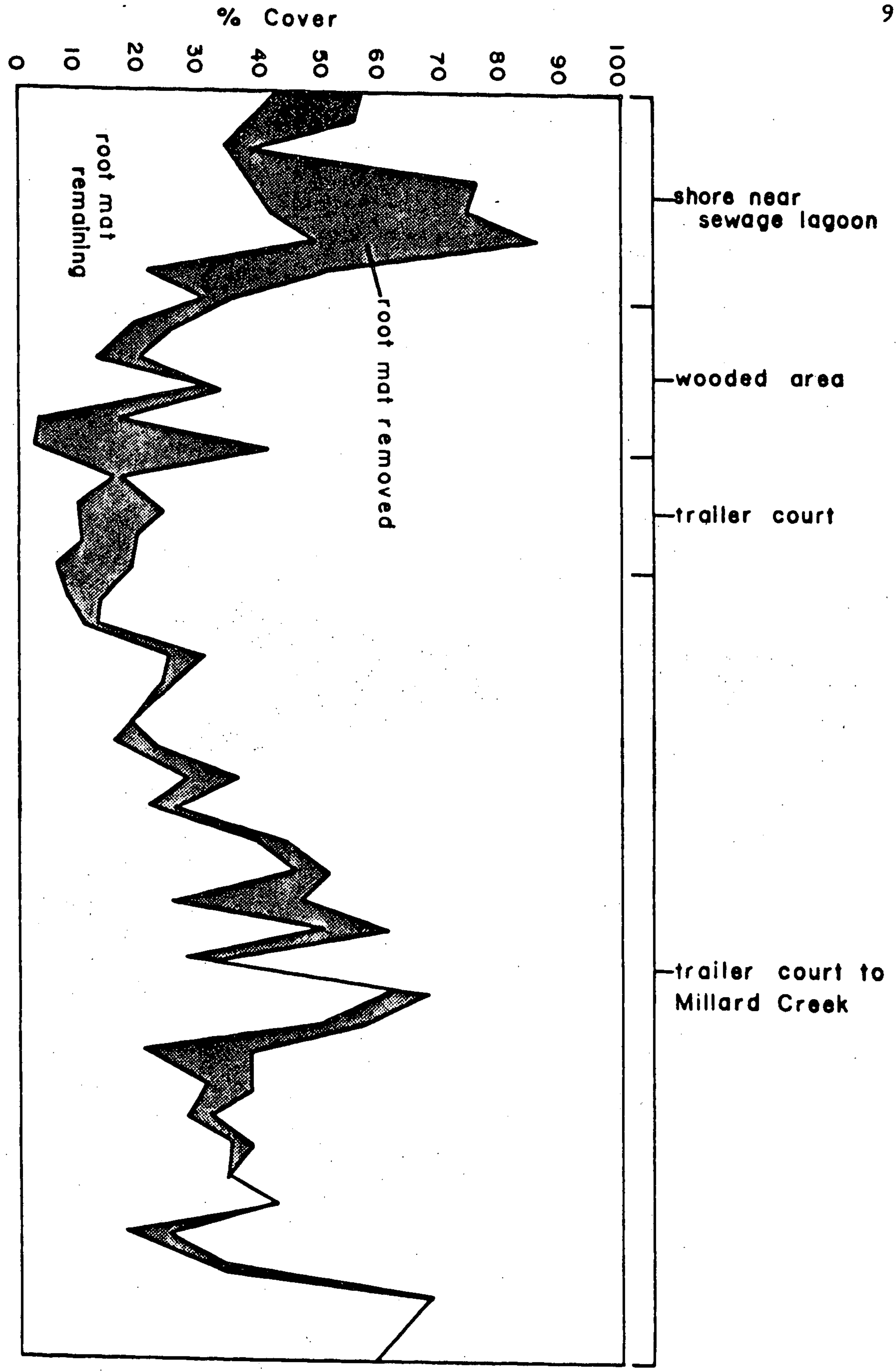

% Cover
0
10
20
30
40
50
60
70
80
90
100
root mat remaining
root mat removed
shore near sewage lagoon
wooded area
trailer court
trailer court to Millard Creek

Table 14. Estimated biomass of food consumed by Trumpeter Swans feeding on emergent plants at Comox Harbour, 1978-79 and 1979-80.

Average area of root mat between the Sewage Lagoon and Millard Creek (from the air photos of May 1979 and May 1980	21000m^2
Area removed	
1978-79 (strip transect)	1100m^2
1979-80 (point sampling)	1900m^2
Biomass/m^2 (Table 2)	1.452 kg/m^2
Biomass removed	
1978-79	1540 kg
1979-80	2660 kg
Swan-use days	
1978-79	9926 days
1979-80	8009 days
Biomass removed per swan-day	
1978-79	155.1 g/day
1979-80	332.1 g/day

approximately 266.2 swan-use days/ha, which resulted in the removal of about 326.0 kg/ha (dry weight) of grass (Table 15 and Fig. 23C).

DISCUSSION

FOOD CONSUMPTION ON THE ESTUARY

Even though large numbers of Trumpeter Swans wintered at Comox Harbour during this study, they appeared to have removed only a relatively small portion of the available food resource annually (less than 10% by area (Table 13)). Although the productivity of the below-ground biomass of the emergent plants at Comox Harbour was not measured, some speculations about the carrying capacity of Comox Harbour, based on current levels of use, are possible. Based on observations of emergent plant regeneration on the Fraser River estuary, it is estimated that root mat removed by feeding swans would take 2-5 years to regrow (C. Levings pers. comm.). Taking the upper limit for regeneration time at Comox Harbour means there should be a large enough standing crop to sustain current levels of use for about 10 years. Comox Harbour, therefore, may be able to support a wintering population of Trumpeter Swans at levels somewhat higher than those observed in 1978-79 and 1979-80. This does not necessarily mean that Comox Harbour could support more swans than it currently has, only a slightly higher level of use. Recent levels of use seem to fluctuate, and may even be declining, even though peak numbers of swans using the harbour have increased over the last three winters (Figs. 10B and 23). It is possible therefore that the use of the emergent plant community by the swans has already reached its peak level and will not change much even if more swans do winter there.

Levels of use of food plants by waterfowl in general seem to vary widely.

Table 15. Biomass (dry weight) of food consumed by Trumpeter Swans grazing on fields at the Beaver Meadow Farm, Comox, 1979-80. Numbers in ( ) are standard errors.

Biomass before swan use (kg/ha)	484.8 (69.2) n = 34
Ungrazed biomass after swan use (kg/ha)	952.0 (69.2) n = 17
Grazed biomass after swan use(kg/ha)	626.0 (88.8) n = 17
Amount removed per hectare(kg)	326.0 (209.2)
Swan use days per hectare(kg)	266.2
Consumption per swan per day(kg/ha)	1.2 (.8)

Anderson and Low (1976) estimated that 40.4% of the standing crop of foliage and 42.9% of the standing crop of tubers of sago pondweed (Potamogeton pectinatus) were removed by fall staging waterfowl at the Delta Marsh, Manitoba. Cornelius (1977) calculated that Redhead Ducks (Aythya americana) on Laguna Madre, Texas, consumed only 4% of the standing crop of the available preferred food item, the rhizomes of shoal grass (Halodule beaudettei). Burton (1977) estimated that Snow Geese wintering on the Fraser River estuary could consume from 32% to 100% of the standing crop of the rhizomes of Scirpus americanus, though his calculations are based on dubious methods. Rates of removal of food by Trumpeter Swans at Comox Harbour certainly fall within these reported ranges for other waterfowl, and tend to be on the low side of the scale.

The estimate of the quantity of material removed per swan per day seems very high. However, a large proportion of that material may have been wasted. The samples used for biomass estimation at Comox Harbour all came from the Scirpus americanus - Triglochin maritimum community and were 5-10 times greater than standing crop estimates of S. americanus on the Fraser River estuary (Burton 1977:29). Much of that greater mass from the Comox Harbour samples may have been due to Triglochin maritimum roots, which were not recorded as a food item for swans at Comox Harbour. If swans are as wasteful in their feeding methods as, for example, Snow Geese are thought to be (McIlhenney 1932) and if Scirpus americanus rhizomes constitute only a fraction of the plant biomass disturbed, actual consumption rates of emergent plant food may be quite low. However, the important point is that large amounts of emergent vegetation at Comox Harbour still must be processed during feeding; the estimates reported here are realistic.

COMPARISON OF METHODS USED

The three methods used to assess the rate of removal of food from Comox Harbour produced different results. I believe two of the methods (strip transect mapping and point sampling) produced results which accurately reflected the use of the food resource rather than results due to differences in methodology. Both methods were estimating the same thing (cover of root mat) but with different precision, based on sample size, and both were operating under the assumption that what constituted root mat could be decided in the field. Although the methods were not tested against each other, the differences they detected between years were highly significant; there are no reasons to believe the two assessments did not have equal levels of repeatability. Of the three procedures used the point sampling method was the simplest and least expensive. It was simple because information necessary for the delineation of plant communities, and for deciding what to sample (i.e. what constituted root mat and what did not), was gathered in the course of other work, such as the strip transect sampling. If decisions are made before sampling as to what will constitute plant cover and what will not, point sampling is a very fast and simple method.

The point sampling technique is actually used to estimate plant cover (Mueller-Dombois and Ellenberg 1974). In this study, it was not used to estimate the cover of a single emergent plant species, but rather of an association of plant species, represented by the Scirpus-Triglochin root mat. Because I wished to know the change in the area of that root mat, this technique allowed the rapid collection of a large amount of data amenable to good statistical analysis.

The strip transect sampling procedure was time consuming and involved a fair amount of decision making in the field. The disadvantage of continually having to make decisions in the field is that they may not be made consistently, thus introducing an unmeasurable amount of error into the data.

One method that would increase the accuracy of the strip mapping technique would be the use of a pantograph (Mueller-Dombois and Ellenberg 1974:83), if one, large and robust enough, could be developed for use on an estuary. Working from a string grid and sketch maps is a relatively fast method of collecting data, but an unknown degree of error is inherent in the sketching of the maps.

Visual interpretation of 70 mm air photographs did not provide sufficient resolution to detect habitat changes at the levels found in this study by other methods. Different plant communities were separable, but such subtleties as areas of sparse growth, growth of annuals, and areas of no growth, although sometimes visible, were too finely associated to separate by eye.

Machine procedures that can detect the levels of changes desired do exist but are expensive (G. Tomlins, pers. comm.). Densitometry of air photos to measure colour intensity objectively, could be combined with a digital process of assigning plant types to areas of specific colours. The frequency of occurrence of those coloured areas could then be measured and changes detected between years. Such a system is available for satellite imagery and could be adapted to existing airphotos.

FOOD CONSUMPTION ON THE FIELDS

The swans feeding on the Beaver Meadow Farm in the winter of 1979-80, although limited in how much grazing they were allowed to do, removed a considerable amount of vegetation. However, their grazing pressure was not so severe that there was a net loss of biomass on the fields. Winter growth of the grass was greater than the grazing pressure, there being a net increase in the standing crop of grass on the pastures.

The effect of that grazing on grass yields the following year, however, has not yet been assessed. Reports from farmers in the Comox area indicate that yields are lowered by winter swan grazing (pers. comms.) while others claim not to have noticed any yield changes (E. Smith, pers. comm.). There is evidence from other studies that winter grazing of agricultural crops by waterfowl can actually be beneficial. Kear (1970) found that grazing of cereal and forage crops by Greylag Geese (Anser anser) and Pink-footed Geese (A. brachyrhynchus) wintering in Britain had no adverse effect on crop yield, and in some instances enhanced yields. Clark and Jarvis (1978) found that Canada Geese grazing on ryegrass (Lolium spp.) in the Willamette Valley, Oregon, had no effect on eight of ten study fields, and significantly increased the yields on the other two fields.

Yield increases may be due to the effective nutrient recycling and enrichment by waterfowl droppings (Marriot 1973), and a whole complex of responses by the grazed plants (McNaughton 1979). Because of the ever-increasing number of swans wintering in the Comox area and the potential for swan/farmer conflicts, studies are continuing to determine the effect of winter grazing by swans on forage crop yields.

IV. MANAGEMENT RECOMMENDATIONS

The most important finding of this study, in terms of Trumpeter Swan management, is that of the recent acquisition by the swans of the habit of grazing on dairy pastures. That has implications for the estuarine habitat and the dairy farm habitat at Comox, and for the swans. Assuming that we wish to maintain the status quo of the Trumpeter Swan at local and other levels (McKelvey and Stroops, in press) there are a number of management procedures possible in the Comox area and at Port Alberni. Although there are no dairy farms at Port Alberni, the opportunity exists for use of some fields by swans, and the Port Alberni habitat in general may be able to support more swans than it does now. Some of those procedures could benefit the Trumpeter Swan throughout its winter range.

ESTUARINE HABITAT AT COMOX

Though the most attractive feature of the Comox area to wintering swans are the dairy farms, swans are still dependent on Comox Harbour throughout the winter. The Harbour is used day and night throughout the winter by a certain number of swans for feeding and resting; it is used at night by most of the swans in the Comox area for feeding and resting; and it becomes the only piece of useable habitat in the area during the coldest part of the winter, when dairy fields may be snow covered, and inland freshwater bodies frozen.

Food Resources

The estuarine food resources consist of both the rather extensive eelgrass beds in the Harbour, and the narrow band of emergent vegetation near the

Courtenay River, from the Sewage Lagoon to about Millard Road. The following recommendations are made to protect that food resource:

1. Acquire key pieces of property along the southern shore of the Harbour, to ensure control of access to, and development of, that foreshore. Descriptions of those properties appear in McKelvey (1980).

2. Ensure that no developments are permitted that will in any way adversely affect the eelgrass beds in the harbour.

3. Secure other pieces of habitat that may become important sources of emergent plant food, should the pressure on areas used most intensely now cause overuse of those areas. Such pieces of habitat include areas near the mouth of the Courtenay River, on the dredge spoil islands in the river channel, and along the northwest shore of the harbour (Fig. 1).

4. Determine what the regeneration time is of the emergent plants now used extensively for winter food, to better assess the carrying capacity of the area. Overuse of the habitat might be construed as mismanagement of the swan population, and could be taken as an excuse to develop the foreshore, if overutilization caused the presence of the swans at Comox to become less obvious. Excessive habitat changes might also cause a change in the rate of use of other bird species, ultimately making Comox Harbour less attractive to wintering waterbirds in general.

Resting Areas

Three areas were used consistently for resting: the gravel spit near the Sewage Lagoon; the mouth of Millard Creek at lower tides; and the harbour centre itself, where swans sleeping on the water were drifted by the tides. Habitat acquisitions to preserve the emergent plant food resource would secure the gravel spit and the mouth of Millard Creek. Maintaining the integrity of the eelgrass beds would keep much of the centre portion of the harbour available for birds sleeping on the water. Harassment, intentional or otherwise, of swans roosting at the shore, however, could be prevented.

5. Control access of people on foot to the Sewage Lagoon area. Swan viewing with little disturbance can be accomplished from vehicles, along the dyke of the Sewage Lagoon.

6. If the Sewage Lagoon is phased out and the area turned into a park (McKelvey 1980) viewing of swans in that area could be accomplished by a system of blinds and covered walkways on the existing Sewage Lagoon dyke.

ESTUARINE HABITAT AT PORT ALBERNI

A large portion of the estuarine habitat at Port Alberni has already been lost through municipal and industrial developments, and much of what remains is polluted with logging debris. The remaining habitat could be protected and enhanced by:

7. Acquiring any available areas of estuarine habitat to ensure the safety of what remains of the Somass River delta from further industrialization.

8. Stop the pollution of the estuary by log and wood chip debris, and remove driftwood wherever possible. Both operations combined will stop and reverse the erosion of the remaining habitat.

DAIRY FARM HABITAT

The greatest problem associated with the swans' acquisition of the grazing habit is the potential conflict, real or imagined, between farmers and swans. Research in progress to assess the impact of winter grazing by swans on the yield of forage crops must be completed. Depending on the outcome of those grazing studies two recommendations are made:

9a. If grazing by swans depresses yields of forage crops, farming "for the swans" must be initiated. Acquisition of farms to the north of the Dike Road at Comox Harbour would help maintain the integrity of Comox Harbour in general as an important wintering area by precluding the urbanization or industrialization of lands adjacent to the harbour. "Swan farms" could be lease farmed at other times of the year to offset the expense of maintaining the pastures for the swans.

9b. If swan grazing enhances yields, a public relations program would benefit both the swans and the farmers.

THE SWANS

The use by the swans of dairy pastures as a source of food during the winter, is the use of a food for which they may not be adapted. Reed (1976) speculated that grazing of pastures by Canada Geese may make goose populations less adaptable to changing environmental conditions through increased winter survival of less fit individuals and an ultimate lowering of productivity. The same thing may happen to Trumpeter Swan populations and now is the time to study that possibility, because they have only recently begun to use pastures as a food source.

10. Make yearly counts of the numbers of adult and immature swans using dairy pastures at Comox and compare yearly productivity to that found in areas where grazing does not occur.

11. Determine the efficiency of digestion and metabolism of Trumpeter Swans feeding on natural foods and on pasture grasses.

APPENDIX I.

Plant Species Occurring in each Community Type

A Comox Harbour Study Area (data from this study)

B Somass River Delta (data from Paish and Associates Ltd. 1973)

Plant communities and prominence values[1] of each species in the emergent plant community at Comox Harbour. Nomenclature after Hitchcock and Cronquist (1973)

Species		Prominence values
<u>Carex</u> community		
Carex lyngbyei	Hornem.	6.12
Deschampsia cespitosa	(L.) Beauv.	28.3
Potentilla pacifica	Howell	14.1
<u>Scirpus</u> community		
Triglochin maritimum	L.	304.9
Scirpus americanus	Pers.	249.8
Scirpus cernuus	Vahl	211.8
Spergularia canadensis	(Pers.) G. Don	57.0
Ruppia maritima	L.	28.3
Glaux maritima	L.	22.6
Distichlis spicata	(L.) Greene	13.2
Cotula coronopifolia	L.	2.8
Juncus balticus	Willd.	2.8
Atriplex patula	L.	1.4
Plantago maritima	L.	1.4
Ranunculus cymbalaria	Pursh	1.4
Salicornia rubra	Nels.	0.5

[1]Prominence value = mean cover X frequency$^{1/2}$ (after Ceska and Roemer 1971).

Plant communities and significant values[1] of species reported by H. Paish and Assoc. Ltd. (1973) for the Somass River delta.

Community	Significance		
Sidalcea - Fritillaria - Solidago Meadow			
	Sidalcea hendersonii	Wats.	4
	Fritillaria camschatcensis	(L.) Ker-Gawl	4
	Oenanthe sarmentosa	Presl.	4
	Solidago canadensis	L.	3
	Plantago macrocarpa	Cham. & Schlecht.	3
	Dodecatheon hendersonii	Gray	3
	Potentilla pacifica	Howell	3
	Juncus balticus	Willd.	3
	Carex lyngbyei	Hornem.	3
	Sium suave	Walt.	2
	Veronica americana	Schwein.	2
	Ranunculus occidentalis	Nutt.	2
	Trifolium wormskjoldii	Lehm.	2
	Hierochloe odorata	(L.) Beauv.	2
	Agrostis exarata	Trin.	2
	Rumex occidentalis	Wats.	2
	Achillea millefolium	L.	2
	Calamagrostis canadensis	(Michx.) Beauv.	2
	Angelica lucida	L.	1
	Conioselinum pacificum	(Wats.)Coult. & Rose.	1
	Heracleum lanatum	Michx.	1
	Deschampsia cespitosa	(L.) Beauv.	1
	Festuca rubra	L.	1
	Hordeum brachyantherum	Herski	1
	Brassica campestris	L.	1
	Equisetum fluviatile	L.	1
	Vicia gigantea	Hook.	1
	Ranunculus orthorhynchus	Hook.	x
	Glaux maritima	L.	x

Camassia quamash	(Pursh) Greene	x
Lupinus sp.		x
Juncus effusus	L.	x
Galium trifidum	L.	x
Cicuta douglasii	(DC.) Coult. & Rose	x

Juncus - Deschampsia Meadow

Juncus balticus	Willd.	6
Deschampsia cespitosa	(L.) Beauv.	5
Potentilla pacifica	Howell	5
Plantago macrocarpa	Cham. & Schlecht.	4
Dodecatheon hendersonii	Gray	4
Triglochin maritimum	L.	4
Carex lyngbyei	Hornem.	4
Eleocharis palustris	(L.) R. & S.	3
Trifolium wormskjoldii	Lechm.	3
Glaux maritima	L.	2
Plantago maritima	L.	2
Sium suave	Walt.	2
Festuca rubra	L.	2
Ranunculus occidentalis	Nutt.	2
Pastinaca sativa	L.	1
Ranunculus orthorhynchus	Hook.	1

Carex meadow

Carex lyngbyei	Hornem.	9-10
Lilaeopsis occidentalis	Coult. & Rose.	4
Triglochin maritimum	L.	4
Plantago maritima	L.	2
Juncus balticus	Willd.	1
Eleocharis palustris	(L.) R. & S.	1

Scirpus variant of Carex meadow

Carex lyngbyei	Hornem.	7-8
Scirpus acutus	Muhl.	7
Typha latifolia	L.	4
Eleocharis palustris	(L.) R. & S.	4
Triglochin maritimum	L.	4
Lilaeopsis occidentalis	Coult. & Rose	2
Juncus balticus	Willd.	2
Scirpus validus	Vahl	1

Myriophyllum - Potamogeton type

Myriophyllum spicatum	L.	2
Potamogeton natans	L.	x

[1]Species significance, based on qualitative estimates of Paish and Assoc. Ltd. (1973).

x - isolated, cover small
1 - scarce, cover small
2 - very scattered, cover small
3 - scattered, cover small
4 - abundant, cover 5%
6 - cover 25-33%
7 - cover 33-50%
8 - cover 50-70%
9 - cover 75%
10 - cover 100%

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