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Waterfowl utilization of a submerged vegetation (Zostera marina and Ruppia maritima) bed in the lower Chesapeake Bay

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WATERFOWL UTILIZATION OF A SUBMERGED VEGETATION (*ZOSTERA MARINA* AND *RUPPIA MARITIMA*) BED IN THE LOWER CHESAPEAKE BAY

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Master of Arts

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APPROVAL SHEET

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ABSTRACT

A study of waterfowl use of a bed of submerged aquatic vegetation was conducted over two winters in the Lower Chesapeake Bay (Virginia). In the season of 1978-1979, Canada geese (*Branta canadensis*) were the dominant waterfowl in the study area. Goose foraging activity was correlated with tide stage, and was greatest at low tide. Consumption by grazing waterfowl was calculated from bird densities, and was approximately 25% of the standing crop of vegetation in the shallow portion of the habitat. In 1979-1980 diving ducks, primarily buffleheads (*Bucephala albeola*), were dominant. Abundance of waterfowl was influenced by wind parameters, but tide, temperature and time of day had little or no influence on bird numbers. Within-habitat variation in abundance was examined, and highest densities were associated with the deeper *Zostera marina* zone.

Gizzard samples and $\delta^{13}C$ analysis revealed that buffleheads fed primarily on small gastropods and nereid worms characteristic of the grassbed epifauna. Consumption of important invertebrate prey items, calculated from exclosure experiments and waterfowl densities, amounted to nearly 50% of the fall standing crop of these species in *Zostera marina*.

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INTRODUCTION

Submerged aquatic vegetation (SAV) is widely recognized as a valuable food resource for wintering waterfowl populations (Bent 1923, Cottam 1939, Stewart 1962, Bellrose 1976, Munro and Perry 1981). The demise of Zostera marina during the 1930's was thought to cause the precipitous decline of the Atlantic brant (Branta bernicla hrota) (Cottam 1934, Addy and Aylward 1944, Cottam and Munro 1954), although coincidence of poor reproductive success may also have been important in reducing populations (Palmer 1976). Numbers of waterfowl utilizing the traditionally important Susquehanna Flats as a winter feeding ground in the Chesapeake Bay plummeted during the height of the eurasian water milfoil epidemic in the 1960s, but returned to former levels after native aquatics became re-established (Bayley et al. 1978).

Recent surveys indicate that submerged vegetation has declined in most areas of the Chesapeake Bay in the last 15 years (Bayley et al. 1978, Anderson and Macomber 1980, Orth and Moore 1981). The response by several waterfowl species has been to alter feeding habits or distribution patterns rather than sustain population losses (Munro and Perry 1981). Canvasbacks (Aythya valisineria) once fed primarily on wild celery (Vallisneria americana), but since the early 1970's have fed mostly on bivalves (primarily Macoma balthica; Perry and Uhler 1976). Canada geese (Branta canadensis) and to a lesser extent whistling swans (Cygnus columbianus columbianus), now rely on agricultural grain as a major dietary component on the wintering grounds (Bellrose 1976). Other species such as redheads (Aythya americana), wigeon (Anas americana) and pintails (Anas acuta), which indicate a continued preference for SAV, have declined in the Bay in recent years, and it is likely that their winter distribution now coincides with areas of greater SAV abundance (Munro and Perry 1981).

Past or current preference for submerged vegetation in the diet is well documented for the above species (Martin and Uhler 1951, Stewart 1962, Munro and Perry 1981). With the exception of canvasbacks and redheads, all are non-divers, or dabblers, which feed in shallow water by tipping up rather than diving to obtain food. Many diving species also feed in SAV habitats on benthic invertebrates. Animal communities associated with grassbeds differ markedly from those in unvegetated areas, both in structural and functional aspects. Submerged aquatic vegetation supports a dense and diverse epifaunal assemblage not found on bare substrates (Marsh 1970), and organisms living on or within sediments are also more abundant due to greater sediment stability and microhabitat complexity (Thayer et al. 1975, Orth 1977). Grassbeds should therefore attract waterfowl which feed on invertebrates as well as those which rely on vegetation, although there is scant evidence to this effect. Nilsson (1969) reported that in shallow water in the Oresund, Sweden, two diving duck species studied fed preferentially over Zostera marina and one fed over patchy Ruppia sp. and Z. marina, whereas an intervening belt of vegetation-free sand contained no fauna of trophic importance for these species.

In spite of the food resources available to waterfowl in SAV habitats, Munro and Perry (1981) found few significant relationships between the distribution and abundance of submerged vegetation and waterfowl populations in the upper Chesapeake Bay. Several species, such as whistling swans, black ducks (*Anas rubripes*), mallards (*Anas platyrhynchos*) and buffleheads (*Bucephala albeola*), showed positive associations with SAV in certain areas, but results were not consistent over all survey zones. In the Lower Bay, the current relationship between waterfowl and SAV is largely unknown. The purpose of this research was to provide detailed information regarding waterfowl use of a particular bed of submerged vegetation in the Lower Bay. Specific objectives were to examine short term patterns of utilization, and to identify and estimate consumption of important waterfowl foods within the study area.

Waterfowl foraging studies have traditionally emphasized gizzard analysis, but more recent research has sought to quantify consumption in addition to describing food habits. A common approach employs average population estimates, theoretical daily ration based on body weight, and knowledge of trophically important foods to arrive at values for annual consumption. These values may then be compared with either standing crop or production of food items to determine grazing or predation pressure. In the saline Lake Grevelingen, The Netherlands, Wolff et al. (1975) and Neinhuis and van Ierland (1978) reported that waterfowl consumed less than 1% of the annual production of *Zostera marina*, whereas Jacobs et al. (1981) calculated that consumption by waterfowl amounted to 50% of the standing crop of

Zostera noltii near Terschelling, The Netherlands. Intermediate values for grazing pressure have been obtained by other investigators using similar methods (Sincock 1962, Steiglitz 1966, Cornelius 1977). Another technique compares biomass samples taken before arrival and after the departure of seasonally-resident birds (Ranwell and Downing 1959, Burton 1961). Values obtained in this way tend to overestimate consumption during the non-growing season, as seasonal declines related to physical factors are also included in these estimates (Charman 1977).

Exclosure experiments have provided additional estimates of consumption, using differences in biomass between grazed and ungrazed (caged) plots to quantify waterfowl feeding. Verhoeven (1978) used exclosures to estimate the impact of foraging by European coots (Fulica atra) and found a marked reduction in the biomass of Ruppia cirrhosa outside exclosures. Jupp and Spence (1977) protected plots of Potamogeton spp. in Loch Leven, Scotland, and reported a similar decline in plant biomass due to waterfowl grazing. Charman (1977) did not estimate grazing pressure, but attributed early seasonal depletion of Zostera to the foraging activities of brent geese based on the results of his previous exclosure experiments.

Similar information for non-grazing waterfowl is almost entirely lacking. Nilsson (1969) calculated that diving ducks consumed less than 10% of the standing crop of invertebrates in a Zostera and Ruppia bed. Sincock (1962) estimated consumption by a number of non-grazing waterfowl but did not relate these values to standing crop. The diversity and patchy distribution of potential food organisms, and the difficulties associated with gizzard analysis may account for the lack of quantitative data.

A technique recently employed to characterize trophic relationships in seagrass communities involves analysis of stable carbon isotope ratios in tissues of herbivores or higher-level consumers. Based on differential uptake of ^{13}C by plants, ^{13}C:^{12}C ratios (expressed in $\delta^{13}C$ units) have been used to identify primary sources and fluxes of organic carbon in grassbeds and other habitats. Comparisons of animal $\delta^{13}C$ values with known or estimated dietary values indicate that isotope ratios are conserved through the food chain (Haines 1976, Fry et al. 1978, Haines and Montague 1979), with only slight variation due to effects of metabolic fractionation (De Niro and Epstein 1978). Seagrasses exhibit $\delta^{13}C$ values of -3 to -13^{o}/oo which are readily distinguished from those of phytoplankton (-18 to -24.5 ^{o}/oo), with benthic diatoms having intermediate values (Fry and Parker 1979). Resolution of dietary components is thus limited to fairly broad taxonomic or functional groups, but the technique is much less tedious than examination of gut contents.

Application of $\delta^{13}C$ analysis to waterfowl trophic studies has thus far been limited, but suggests a similar strong relationship between isotope ratios of bird tissue and dietary values. Patrick Parker and James Winters (pers. comm.) have used $\delta^{13}C$ values from liver and other tissues to study redheads foraging in shoalgrass (<u>Halodule wrightii</u>). Bird $\delta^{13}C$ values exhibited a positive seasonal shift of about 8 $^{o}/oo$ soon after arrival of birds from the breeding grounds, indicating rapid carbon turnover in bird tissue associated with the new winter diet. McConnaughey and McRoy (1979) reported a similar seasonal shift in values for waterfowl species in the Izembek Lagoon, Alaska. Although turnover may be very rapid, dietary information is time-integrated in the short term, whereas gizzard samples represent single foraging episodes.

Details of diet and reliable consumption estimates are needed to assess the functional role of waterfowl in SAV habitats and to evaluate the importance of this resource for wintering waterfowl. In this study, several of the above methods were combined, as it was felt that an integrative approach would provide more information than the use of a single technique, and would allow for comparison of results obtained by different methods.

METHODS

The Study Area

Vaucluse Shores is located on the Delmarva Peninsula in the lower Chesapeake Bay, just north of Hungar's Creek in Northampton County, Virginia (37°25'N latitude, 75°39'W. longitude) (Figure 1). The site consists of approximately 150 hectares vegetated subtidally by Ruppia maritima and Zostera marina (hereafter Ruppia and Zostera) which dominate beds of submerged vegetation in meso- and polyhaline regions of the Bay. These species are distributed according to depth, with Ruppia dominant in shallow water [less than 0.5 m at mean low water (MLW)], Zostera dominant in deeper water (greater than 1.0 m) and a mixed vegetation zone present at intermediate depths. Areal extent of the grassbed is delimited bayward by a series of parallel offshore sandbars oriented obliquely to the shoreline. Six transects (A-F) were established in the study area in 1978 for use in mapping vegetation at the site (Orth et al. 1979) and these provided convenient boundaries for waterfowl censuses.

Biomass data for Zostera at Vaucluse Shores indicate a seasonal maximum coinciding with seed production in June and July, averaging 85 g m^{-2} in 1978 (Orth et al. 1979). A second smaller peak in biomass takes place in the fall, followed by winter values of less than 50 g m^{-2}. Ruppia has a slightly different growth cycle, with one major biomass peak occurring in August and September. Both species may

Figure 1. The Vaucluse Shores study area, showing previously established transects A-F, and the location of waterfowl exclosures within transect interval B-C.

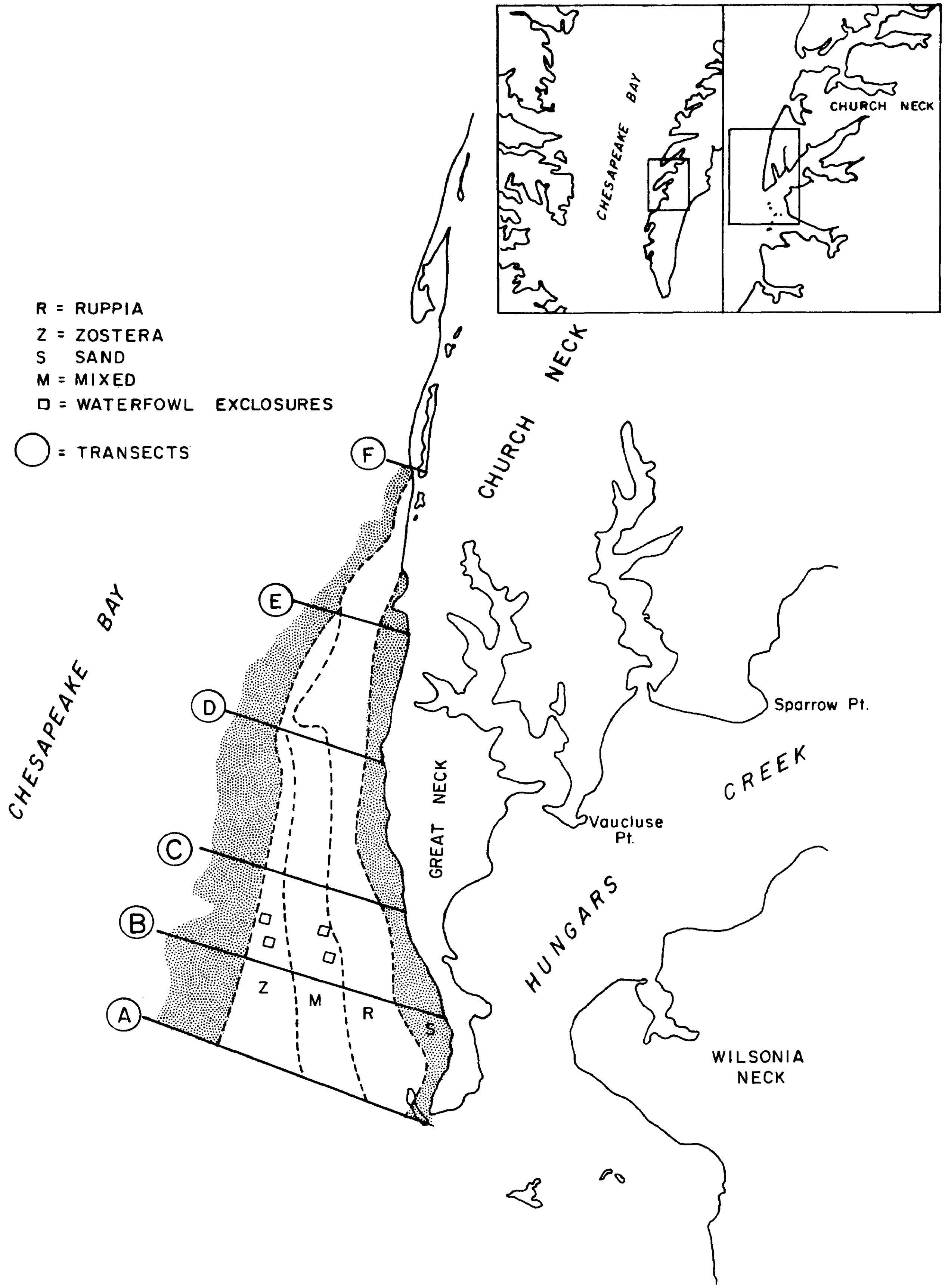

R = RUPPIA
Z = ZOSTERA
S SAND
M = MIXED
□ = WATERFOWL EXCLOSURES
○ = TRANSECTS
CHESAPEAKE BAY
CHESAPEAKE BAY
CHURCH NECK
CHURCH NECK
A
B
C
D
E
F
Z
M
R
S
GREAT NECK
Sparrow Pt.
Vaucluse Pt.
HUNGARS CREEK
WILSONIA NECK

exhibit different patterns of growth at mixed vegetation sites (P. A. Penhale, pers. comm.).

Salinity at the site varies from 14 ^{o}/oo to 24 ^{o}/oo and water temperatures range from -2C to 28C. In winter months, extreme low temperatures may cause ice formation in the shallow areas.

The same site was the focus of a broad scale interdisciplinary study (EPA-CBP contract #R80-59-74) designed to describe the principal components of seagrass communities in the lower Chesapeake Bay, and to elaborate important aspects of the functional ecology of these systems. This integrated program included the following investigation of waterfowl use of the habitat.

Waterfowl Abundance Estimates

1978-79: A preliminary census effort was undertaken in 1978-79 consisting of 13 census days between 6 December and 22 March, with a variable number of censuses per day. Waterfowl observed between previously established transects A through F were identified and counted with the aid of a spotting telescope and located by transect interval. The duration of each census was 15 minutes, and all birds present during that time were counted. Feeding activity of Canada geese was noted, and the relationship between percent feeding and tide level was tested using the Spearman rank-correlation coefficient r_s, computed as

$$r_s = 1 - \frac{6\ {}^{n}(R_1 - R_2)^2}{n(n^2 - 1)}$$

where R is the variable rank, and n is the sample size (Sokal and Rohlf 1981). Census times were used to obtain approximate tide level data from NOAA tide prediction tables.

1979-80: All observations were made between transects B and C (Figure 1) in 1979-80, allowing a more intense effort in a smaller area (approximately 26.5 ha) which had been consistently utilized by waterfowl the previous year. Waterfowl were censused at intervals averaging 11 days from 8 November to 3 April and on each census date birds were counted at approximately 2-hourly intervals during daylight.

At the outset of the study, four zones were marked in the census area from shore to the offshore sandbar which encloses the grass bed: bare sand, patchy *Ruppia maritima*, mixed *Ruppia* and *Zostera*, and pure *Zostera marina*. Although the zones are not highly discrete, fluorescent stakes were placed at transitions along transects B and C such that major vegetation type was indicated between pairs of stakes. The position of each bird was recorded in reference to these stakes. In order to express waterfowl numbers in terms of vegetation type, areal extent of each zone was estimated from the results of vegetational transect analysis reported by Wetzel et al. (1979) and from personal observation of transition zones. Density of waterfowl within these zones was then calculated, and differential utilization was tested between each pair by the Wilcoxon nonparametric two-sample rank test. The Wilcoxon statistic is calculated for samples of equal size as follows:

$$C = n^2 + \frac{n(n + 1)}{2} - \Sigma^{n} R$$

where n is sample size and R is the variable rank. This statistic is then compared with $(n^2 - C)$ and the greater of the two quantities is the test statistic U_s (Sokal and Rohlf 1981). The bare sand zone was excluded from analyses, as waterfowl rarely utilized that area.

A tide gauge consisting of a stake graduated in 5 cm increments was placed in subtidal shallow water and water level was recorded at the time of each census. The stake was destroyed by ice floes and replaced twice, but after 1 February tide data were obtained from NOAA tables as in 1978-79. Time and air temperature were also recorded, and wind speed and direction were obtained from the National Weather Service station in Norfolk, Virginia. The above parameters were related to waterfowl abundance using nonparametric correlation statistics as described above. In the case of tide, separate correlations were run for each vegetation zone in order to minimize the effect of the onshore-offshore depth gradient. One census date, 23 March, was eliminated from the above correlations because of the presence of a single large flock of redheads which would have obscured major trends.

Food Habits

Waterfowl gizzards and livers were obtained from birds collected by local hunters and scientific personnel in the study area and in the mouth of Hungar's Creek between October 1979 and March 1980. Because buffleheads were predominant in the second year of study, the diet of this species was the focus of food habits studies. Bufflehead gizzards were analyzed for food items, and livers of all species were analyzed for stable carbon isotope ratios ($\delta^{13}C$). Gizzards were kept frozen before laboratory processing, and contents were then sieved into two fractions for ease of examination. The coarse and fine fractions were retained on 0.5 mm and 62µ sieves, respectively. Material which passed through the 62µ sieve was negligible and therefore was discarded. Both fractions were preserved in 10% formalin. Contents of intact esophagi were examined, but were sieved on 62µ mesh only.

Identifiable species were enumerated under a dissecting microscope and noted as present or absent in the case of fragmented remains. Total contents of individual gizzards were not weighed, as it was felt that differential digestion would bias these quantities to a great extent. Instead, a representative sample of entire specimens of each prey species was obtained and dried to constant weight. Ash-free dry weights were estimated using conversion factors in Cummins and Wuycheck (1971) and values provided by J. Lunz and D. Weston (pers. comm.) for two mollusc species, as follows:

Peracarida 0.82 x Dry weight

Annelida	0.82
Decapoda	0.74
Mollusca	0.10 (For *Bittium varium* and *Crepidula convexa*)

These weights were multiplied by abundance per gizzard in order to calculate percent composition by dry weight and ash-free dry weight. The aggregate percent method was used to calculate mean composition, where the proportion of a species in each gizzard is averaged over all gizzards (Swanson et al. 1974). By this method, each gizzard has equal importance despite differences in volume of contents. Dietary importance was determined using the 'index of relative importance' (IRI) (Pinkas et al. 1971):

$$\mathrm{IRI} = (\%\,N + \%\,W) \times \%\,F$$

where N is numerical abundance, W is weight, (substituted here for volume) and F is frequency of occurrence.

Bufflehead dietary electivity was calculated within mollusc prey species only, as the numerical importance of softer-bodied forms may not be as accurately reflected in gizzard samples. The Jacobs index (L) was used to measure electivity because the degree of departure from zero (non-selectivity) can be statistically tested (Gabriel 1978). L is calculated as follows:

$$L = \ln (O) \quad \text{where } O = \frac{p_1 q_2}{p_2 q_1}$$

and p_1 = proportion of diet comprised by a given prey taxon

q_1 = proportion of diet comprised by all other prey taxa

p_2 = proportion of food complex in environment comprised by given taxon

q_2 = proportion of food complex in environment comprised by all other taxa

Estimates of environmental abundance of prey items were obtained from cores collected in January, and only gizzard samples which were collected within two weeks of benthic sampling were used to obtain dietary values.

Stable Carbon Isotope Analysis

Waterfowl livers were rinsed in distilled water, dried at 65°C for 96 hr and ground in a Wiley Mill to a fine powder. These samples were analyzed by Dr. Evelyn Haines at the University of Georgia Marine Science Institute and Drs. Patrick Parker and James Winters of Coastal Science Laboratories, Inc., at Port Aransas, Texas. Details of further sample preparation and analyses by these labs are described in Haines (1976) and Parker et al. (1972), respectively. In general samples are first combusted to convert organic carbon into CO_2, which is then isolated from other evolved gases. Isotopic analysis of CO_2 is carried out on a mass spectrometer, and isotope ratios are reported relative to a carbonate standard, in $\delta^{13}C$ units (parts per mil):

$$\delta^{13}C = \left(\frac{^{13}C/^{12}C \text{ sample}}{^{13}C/^{12}C \text{ standard}} - 1\right) \times 10^3$$

Tissues of important waterfowl foods (invertebrates from the study area) were prepared and analyzed in the same manner, except that in many cases specimens were pooled to obtain sufficient tissue

(≃60 mg). For comparison with observed bufflehead $\delta^{13}C$ values, an expected value was calculated by multiplying the mean percent contribution of each prey species to the diet (ash-free dry weight) by its $\delta^{13}C$ value, and summing these values over all gizzards (Fry et al. 1978).

Waterfowl Exclosure Experiments

To investigate the impact of grazing waterfowl (primarily Canada geese and redheads) on vegetation density at the study site, two areas between transects B and C were chosen to locate exclosures: a shallow mixed *Ruppia* and *Zostera* zone and a deeper pure *Zostera* zone (Figure 1). Between 14 and 18 October 1979, two caged plots were established in each of these zones at depths of approximately 0.5 m and 1.2 m at MLW, respectively. Cage pairs included one cage (cage I) to be sampled at two intervals during waterfowl residence and another (cage II) to be sampled only if cage I was damaged.

Exclosures measured 2m x 2m x 0.5m and were constructed with 2.5 cm mesh vinyl-coated wire sides and crab pot wire tops (2.5 cm hexagonal mesh), hinged on two sides to open from the center during sampling. A frame consisting of a length of shaped concrete reinforcing rod supported the top and penetrated the sediment to 50 cm. In addition, a 1 m length of reinforcing rod was attached to each corner and buried to 50 cm.

Benthic samples were taken with a 0.031 m^2 plexiglass corer to a depth of approximately 15 cm during three sampling periods: 18 October

1979, 16-19 January 1980, and 19 March 1980. On 18 October, six replicate cores were taken in the vicinity of cages located in the Zostera and mixed vegetation zones. Sample size was chosen based on previous estimates of variability in plant biomass in the study area (Orth et al. 1979). These samples were processed for vegetation only, which was separated into above and below ground fractions, then dried in an oven at 55°C for 48 hours and weighed.

During the second sampling period methodolgy was modified based on the near-absence of Canada geese from the grassbed (see results). As the dominant species was the bufflehead, which feeds primarily on invertebrates (Stewart 1962), samples were processed for animal abundance as well as quantity of vegetation. Sample size was increased to ten cores each from caged and uncaged sites to account for greater patchiness of the invertebrate species.

Cores from uncaged areas were taken in a pattern radiating from the center of the cage using random compass headings and distances between 6 m and 12 m from the cage. Within exclosures, cores were taken randomly from a 2m x 2m grid. Care was taken to position and remove the corer with the least possible disturbance to adjacent bottom. Samples were placed in muslin bags, refrigerated and washed the following day on a 0.5 mm sieve. Cores collected in January were frozen after sieving, but this resulted in damage to soft-bodied invertebrates and thus samples collected in March were stored in 10% formalin.

In the lab, samples were rinsed and elutriated repeatedly to separate vegetation from the animal and sediment component, which was then sieved into two fractions. The coarse fraction (>2 mm) was sorted and identified in its entirety, and the fine fraction (<2 mm >0.5 mm) was distributed evenly on the sieve by flotation and then split into quarters. Two quarters were chosen randomly for sorting and the counts obtained were then doubled. Split counts were compared to total counts for two samples. Total number of individuals was 3.0% in error for one comparison and 3.1% for the other. Error by species varied, with the rarest species most affected by the technique. All organisms were identified to lowest taxa, with some exceptions. In the January samples polychaetes, oligochaetes, and nemertea were eliminated from analysis because damage from freezing rendered numbers unreliable. Only two dominant epifaunal polychaetes, _Nereis succinea_ and _Polydora ligni_, were identified to species in the March samples.

Sediment cores were taken to determine effects of exclosures on sedimentation processes. Three cores were taken from each treatment in January and five were taken from each treatment in March. Percent sand and silt-clay were determined by sieving and pipette analysis outlined by Folk (1961).

Differences between treatment means were tested using the Wilcoxon statistic, with the exception of sediment data, which were arcsin transformed (Sokal and Rohlf 1981) and compared between treatments using a standard t-test.

Estimates of Consumption from Waterfowl Density

Mean waterfowl abundances, theoretical daily intake, and days in residence were used to estimate total consumption of biomass by birds utilizing the study area. Methods for determining daily intake are from Wolff et al. (1975) where standard metabolism M is multiplied by 5 to obtain consumption in kcal/day. M is determined by the formula:

$$\text{Log } M = \text{Log } 78.3 + 0.723 \log W$$

where W is body weight in kg. Kcal were converted to grams ash-free dry weight (AFDW) by multiplying by a factor of 0.2. These values were then used in the following formula for consumption:

$$C = I \cdot A \cdot R$$

where I = daily intake in grams AFDW
A = mean abundance
R = residence (estimated as 150 days)

Consumption was calculated over the total habitat as well as more restricted areas, based on patterns of utilization within the habitat. Estimates were partitioned according to predominant feeding type (animal vs vegetation) according to Stewart (1962) and Munro and Perry (1981).

RESULTS

Waterfowl Abundance

1978-79: The Canada goose was the most important waterfowl species in the study area in 1978-79, and averaged 526 individuals per 100 hectares (Table 1). The overwhelming dominance demonstrated by the species is obvious when plots of total waterfowl and Canada goose abundance are compared (Figure 2). Second in importance was the bufflehead, which averaged 46 birds per 100 ha and was the only species present on every census date. Large flocks of redheads utilized the study area, but occurred on only 5 of the 13 census days. It is uncertain whether this species was adequately censused, as foraging may have been primarily nocturnal. Redheads were most often observed at dawn and dusk, and did not generally remain in the area throughout the day.

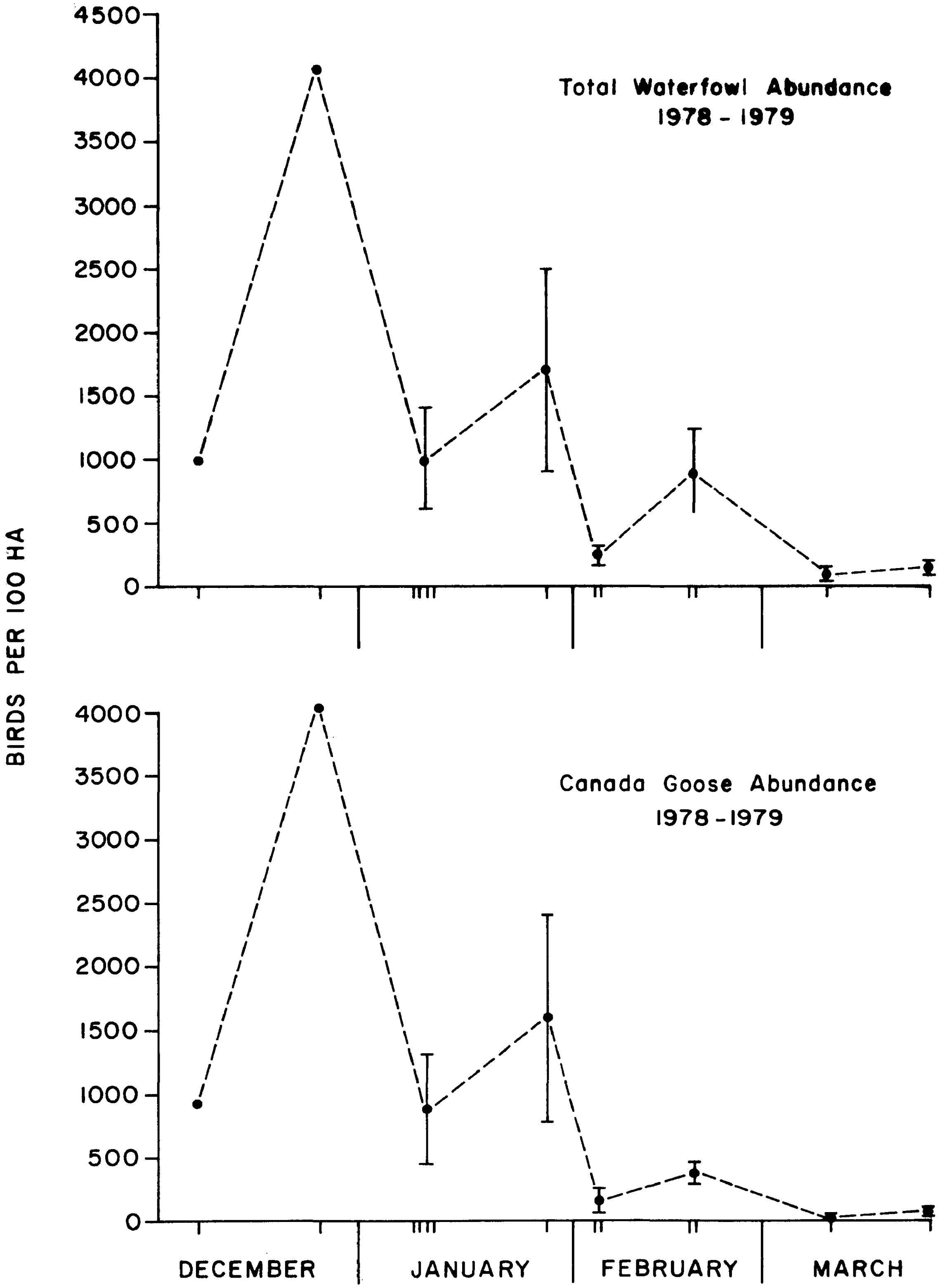
Brant occurred on only two census dates, but one flock of approximately 1300 birds inflated the relative importance of the species. Whistling swans and wigeon were present regularly (in more than 60% of censuses) but in low numbers. Red-breasted mergansers (*Mergus serrator*) occurred less frequently but in flocks with an average density of 19 birds per 100 ha. Although non-divers (primarily Canada geese) were more abundant than diving ducks, both groups were represented by nearly equal numbers of species throughout the season.

Table 1. Mean abundances of waterfowl species at Vaucluse Shores 1978-1979.

Birds Per 100 Hectares

		1978		1979											Overall Mean Abundance (Weighted)
		12/6	12/24	1/7	1/8	1/9	1/10	1/27	2/3	2/4	2/17	2/18	3/7	3/22	
# Censuses		1	1	5	1	4	5	3	4	4	8	4	4	10	
Canada goose (*Branta canadensis*)	$\bar{x}$	964	4052	1965	0	34	531	1623	168	147	194	643	6	52	526.5
	±S.E.	--	--	±198.1	--	±33.8	±413.3	±812.3	±141.00	±99.5	±79.6	±80.2	±6.2	±17.3	
Bufflehead (*Bucephala albeola*)	$\bar{x}$	17	3	19	35	35	39	85	59	51	35	102	41	46	46.1
	S.E.	--	--	±26.8	--	±4.2	±9.5	±20.2	±19.9	±29.0	±12.2	±64.1	±10.2	±12.3	
Redhead (*Aythya americana*)	$\bar{x}$	0	0	48	61	30	0	0	0	0	91	302	0	0	44.2
	S.E.	--	--	±30.7	--	±67.5	--	--	--	--	±113.9	±191.6	--	--	
Brant (*Branta bernicla*)	$\bar{x}$	0	0	0	0	0	0	0	1	0	0	404	0	0	29.9
	S.E.	--	--	--	--	--	--	--	0.8	--	--	±348.8	--	--	
Red-breasted merganser (*Mergus serrator*)	$\bar{x}$	0	0	43	135	0	0	0	0	33	0	0	32	28	18.9
	S.E.	--	--	±27.6	--	--	--	--	--	±27.2	--	--	±11.3	±12.0	
American wigeon (*Anas americana*)	$\bar{x}$	0	0	64	23	5	4	0	0	8	0.2	38	13	3	12.0
	S.E.	--	--	±17.9	--	±4.8	±2.5	--	--	±7.8	±0.2	±27.6	±12.4	±1.7	
Whistling swan (*Cygnus columbianus*)	$\bar{x}$	15	15	7	23	0	7	0	0	0	12	3	1	0	4.4
	S.E.	--	--	±4.1	--	--	±5.1	--	--	--	±6.9	±1.7	±1.2	--	
Pintail (*Anas acuta*)	$\bar{x}$	0	0	13	0	6	9	0	0	0	1	2	0	0	2.7
	S.E.	--	--	±9.2	--	±6.5	±9.0	--	--	--	±0.8	±1.8	--	--	
Black duck (*Anas rubripes*)	$\bar{x}$	0	0	1	0	0	0	0	1	8	1	14	1	2	2.2
	S.E.	--	--	±11.9	--	--	--	--	±1.8	±3.9	0.8	±12.8	±0.3	±0.9	
Common goldeneye (*Bucephaea clangula*)	$\bar{x}$	0	0	2	0	0	1	1	0	1	0	0	2	0.4	2.2
	S.E.	--	--	±1.8	--	--	±1.3	±1.1	--	±0.7	--	--	±1.8	±0.1	
Scaup sp. (*Aythya* spp.)	$\bar{x}$	0	0	0	0	0.4	0	0	0	0	0	12	0	0	0.9
	S.E.	--	--	--	--	±0.4	--	--	--	--	--	±12.5	--	--	
Surf scoter (*Melanitta perspicillata*)	$\bar{x}$	0	0	0	0	--	2	0	3	0	0	0	0	0	0.4
	S.E.	--	--	--	--	--	±1.8	--	±1.5	--	--	--	--	--	
Mallard (*Anas platyrhynchos*)	$\bar{x}$	0	0	2	0	0	0	0	0	0	1	0	0	0	0.3
	S.E.	--	--	±1.3	--	--	--	--	--	--	±1.2	--	--	--	

Figure 2. Abundances of total waterfowl and Canada geese at Vaucluse Shores, 1978-1979. Points represent means and bars are standard errors of the mean.


BIRDS PER 100 HA
Total Waterfowl Abundance
1978 - 1979
4500
4000
3500
3000
2500
2000
1500
1000
500
0
Canada Goose Abundance
1978-1979
4000
3500
3000
2500
2000
1500
1000
500
0
DECEMBER
JANUARY
FEBRUARY
MARCH

Abundances of most species fluctuated without respect to seasonality in 1978-79. However, Canada geese were most abundant in the first few censuses, and this trend would probably have been more pronounced had the earliest part of the season (November to early December) been included.

Utilization of the study area by foraging Canada geese was influenced by tide level (Figure 3). At the lowest water levels (2 hr. before and after low tide) the majority of geese present were feeding, whereas geese almost never attempted to feed at higher tide levels, and instead remained on the offshore sandbar. A negative rank correlation between percent feeding and departure from low tide in hours was significant at $p < 0.001$.

<u>1979-80</u>: Patterns of waterfowl abundance changed dramatically in the second year of observations. Fewer species utilized the area consistently (four per day average) and the proportion of non-diving to diving species decreased to less than 0.2 per day (Figure 4). Although large numbers of Canada geese were noted in the vicinity of Hungar's Creek, no large flocks were censused within the study area (Table 2). During a number of censuses, rafts of several hundred geese were observed directly offshore at a distance of approximately 500 m beyond the sandbar (numbers in parentheses in Table 2), but they did not come into the grassbed.

The bufflehead was the dominant species in 1979-80, and total waterfowl numbers closely tracked the abundance of this diving duck (Figure 5). Again, they occurred on every census date, and mean

Figure 3. Relationship between tide stage and foraging activity in Canada geese at Vaucluse Shores, 1978-1979. Curve fit by eye.

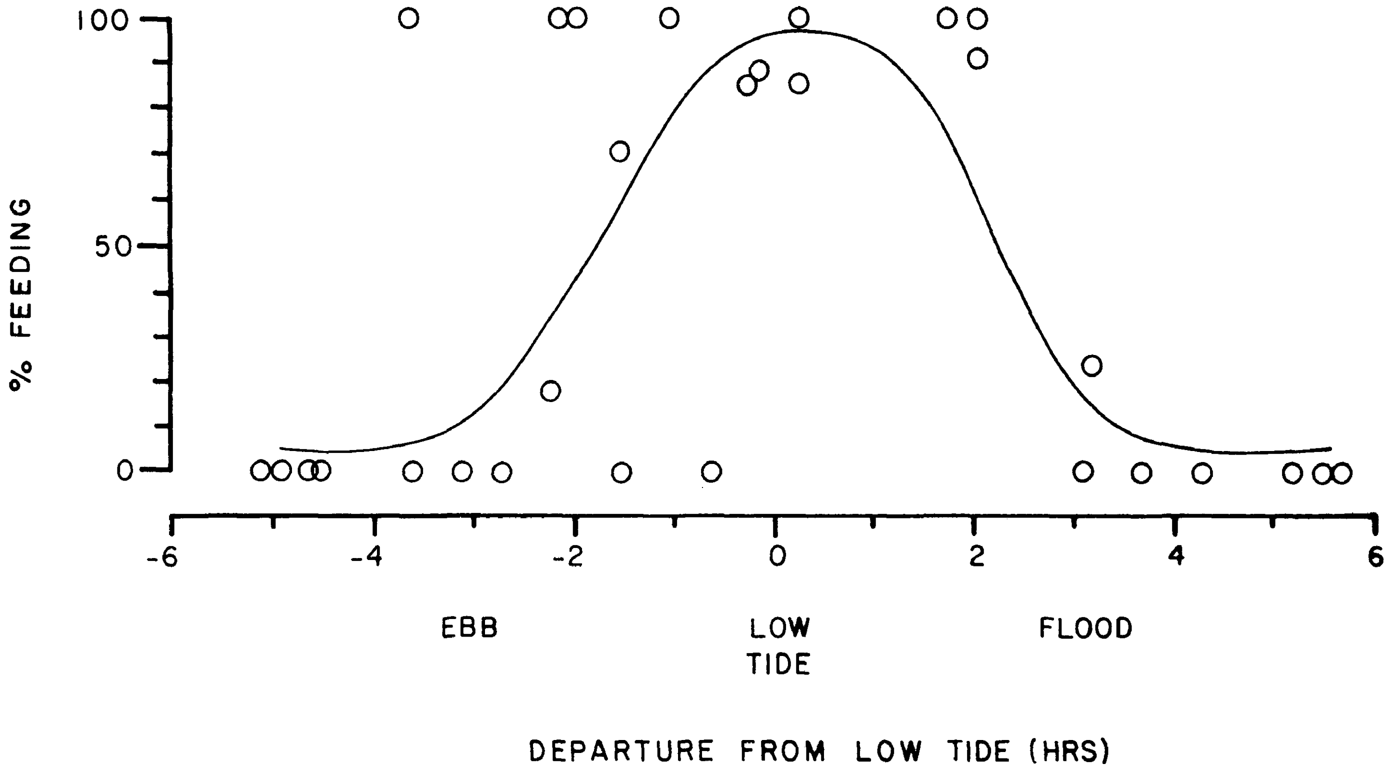

100
50
0
% FEEDING
-6
-4
-2
0
2
4
6
EBB
LOW
TIDE
FLOOD
DEPARTURE FROM LOW TIDE (HRS)

Figure 4. Numbers of diving vs. non-diving waterfowl, as a percentage of total waterfowl during 1978-1979, compared to 1979-1980.

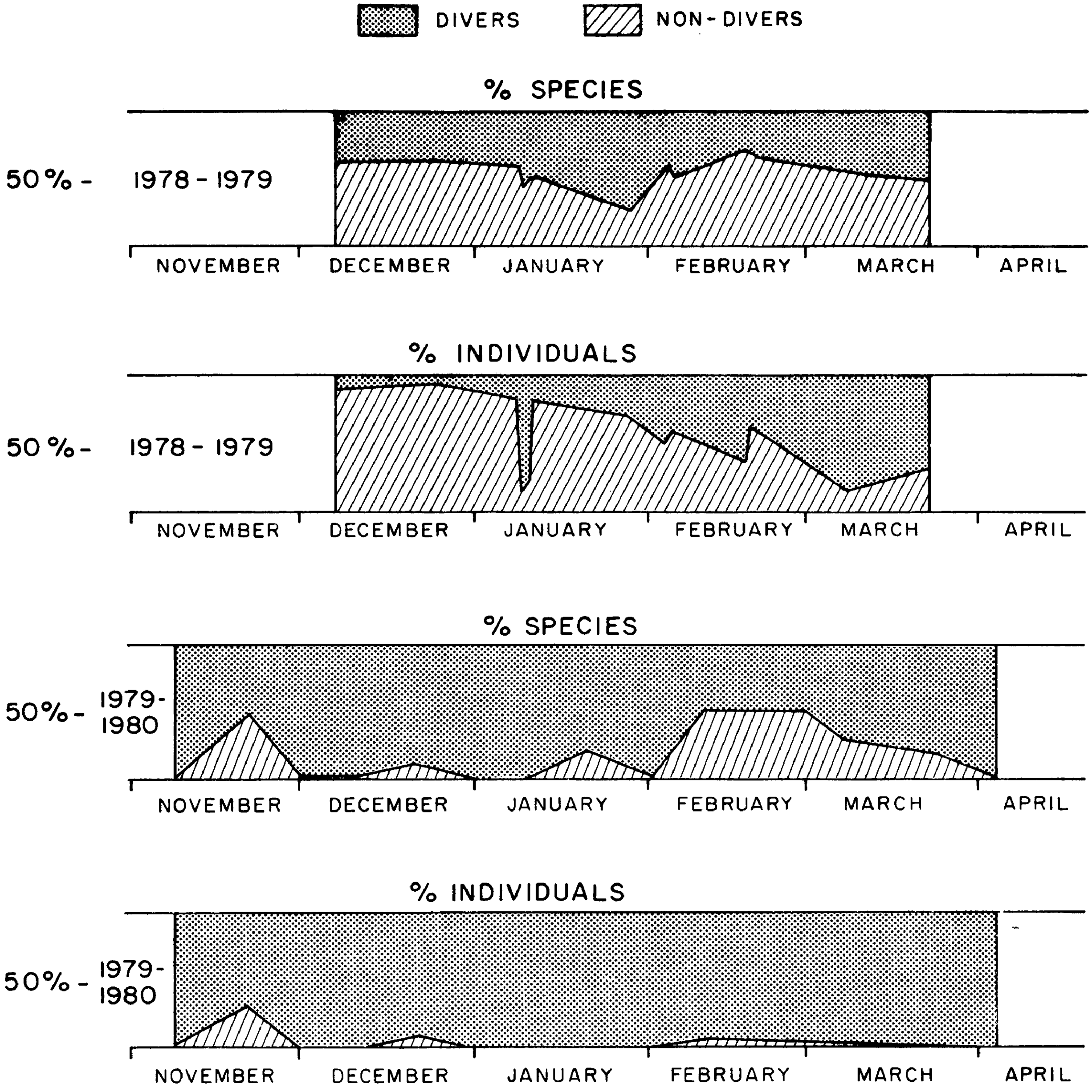
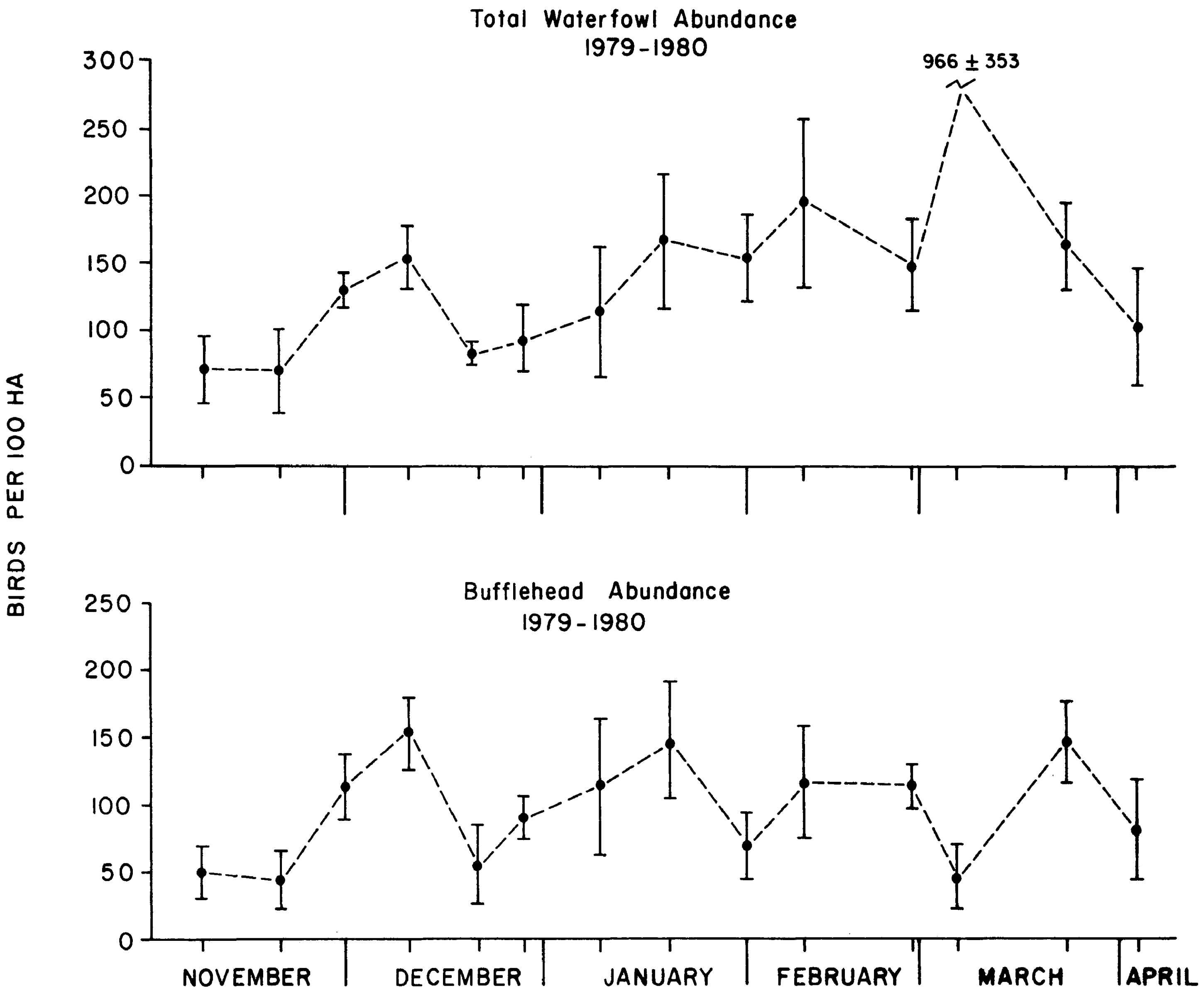

DIVERS
NON-DIVERS
% SPECIES
50% -
1978 - 1979
NOVEMBER
DECEMBER
JANUARY
FEBRUARY
MARCH
APRIL
% INDIVIDUALS
50% -
1978 - 1979
NOVEMBER
DECEMBER
JANUARY
FEBRUARY
MARCH
APRIL
% SPECIES
50% -
1979-
1980
NOVEMBER
DECEMBER
JANUARY
FEBRUARY
MARCH
APRIL
% INDIVIDUALS
50% -
1979-
1980
NOVEMBER
DECEMBER
JANUARY
FEBRUARY
MARCH
APRIL

Table 2. Mean abundances of waterfowl species at Vaucluse Shores, area B-C, 1979-1980.

Birds Per 100 Hectares

		1979						1980								Overall Mean Abundance (Weighted)
		11/8	11/20	11/30	12/10	12/21	12/28	1/9	1/20	2/1	2/10	2/27	3/6	3/23	4/3	
	# Censuses	6	6	6	6	6	6	5	6	6	5	6	6	7	7	
Bufflehead (Bucephala albeola)	$\bar{x}$	51	46	126	153	56	85	113	149	69	115	114	46	145	78	96.1
	±S.E.	±16.9	±19.8	±18.8	±23.0	±25.6	±24.2	51.3	±39.3	±23.7	±40.3	±13.7	±22.0	±29.2	±36.3	
Redhead (Aythya americana)	$\bar{x}$	0	0	0	0	0	0	0	0	40	0	0	802	0	0	60.1
	±S.E.	--	--	--	--	--	--	--	--	±95.5	--	--	±335.4	--	--	
Scaup spp. (Aythya spp.)	$\bar{x}$	0	0	0	0	4	2	0	0	45	69	38	53	0	0	15.0
	±S.E.	--	--	--	--	±3.1	±1.9	--	--	±21.6	±42.1	±25.5	±24.6	--	--	
Red-breasted merganser	$\bar{x}$	10	0	1	2	0	1	0	0	0	0	1	1	15	12	3.1
(Mergus serrator)	±S.E.	±10.1	--	±0.8	±1.9	--	±1.3	--	--	--	--	0.6	±0.8	±14.5	±6.1	
Surf scoter	$\bar{x}$	0	0	1	2	25	4	0	0	0	0	0	0	0	0	2.2
(Melanitta perspicillata)	±S.E.	--	--	±0.6	±12.9	±11.1	2.4	--	--	--	--	--	--	--	--	
Brant (Branta bernicla)	$\bar{x}$	0	22	0	0	0	0	0	0	0	3	0	0	0	0	1.8
	±S.E.	--	±23.3	--	--	--	--	--	--	--	±3.0	--	--	--	--	
American wigeon	$\bar{x}$	0	0	0	0	0	0	0	0	0	0	6	16	0	0	1.6
(Anas americana)	±S.E.	--	--	--	--	--	--	--	--	--	--	±5.7	±9.2	--	--	
Whistling swan	$\bar{x}$	0	0	0	0	0	0	0	1	0	3.0	0	17	0	0	1.5
(Cygnus columbianus)	±S.E.	--	--	--	--	--	--	--	±0.6	--	±1.8	--	±14.2	--	--	
Horned grebe	$\bar{x}$	8	0	2	0	1	0	0	1	0	0	0	0	1	0	0.9
(Podiceps auritus)	±S.E.	±4.2	--	±1.3	--	±0.6	--	--	±0.6	--	--	--	--	±0.7	--	
Canada goose	$\bar{x}$	0	0	0	0	4	0	0	0	0	0	1	0	0	0	0.4
(Branta canadensis)	±S.E.	--	--	--	--	±4.4	--	--	--	--	--	±0.6	--	--	--	
(outside study area)		--	(966)	--	(436)	(333)	--	(1100)	(338)	--	(500)	--	--	--	--	
Pintail (Anas acuta)	$\bar{x}$	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0.3
	S.E.	--	--	--	--	--	--	--	--	--	--	±4.1	--	--	--	
Oldsquaw	$\bar{x}$	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0.3
(Clangula hyemalis)	S.E.	--	--	--	--	±2.0	--	±0.8	--	--	--	--	--	--	--	
Common goldeneye	$\bar{x}$	0	0	0	0	0	2	1	1	0	0	0	0	1	1	0.3
(Bucephala clangula)	±S.E.	--	--	--	--	--	±1.9	±0.7	±0.6	--	--	--	--	±0.5	±0.5	
Black duck (Anas rubripes)	$\bar{x}$	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0.1
	S.E.	--	--	--	--	--	--	--	--	--	--	--	--	±1.1	--	
Common loon (Gravia immer)	$\bar{x}$	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0.04
	S.E.	--	--	±0.6	--	--	--	--	--	--	--	--	--	--	--	

Figure 5. Abundances of total waterfowl and buffleheads at Vaucluse Shores, area B-C 1979-1980. Points are means and bars are standard errors of the mean.


Total Waterfowl Abundance
1979-1980
966 ± 353
300
250
200
150
100
50
0
BIRDS PER 100 HA
Bufflehead Abundance
1979-1980
250
200
150
100
50
0
NOVEMBER
DECEMBER
JANUARY
FEBRUARY
MARCH
APRIL

density of this species (96 birds per 100 ha) was approximately twice as great as in 1978-79. Redheads were also important though infrequent the second year, primarily due to a flock of approximately 500 birds which fed in shallow Ruppia on 6 March. In contrast to the previous year, scaup (Aythya spp.) were important and were present in greatest numbers (45-60 per 100 ha) in February and early March.

In 1979-80 waterfowl abundance was independent of tide level, except in the shallow Ruppia zone, where numbers of birds were generally low but increased with higher tide levels (Figure 6). Rank correlation coefficients for the mixed and Zostera zones and the total study area were not significantly different from zero (Table 3).

Temperatures ranged from -6C to 22C but did not influence waterfowl abundance in the study area. Winds were predominately NNW, but direction had some effect on waterfowl numbers. A positive correlation was found between abundance and direction (from 10-360°), and higher numbers were associated with winds from the NNW ($p < 0.05$). Wind speed alone did not have a significant effect, but when wind direction was held constant, wind speed had a positive influence on bird numbers in the case of NNW winds ($p < 0.05$). When wind speed was held constant (in 5 knot increments) direction had a positive effect only at 21-25k ($p < 0.05$). No correlation was found between waterfowl abundance and time of day during daylight hours.

Within the grassbed, vegetation zone had a pronounced effect on waterfowl use (Figure 7). Mean densities of birds within these zones indicated an increasing inshore to offshore trend, with maximum

Figure 6. Relationships between numbers of waterfowl and tide levels in three vegetation zones, 1979-1980. Numbers in parentheses refer to a single flock of redheads which were not included in analyses. Means are indicated by the height of blocks, and points are individual observations.

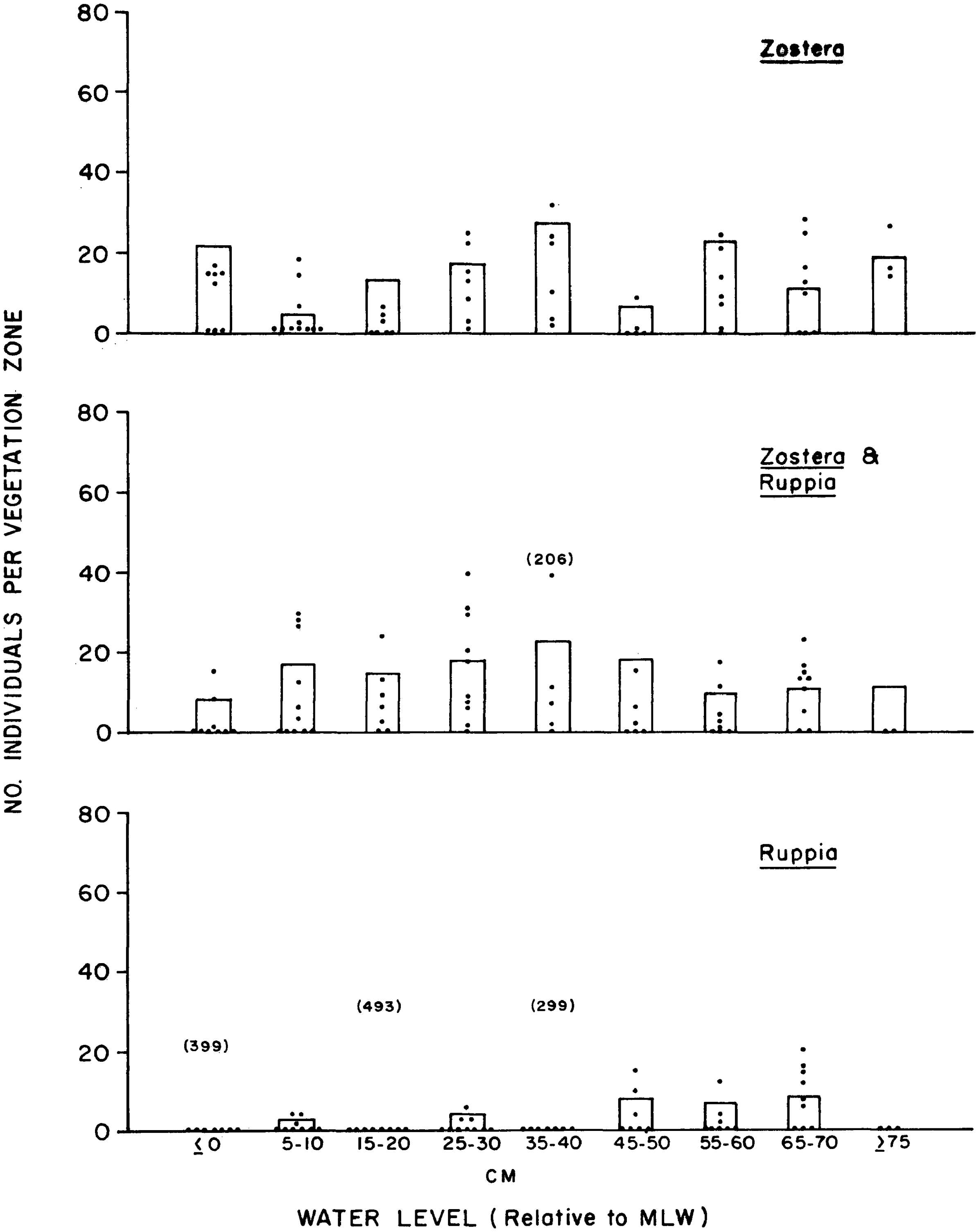
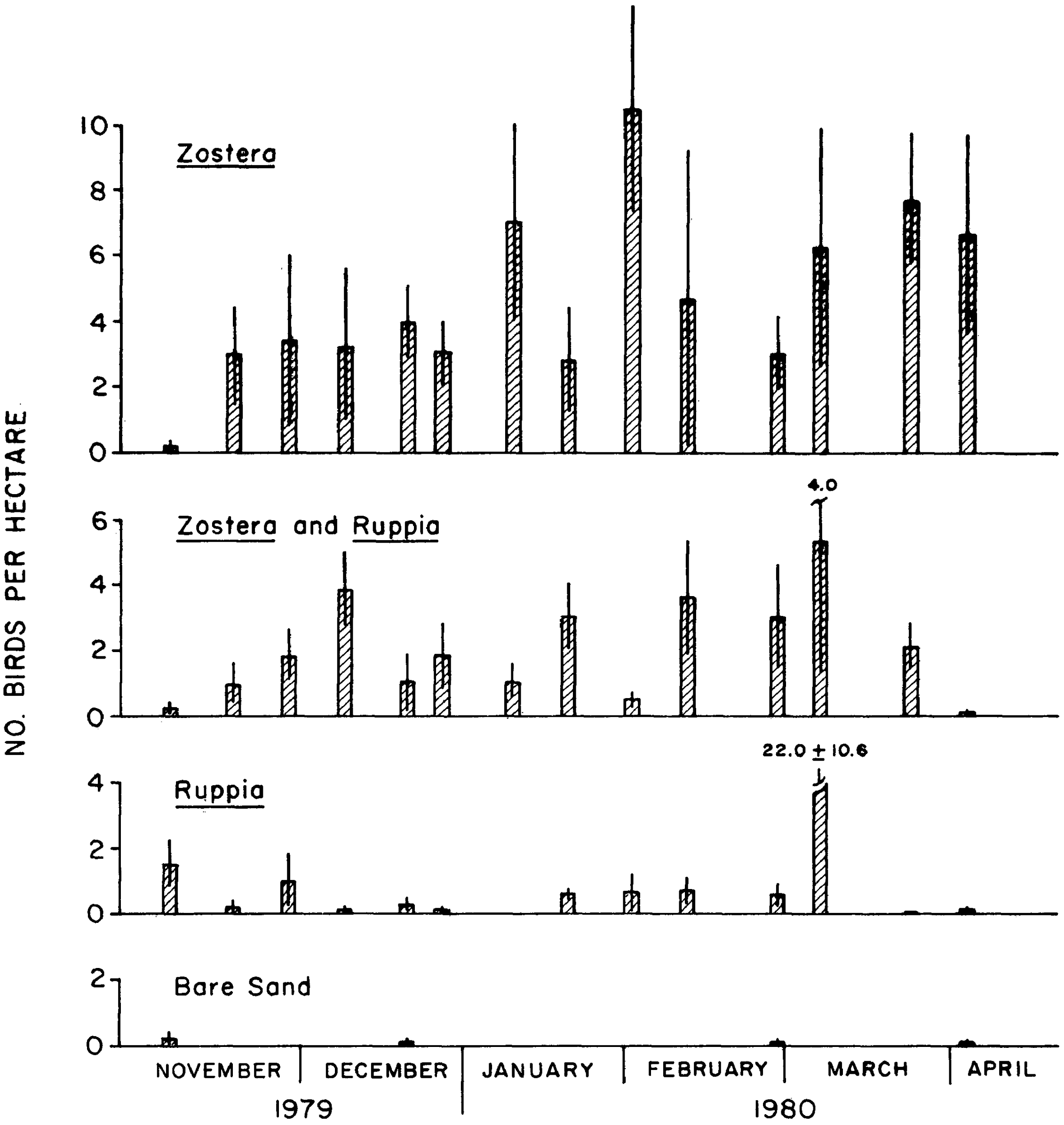

80
60
40
20
0
Zostera
Zostera & Ruppia
(206)
Ruppia
(399)
(493)
(299)
≤0
5-10
15-20
25-30
35-40
45-50
55-60
65-70
≥75
CM
WATER LEVEL (Relative to MLW)
NO. INDIVIDUALS PER VEGETATION ZONE

Table 3. Nonparametric correlation analysis of waterfowl abundance, 1979-1980.

					r_s
Tide Level	With	Abundance	Shallow	(*Ruppia*)	0.3128*
			Mixed		0.0881
			Deep	(*Zostera*)	0.0846
		Total Abundance			0.1002
Time of Day	With	Total Abundance			0.1463
Temperature	With	Total Abundance			0.0235
Wind Direction, Variable Speed	With	Total Abundance			0.2271*
1-5 knots	(N=9)				-0.3291
6-10	(25)				-0.2862
11-15	(20)				0.3807
16-20	(10)				0.1042
21-25	(5)				0.9487*
Wind Speed, Variable Direction					0.1837
NNE	(12)				-0.0808
ENE	(11)				0.0605
SSW	(5)				0.8208
WNW	(6)				0.6088
NNW	(35)				0.3281*

* $p<0.05$.

Figure 7. Within-habitat variation in waterfowl density at Vaucluse Shores, 1979-1980. Means and standard errors are indicated.


NO. BIRDS PER HECTARE
Zostera
Zostera and Ruppia
4.0
Ruppia
22.0 ± 10.6
Bare Sand
0
2
4
6
8
10
NOVEMBER
DECEMBER
JANUARY
FEBRUARY
MARCH
APRIL
1979
1980

densities in the Zostera zone. Numbers of birds were very low in bare sand and Ruppia, rarely exceeding one individual per hectare. Multiple comparisons indicated that these differences were highly significant for each pair considered (Table 4).

Again, few seasonal trends were evident in waterfowl abundance. A gradual increase in total numbers from January through March 1980 reflects primarily the occurrence of greater numbers of scaup and redheads, while bufflehead numbers fluctuated around the overall mean with no sustained increases or decreases.

Food Habits: Gizzard Analysis

Gizzards from 32 buffleheads were examined. Due to the difficulties of collecting waterfowl during active feeding, most gullets and a number of gizzards contained very little or no food. Of 25 esophagi collected, 22 were empty. Therefore, results are presented for gizzards only, two of which were completely empty and were also omitted from analysis. All other gizzards were analyzed regardless of fullness, in order to obtain an adequate sample size.

A total of 27 taxa were identified in bufflehead gizzards, including 23 invertebrate species, three plant species and fish vertebrae (Table 5). Molluscs and peracaridan crustaceans accounted for 18 of the 23 invertebrate species and the remainder included polychaetes, decapods, bryozoans and barnacles. Plant material in the diet consisted primarily of Ruppia maritima and Zostera marina, with corn (Zea mays) present in a single gizzard.

Table 4. Effect of vegetation zone on waterfowl density in the study area. Comparisons tested by the Wilcoxon statistic U_s.

	Ruppia	Mixed	*Zostera*	U_s
Mean density (Birds/ha) ± Std. Error N=76	0.43 ±0.110	1.71 ±0.263	4.92 ±0.697	
Mean Ranks R/M	60.62	92.38	--	7021.0***
M/Z	--	66.30	86.70	5038.5**
Z/R	55.72	--	97.28	7393.5***

** $p < 0.01$
*** $p < 0.001$

Table 5. Composition of gizzard contents of 30 buffleheads collected in the vicinity of Vaucluse Shores, 1979-1980.

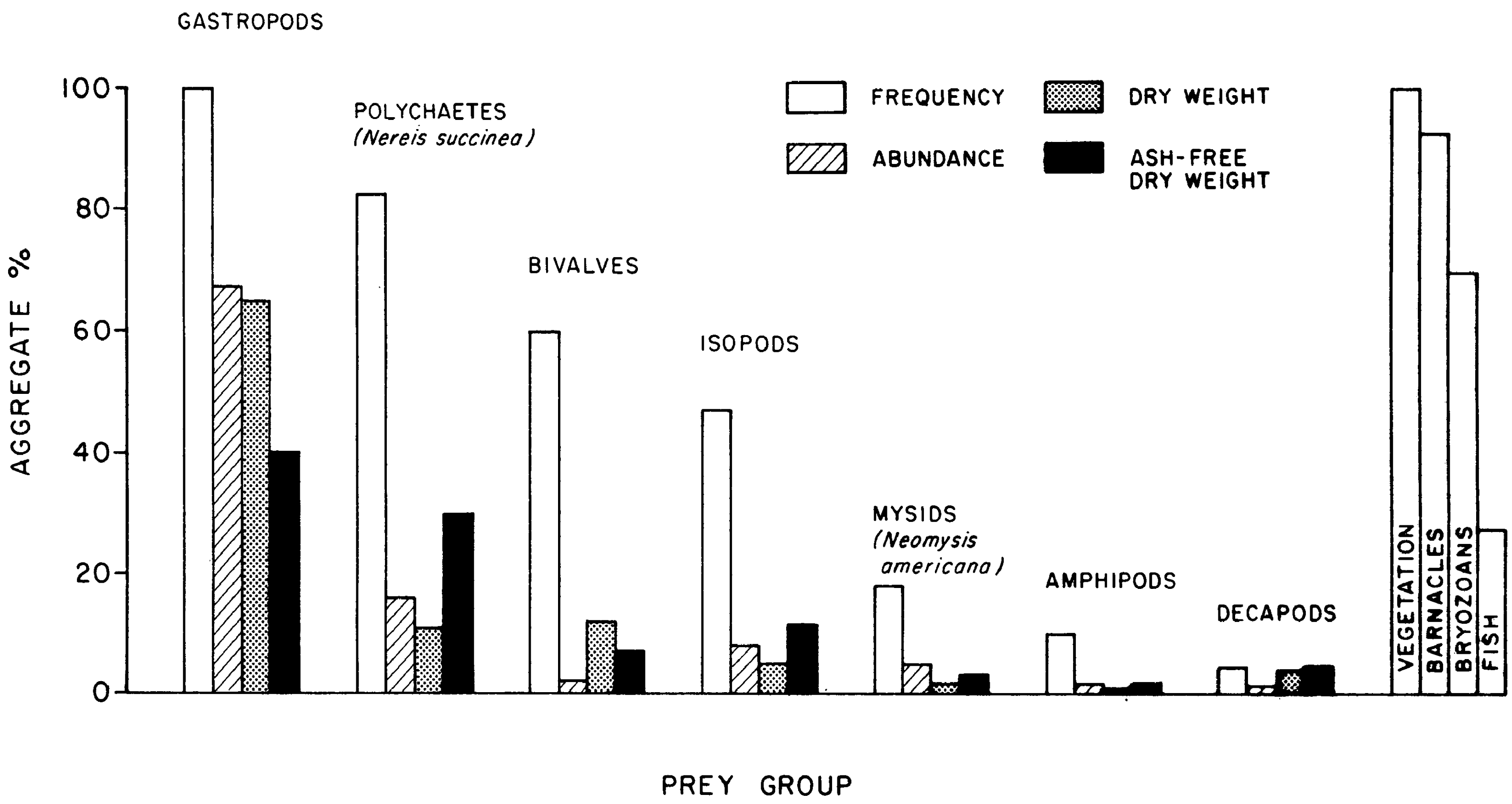
	Mean Abundance	Aggregate %	Mean Dry Weight (mg)	Aggregate %	Mean Ash-free Dry Weight (mg)	Aggregate %	Frequency of Occurrence %	IRI (DW)	IRI (AFDW)
Animal Contents									
Mollusca									
Gastropoda									
Crepidula convexa	49.4	32.8	43.0	24.6	4.3	16.4	76.7	22.0	18.9
Pyramidellidae sp.	20.2	16.3	12.9	9.6	1.3	6.1	66.7	8.6	7.5
Bittium varium	7.3	8.6	7.9	7.7	0.8	4.1	73.3	6.0	4.7
Astyris lunata	3.6	6.0	20.7	14.9	2.1	9.0	60.0	6.3	4.5
Acteocina canaliculata	0.7	1.6	1.3	1.5	0.1	0.8	30.0	0.5	0.4
Triphora nigrocinta	0.7	1.0	1.7	1.4	0.2	0.7	33.3	0.4	0.3
Nassarius vibex	0.2	0.6	9.8	5.5	1.0	4.0	16.7	0.5	0.4
Epitonium rupicola	0.1	0.3	0.3	0.2	tr	0.2	10.0	-	-
Acteon punctostriatus	tr	0.2	tr	0.1	tr	0.1	3.3	-	-
Bivalvia									
Anadara transversa	1.5	2.0	19.0	10.2	1.9	6.1	46.7	2.8	1.9
Gemma gemma	0.6	1.7	1.1	1.9	0.1	0.8	40.0	0.7	0.5
Annelida									
Polychaeta									
Nereis succinea	8.6	15.9	12.5	11.0	10.0	29.6	83.3	11.2	19.0
Arthropoda									
Crustacea									
Cirripedia									
Balanus improvisus		-	-	-	-	-	83.3	-	-
Malacostraca									
Crangon septemspinosa	0.2	0.2	8.7	4.5	6.4	5.0	6.7	0.4	0.2
Xanthidae sp.	tr	tr	0.2	tr	0.1	0.4	3.3	-	-
Mysidacea									
Neomysis americana	5.0	5.4	0.7	1.2	0.6	3.0	16.7	0.5	0.7
Isopoda									
Erichsonella attenuata	2.8	5.4	3.5	3.9	2.8	9.8	43.3	2.0	3.3
Edotea triloba	0.7	1.0	0.3	0.3	0.2	0.9	26.7	0.2	0.3
Idotea balthica	0.1	0.2	0.1	0.5	0.1	1.7	6.7	-	0.1
Paracerceis caudata	tr	tr	tr	tr	tr	0.2	3.3	-	-
Amphipoda									
Gammarus mucronatus	0.2	0.3	0.2	0.1	0.2	0.6	13.3	-	0.1
Cymadusa compta	0.1	0.3	0.1	0.1	0.1	0.4	6.7	-	-
Bryozoa spp.	-	-	-	-	-	-	60.0	-	-
Chordata									
Vertebrata									
Osteichthyes							36.7		
Vegetation									
Zostera marina							70.0		
Ruppia maritima							96.7		
Zea mays							3.3		

Crepidula convexa was the dominant prey item by numerical abundance and dry weight, with a mean abundance of 49 individuals and mean dry weight of 43 mg per gizzard. In terms of ash-free dry weight, C. convexa was less important than the polychaete, Nereis succinea, which averaged 30% of gizzard contents by ash-free weight. However, abundance of N. succinea was relatively low (nine individuals per gizzard). Only chitinous jaws and setae of this polychaete were evident in gizzards due to rapid digestion of softer tissue, but numbers of individuals (and thus reconstructed weights) were obtained by counting pairs of jaws.

By taxonomic group, gastropods dominated gizzard contents (Figure 8). Of the five most important prey species by the index of relative importance (IRI) four were gastropods: Crepidula convexa, Pyramidellidae sp., Bittium varium and Astyris lunata. These four species accounted for nearly 60% of gut contents by dry weight (36% by AFDW) and 64% by abundance, and occurred with an average frequency of 70%.

Polychaetes were represented in gizzards only by Nereis succinea, although the contribution to the diet by this group may be underestimated. Bivalves (primarily Anadara transversa) and isopods (dominated by Erichsonella attenuata) were of roughly equal importance averaging from 5-12% of gizzard contents by dry and ash-free dry weight. Mysids (Neomysis americana) were abundant in several samples, but dry weight contribution was minor. Identifiable amphipods and decapods were encountered rarely and in low numbers.

Figure 8. Aggregate percent composition of gizzard contents, by major prey taxa, from 30 buffleheads collected in 1979-1980.


GASTROPODS
POLYCHAETES
(Nereis succinea)
BIVALVES
ISOPODS
MYSIDS
(Neomysis americana)
AMPHIPODS
DECAPODS
VEGETATION
BARNACLES
BRYOZOANS
FISH
FREQUENCY
ABUNDANCE
DRY WEIGHT
ASH-FREE DRY WEIGHT
AGGREGATE %
100
80
60
40
20
0
PREY GROUP

The barnacle Balanus improvisus was a consistent prey species, with shell fragments found in 25 gizzards. Exoskeletal fragments of bryozoans were also found frequently (70% occurrence). Because numbers could not be determined for either of these groups, dietary importance was not assigned. Importance was not determined for plant material as no quantitative measure of percent composition was made. However, it appeared by visual estimate that vegetation was a minor dietary component, taken with invertebrate prey items found among vegetation.

Results of electivity calculations among mollusc prey species indicate that buffleheads may be at least partially selective (Table 6). Crepidula convexa was eaten in proportionally low numbers relative to its abundance in the grassbed, resulting in a significantly negative L value ($p < 0.001$) although it was still the dominant prey item. The gastropods Bittium varium, Pyramidellidae spp., Astyris lunata, and the bivalves Gemma gemma and Anadara transversa are apparently preferred (i.e. had significantly positive L values), but are found in much lower abundances in the environment than is C. convexa. The gastropods Triphora nigrocincta, Acteon punctostriatus and Acteocina canaliculata contributed to the diet in close proportion to their environmental abundances.

Food Habits: Stable Carbon Isotope Ratios

Bufflehead livers were fairly consistent in carbon isotope composition, with an average $\delta^{13}C$ of -17.2 ± 0.81 $^{o}/oo$ (Table 7). $\delta^{13}C$ values were obtained directly for 11 prey species (van Montfrans

Table 6. Bufflehead dietary electivity within molluscan prey species only, as measured by the Log of Jacobs' odds Ratio (L) (Gabriel, 1978).

Prey Item	% Abundance in environment	Mean % abundance in diet (n=15)	L	S.E. (L)	Z
Crepidula convexa	94.40	51.82	-2.75	0.270	-12.689***
Bittium varium	1.37	19.51	+2.86	0.290	9.872***
Pyramidellidae spp.	1.01	12.78	+2.66	0.343	7.770***
Anadara transversa	0.95	4.05	+1.49	0.583	2.563**
Gemma gemma	0.95	3.46	+1.35	0.580	2.326*
Astyris lunata	0.48	6.42	+2.65	0.473	5.613***
Triphora nigrocincta	0.46	0.64	+0.47	1.321	0.358 ns
Acteon punctostriatus	0.23	0.51	+0.79	2.213	0.359 ns
Acteocina canaliculata	0.15	0.58	+1.35	1.416	0.954 ns

* $p<0.05$
** $p<0.01$
*** $p<0.001$

TABLE 7. Carbon isotope composition of buffleheads collected near Vaucluse Shores, 1979-1980.

$\delta^{13}C$ Values Bufflehead Livers $^{o}/oo$	Date Collected
-15.8	12/18/79
-17.1	12/18/79
-16.4	12/18/79
-18.0	12/18/79
-17.2	12/18/79
-17.4	12/19/79
-18.0	12/19/79
-18.0	12/19/79
-17.8	12/19/79
-15.5	12/24/79
-16.8	12/26/79
-17.8	01/02/80
-17.0	01/14/80
-17.3	01/14/80
-16.5	01/15/80
-17.5	01/16/80
-18.4	01/16/80
-17.7	01/16/80
-17.6	01/16/80
-17.9	01/16/80
-16.4	01/23/80
-16.7	01/23/80
-17.0	01/23/80
-18.3	01/23/80
-15.3	01/23/80
-18.1	01/23/80
-15.3	01/23/80
-18.1	01/23/80
-18.5	01/23/80
-16.9	01/23/80
-18.0	02/22/80
-16.5	02/22/80
-17.3	02/22/80
-16.8	02/23/80

$\overline{X} = -17.2$ o/oo
S.D. ± 0.81

1981) and were estimated by taxonomic group or feeding category for the remaining species (Table 8). In general, values were slightly less negative than bufflehead liver tissue and varied widely among taxa. The polychaete *Nereis succinea* (-13.3 ^{o}/oo), the gastropod *Bittium varium* (-13.4 ^{o}/oo) and the isopod *Erichsonella attenuata* (-13.4 ^{o}/oo) had the highest $\delta^{13}C$ values, while the gastropods *Crepidula convexa* (-20.2 ^{o}/oo), *Astyris lunata* (-16.4 ^{o}/oo) and the amphipod *Cymadusa compta* (-16.8 ^{o}/oo) were less $\delta^{13}C$-enriched. The suspension feeding bivalves *Anadara transversa* and *Gemma gemma* were assigned a value of -17.5 ^{o}/oo based on measured ^{13}C:^{12}C ratios for the clams *Mya arenaria* and *Mercenaria mercenaria*. Values for other prey species ranged from -14.0 to -15.9 ^{o}/oo.

From these values for prey items and the percent contribution of each species (by ash-free dry weight) to the diet, the resulting value for bufflehead tissue should approximate -15.4 ^{o}/oo, if all prey items are accounted for in correct porportions. Although this assumption was not strictly met, the observed mean was within 1.8 ^{o}/oo of the predicted value.

$\delta^{13}C$ values for other waterfowl species were also lower than most potential prey species (Table 9). With the exception of a single wigeon liver (-12.7 ^{o}/oo), values were even further removed from those obtained for submerged vegetation. *Ruppia* and *Zostera* ranged in $\delta^{13}C$ values from -7.5 to -10.6 ^{o}/oo, and the value for associated periphyton was -11.2 ^{o}/oo.

TABLE 8. Isotopic composition of bufflehead invertebrate prey species.

PREY SPECIES	$\delta^{13}C$ $^o/oo$	PROPORTION OF DIET BY AFDW	CONTRIBUTION TO TOTAL $\delta^{13}C$
Crepidula convexa	-20.2	0.164	-3.31
Nereis succinea	-13.3	0.296	-3.94
Pyramidellidae sp.	-14.5[a]	0.060	-0.88
Bittium varium	-13.4	0.041	-0.55
Astyris lunata	-16.4	0.090	-1.48
Erichsonella attenuata	-13.4	0.098	-1.31
Anadara transversa	-17.5[b]	0.061	-1.07
Crangon septemspinosa	-14.2	0.050	-0.71
Neomysis americana	-17.5[b]	0.029	-0.51
Nassarius vibex	-14.2	0.040	-0.57
Triphora nigrocincta	-14.7[c]	0.007	-0.10
Edotea triloba	-15.5	0.009	-0.14
Gemma gemma	-17.5[b]	0.008	-0.14
Acteocina canaliculata	-14.7[c]	0.008	-0.12
Gammarus mucronatus	-15.9	0.006	-0.10
Idotea balthica	-14.0	0.017	-0.24
Cymadusa compta	-16.8	0.004	-0.07
Epitonium rupicola	-14.7[c]	0.002	-0.03
Acteon punctostriatus	-14.7[c]	0.001	-0.001
Xanthidae sp.	-14.5[a]	0.004	-0.06
Paracerceis caudata	-14.3[d]	0.002	-0.03

Total = Expected $\delta^{13}C$ = -15.35 $^o/oo$

[a] Mean value for: predator/omnivores
[b] " : suspension feeders
[c] " : gastropods
[d] " : isopods

TABLE 9. Carbon isotope composition of waterfowl other than buffleheads collected near Vaucluse Shores, 1979-1980.

Species	$\delta^{13}C$ Values $^{o}/oo$ (Livers)	Date Collected
Canada goose	-19.6	12/31/79
	-21.6	01/05/80
	-19.6	01/11/80
American wigeon	-19.1	12/17/80
	-17.6	12/17/79
	-16.2	12/17/79
	-16.8	01/01/80
	-15.0	03/14/80
	-16.2	03/14/80
	-12.7	03/14/80
Black duck	-18.8	01/01/80
	-17.8	01/02/80
Pintail	-16.9	01/11/80
Lesser scaup	-18.9	01/23/80
Greater scaup	-19.1	12/31/79
Oldsquaw	-16.5	01/16/80
	-17.7	01/23/80
Surf scoter	-17.1	01/01/80
	-18.3	01/01/80
Red-breasted merganser	-20.8	02/23/80

Waterfowl Exclosures

By 23 January, the inshore exclosures had been removed by ice, and results are presented for cages in pure *Zostera* only. Cage I in *Zostera* was sampled in January but not in March, as the top had been forced open for an unknown length of time. Instead, Cage II was sampled, and therefore the results from the two dates are not strictly comparable.

Samples from both cages (i.e. both sample dates) yielded significantly greater numbers of individuals and species than samples from uncaged areas (Table 10). Species abundances were significantly greater inside cages in approximately half of the comparisons ($p \leq 0.05$) (Figures 9 and 10). Eight species were found in significantly higher numbers in both sets of caged samples: the gastropods *Doridella obscura*, *Crepidula convexa*, *Astyris lunata*, and *Bittium varium*, a bivalve *Anadara transversa*, the isopods *Erichsonella attenuata* and *Edotea triloba*, and an amphipod *Paracaprella tenuis*. With the exception of *P. tenuis* and *D. obscura*, all of these species were found in bufflehead gizzard samples, and most were important components of the diet. Other species with significantly higher abundances inside cages which were not present in gizzard or gullet samples included a number of peracarid crustaceans and juvenile blue mussels (*Mytilus edulis*). Only one species, the gastropod *Ilyanassa obsoleta*, was found in significantly higher numbers outside cages.

For most bufflehead prey species, the magnitude of the observed differences between treatments did not increase with the duration of

Table 10. Number of species and individuals from cores taken in caged and uncaged *Zostera* in January and March 1980. Differences were tested by the Wilcoxon Statistic U_s.

		No. Species		No. Individuals	
		Caged	Uncaged	Caged	Uncaged
		33	29	1257	854
		34	29	1615	937
		30	29	1264	1000
		31	29	978	1335
		32	29	1343	1027
January		31	28	1002	941
N=10		29	26	1360	930
		33	25	1153	694
		29	26	1089	620
		29	25	997	740
	$\bar{X}$	31.1	27.5	1025.8	907.8
	S	1.85	1.78	202.62	202.00
	U_s	92.5***		88.0**	
		45	41	1179	1161
		38	35	1504	1202
		34	32	1987	1522
		38	34	2154	1559
		39	31	2015	1741
March		33	29	2013	1681
N=10		41	29	2098	1444
		31	29	2316	1259
		43	33	2218	1079
		42	32	2607	1556
	$\bar{X}$	38.4	32.5	2069.1	1420.4
	S	4.58	3.66	297.55	230.16
	U_s	84.0**		95.0***	

** $p < 0.01$
*** $p < 0.001$

Figure 9. Rank scores for species abundances in caged vs. uncaged samples taken in January 1980, as designated by the Wilcoxon 2-sample test. Expected score under H_O (that treatment means are equal) = 10.5. Significance level of the U statistic is indicated.

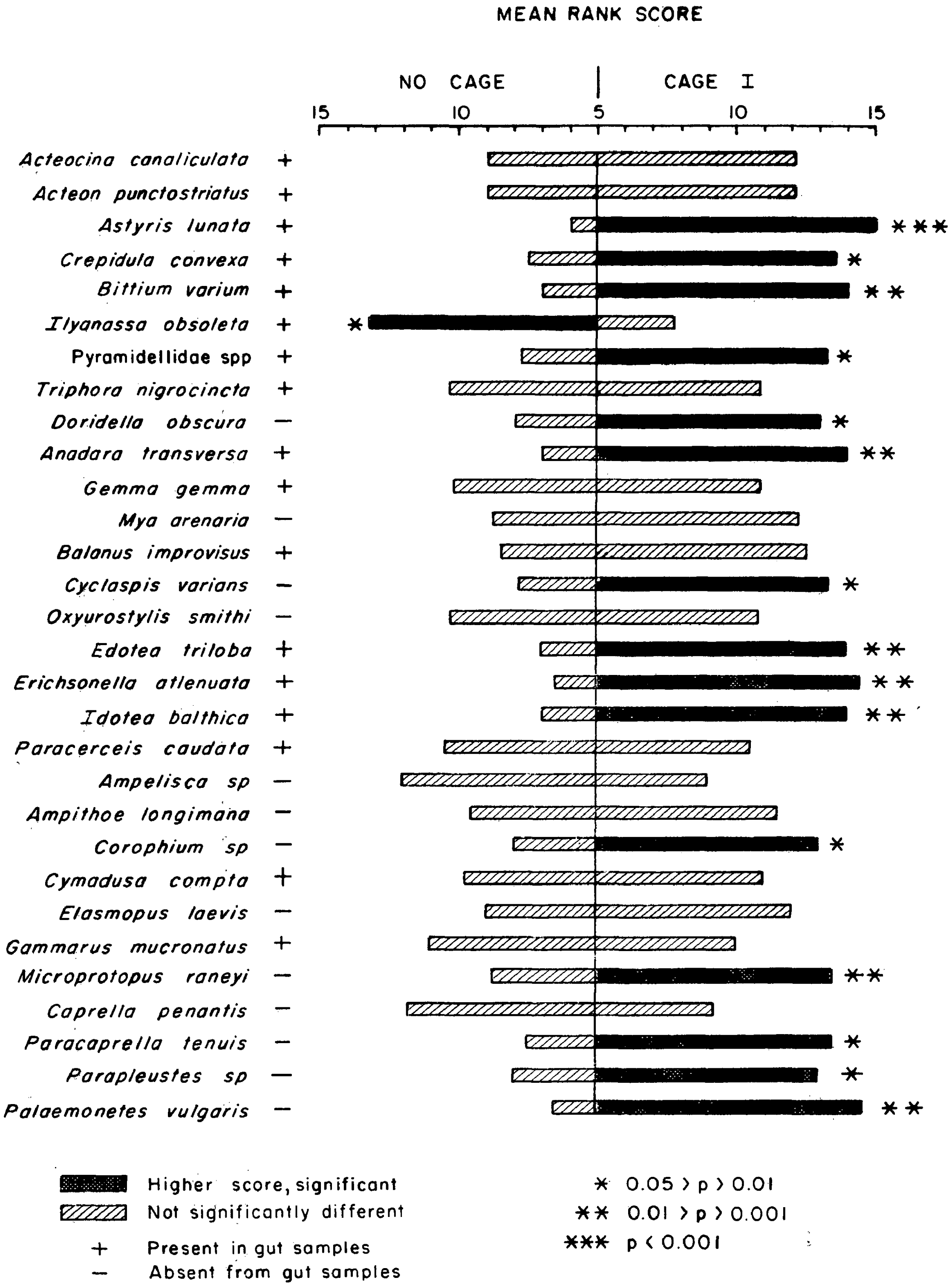
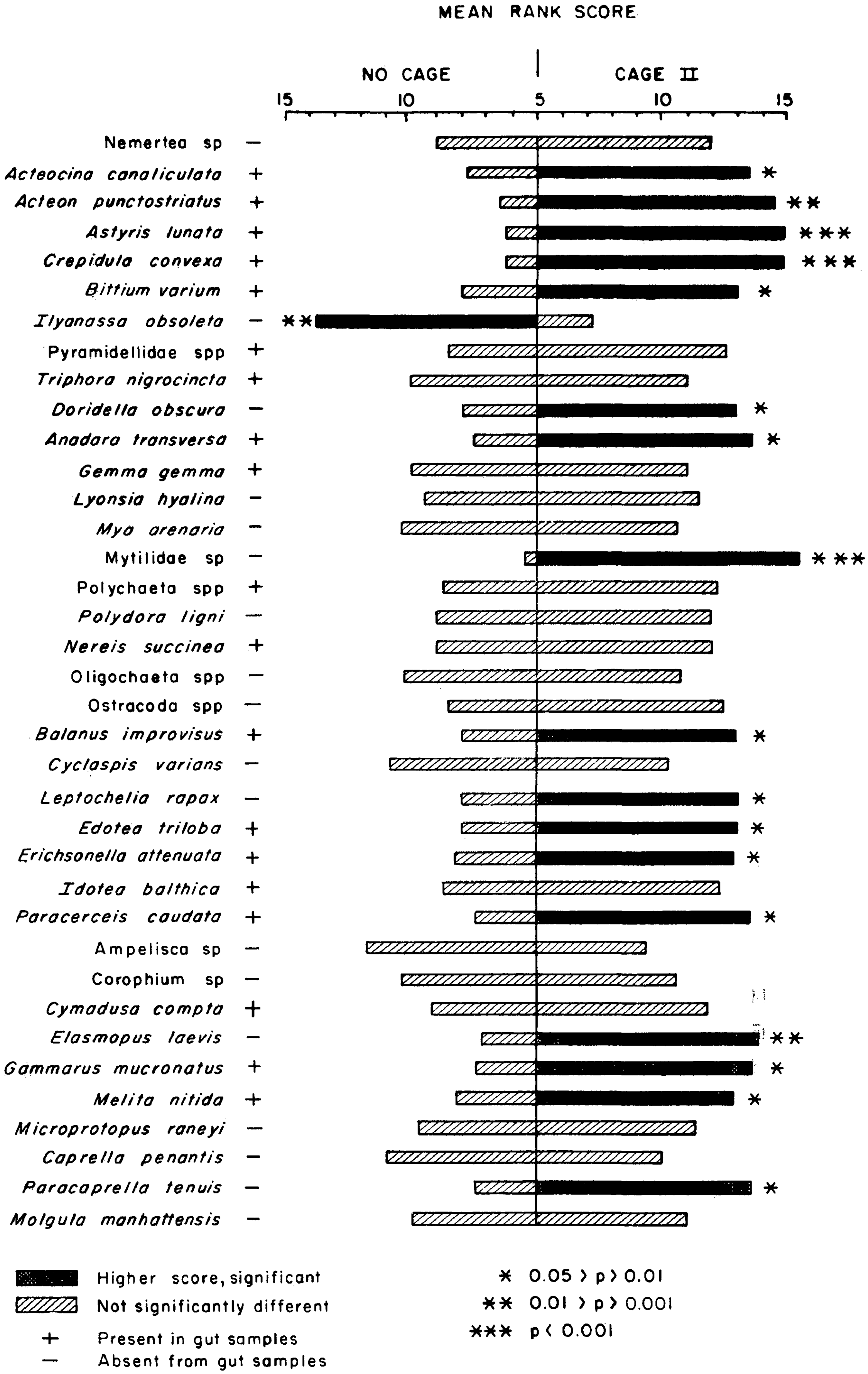

MEAN RANK SCORE
NO CAGE
CAGE I
15
10
5
10
15
Acteocina canaliculata +
Acteon punctostriatus +
Astyris lunata + ***
Crepidula convexa + *
Bittium varium + **
Ilyanassa obsoleta + *
Pyramidellidae spp + *
Triphora nigrocincta +
Doridella obscura − *
Anadara transversa + **
Gemma gemma +
Mya arenaria −
Balanus improvisus +
Cyclaspis varians − *
Oxyurostylis smithi −
Edotea triloba + **
Erichsonella attenuata + **
Idotea balthica + **
Paracerceis caudata +
Ampelisca sp −
Ampithoe longimana −
Corophium sp − *
Cymadusa compta +
Elasmopus laevis −
Gammarus mucronatus +
Microprotopus raneyi − **
Caprella penantis −
Paracaprella tenuis − *
Parapleustes sp − *
Palaemonetes vulgaris − **
■ Higher score, significant
▨ Not significantly different
+ Present in gut samples
− Absent from gut samples
* 0.05 > p > 0.01
** 0.01 > p > 0.001
*** p < 0.001

Figure 10. Rank scores for species abundances in caged vs. uncaged samples taken in March 1980, as designated by the Wilcoxon 2-sample test. Expected score under H_o (that treatment means are equal) = 10.5. Significance level of the U statistic is indicated.


MEAN RANK SCORE
NO CAGE
CAGE II
15
10
5
10
15
Nemertea sp —
Acteocina canaliculata + *
Acteon punctostriatus + **
Astyris lunata + ***
Crepidula convexa + ***
Bittium varium + *
Ilyanassa obsoleta — **
Pyramidellidae spp +
Triphora nigrocincta +
Doridella obscura — *
Anadara transversa + *
Gemma gemma +
Lyonsia hyalina —
Mya arenaria —
Mytilidae sp — ***
Polychaeta spp +
Polydora ligni —
Nereis succinea +
Oligochaeta spp —
Ostracoda spp —
Balanus improvisus + *
Cyclaspis varians —
Leptochelia rapax — *
Edotea triloba + *
Erichsonella attenuata + *
Idotea balthica +
Paracerceis caudata + *
Ampelisca sp —
Corophium sp —
Cymadusa compta +
Elasmopus laevis — **
Gammarus mucronatus + *
Melita nitida + *
Microprotopus raneyi —
Caprella penantis —
Paracaprella tenuis — *
Molgula manhattensis —
Higher score, significant
Not significantly different
\+ Present in gut samples
— Absent from gut samples
* 0.05 > p > 0.01
** 0.01 > p > 0.001
*** p < 0.001

the experiment, as indicated by a Wilcoxon test comparing these trends between January and March samples (Table 11). However, abundances of five prey species were significantly greater inside cages in March but not in January, and the reverse was true for two prey species.

Determinations of plant biomass indicated that the cage structure may have had a negative impact on plant survival and/or growth (Table 12). Orth et al. (1979) reported lower biomass values for Zostera in winter months, and a similar decline was observed from October to January in uncaged cores. However, biomass of vegetation inside cages was reduced to a greater degree, and the difference was significant ($p<0.001$) in March. Cages were observed to be badly fouled with macroalgae and hydrozoans at that time.

Differences in percent sand and silt-clay were not apparent between treatments in January or March (Table 13). Sediments were fine sands, with less than 15% silt-clay.

Consumption Rates

Total consumption estimated from waterfowl density in 1978-79 and 1979-80 amounted to 11.67 and 1.70 g AFDW m^{-2} respectively, over the entire area censused (Tables 14 and 15). In 1978-79 vegetation was the predominant waterfowl food, according to the general food preferences of abundant species. Foraging Canada geese removed approximately 8.26 g AFDW m^{-2}, or 74% of the total for vegetation. Brant, redheads, and whistling swans consumed 2.72 g, while the remaining grazers ate an estimated 0.18 g AFDW m^{-2}. If only the

Table 11. Abundances of prey species which showed significant differences between treatments in January or March 1980 (indicated by *). U_s compares the magnitude of these differences over all species across sample dates. Values are means and standard errors of the mean.

	JANUARY		MARCH	
	NO CAGE	CAGE	NO CAGE	CAGE
Crepidula convexa	22690	28254*	12230	21540***
	±1937.7	±1643.7	±1171.6	±1761.0
Pyranidellidae	280	825*	328	468 n.s.
	±81.0	±254.1	±88.3	±88.4
Bittium varium	255	519**	150	271*
	±47.9	±70.6	±60.5	±48.5
Astyris lunata	92	631***	51	541***
	±21.5	±166.7	±20.3	±147.2
Erichsonella attenuata	370	796**	382	573*
	±31.9	±174.1	±71.7	±87.8
Anadara transversa	169	306**	80	188
	±33.9	±30.5	±15.2	±36.6
Edotea triloba	427	936**	946	1306*
	±99.3	±113.7	±83.9	±179.2
Acteocina canaliculata	57	121 n.s.	22	121
	±27.6	±51.5	±13.5	±34.5
Gammarus mucronatus	866	573 n.s.	940	1436*
	±266.8	±70.3	±101.4	±175.6
Idotea balthica	373	675**	248	338 n.s.
	±30.0	±82.6	±46.9	±53.3
Acteon punctostriatus	70	102 n.s.	54	194**
	±19.5	±22.2	±25.1	±34.4
Balanus improvisus	99	213 n.s.	48	140*
	±28.3	±52.2	±13.6	±36.8
Paracerceis caudata	204	201 n.s.	89	201*
	±19.1	±35.2	±20.6	±44.3

U_s = 88.0 n.s.

Table 12. Above and below-ground biomass of *Zostera marina* from cores taken in October 1979 and in January and March 1980. Differences were tested by the Wilcoxon statistic U_s.

	10/79		1/80				3/80			
			Uncaged		Caged		Uncaged		Caged	
	g m^{-2}		g m^{-2}				g m^{-2}			
	Above	Below	Above	Below	Above	Below	Above	Below	Above	Below
	61.63	59.75	51.98	89.40	28.27	38.06	52.25	88.71	39.96	92.20
	76.40	114.86	45.72	114.17	46.11	46.18	38.66	77.78	23.73	134.84
	83.43	88.07	51.38	157.55	44.51	89.99	49.40	102.55	33.94	77.97
	81.70	66.87	57.25	74.75	54.02	118.87	39.75	89.44	39.26	134.44
	70.22	90.60	46.84	143.77	57.84	104.60	55.91	73.33	28.52	106.67
	61.73	198.24	57.11	59.39	22.84	91.25	45.12	94.09	38.34	79.66
			29.71	53.01	32.63	62.37	52.40	85.87	28.56	112.17
			54.32	100.29	33.14	128.65	48.90	58.31	23.08	88.36
			58.01	88.84	42.36	100.05	56.70	95.34	29.32	69.40
			68.55	119.04	58.69	144.50	62.20	63.05	32.26	50.90
$\bar{X}$	72.52	103.07	52.09	100.08	42.04	92.45	50.13	82.85	31.70	86.36
S	9.58	50.53	10.18	34.19	12.56	34.86	7.44	14.41	6.13	38.53
U statistic			72 n.s.	53 n.s.			97*** $p<0.001$	62 n.s.		

Table 13. Composition of sediments sampled in January and March 1980, from caged and uncaged *Zostera*. Differences were tested by a t-test, on arcsin transformed percentages.

		% Sand		% Silt and Clay	
		Uncaged	Caged	Uncaged	Caged
		91.36	92.09	8.64	7.91
January		91.64	92.68	8.35	7.32
N=3		89.24	92.31	10.76	7.69
	$\bar{X}$	90.75	92.36	9.25	7.64
	S	1.315	0.297	2.329	0.638
	t	1.76 n.s.			
		93.68	89.81	6.32	10.19
March		89.76	88.23	10.24	11.77
N=5		88.83	86.04	11.17	13.96
		89.33	89.25	10.67	10.75
		92.45	90.03	7.55	9.97
	$\bar{X}$	90.81	88.67	9.19	11.32
	S	2.129	1.630	2.259	2.981
	t	2.00 n.s.			

Table 14. Estimates of consumption by waterfowl at Vaucluse Shores, 1978-1979, by predominant food type.

	Daily Consumption g AFDW ind^{-1}	Mean Abundance 100 ha^{-1} (total habitat)	Annual Consumption g AFDW m^{-2}
Canada goose	193.6	284.3*	8.26
Brant	120.6	46.1	0.83
Redhead	83.3	44.2	0.55
Whistling swan	308.1	29.9	1.34
American wigeon	62.1	12.0	0.11
Pintail	73.0	2.7	0.03
Black duck	85.8	2.2	0.03
Mallard	85.8	0.3	<0.01
	Vegetation (over total habitat)		11.15 g
	(over vegetated shallows)		21.44 g
Bufflehead	40.6	46.1	0.28
Red-breasted merganser	73.0	18.9	0.21
Common goldeneye	73.0	2.2	0.02
Scaup spp.	73.0	0.9	0.01
Surf scoter	75.6	0.4	<0.01
	Invertebrates/Fish (over total habitat)		0.52 g

* Foraging geese only.

Table 15. Estimates of consumption by waterfowl at Vaucluse Shores, 1979-1980, by predominant food type.

	Daily Consumption (g AFDW ind^{-1})	Mean Abundance 100 ha^{-1} (total habitat)	Annual Consumption (g AFDW m^{-2})
Redhead	83.3	60.1	0.76
Brant	120.6	1.8	0.03
American wigeon	62.1	1.6	0.01
Whistling swan	308.1	1.5	0.07
Canada goose	195.6	0.4	0.01
Pintail	73.0	0.3	<0.01
Black duck	85.8	0.1	<0.01
	Vegetation (over total habitat)		0.88 g
	(over vegetated habitat)		1.19 g
Bufflehead	40.6	96.1	0.59
Scaup	73.0	15.0	0.17
Red-breasted merganser	73.0	3.1	0.03
Surf scoter	75.6	2.2	0.03
Horned grebe	--	0.9	<0.01
Oldsquaw	59.3	0.3	<0.01
Common goldeneye	73.0	0.3	<0.01
Common loon	--	<0.1	<0.01
	Invertebrates/Fish (over total habitat)		0.82 g
	(over vegetated habitat)		1.09 g
	(over *Zostera* only)		3.32 g

vegetated shallows are considered (approximately half the total area) the adjusted estimate for consumption of vegetation becomes 21.44 g m^{-2}. Of the total for animal material consumed by waterfowl in 1979, buffleheads and red-breasted mergansers consumed 92%, or 0.28 and 0.21 g AFDW m^{-2}, respectively.

In 1979-80, plant and animal foods were consumed in roughly equal proportions, although total consumption was an order of magnitude lower than in the previous year, reflecting primarily the absence of Canada geese. Redheads were the only important grazing species, removing 0.76 of the 0.88 g AFDW m^{-2} vegetation consumed over the entire area. Buffleheads and scaup were the only other abundant waterfowl, and together consumed 0.76 g of animal material per m^2. Consumption by all other species totalled only 0.18 g AFDW m^{-2} over all habitat zones. Because the distribution of birds within these zones was recorded consumption of plant and animal foods was also calculated over the vegetated area (for all species) and the Zostera zone (for non-grazers). Utilization of the bare sand area was negligible and thus consumption rates are higher per m^2 of vegetation than when averaged over the entire habitat. Consumption of animal foods in the Zostera zone was approximately three times the rate averaged over all zones, reflecting higher bird densities associated with Zostera.

The results of the two methods used to estimate consumption of invertebrates in Zostera marina in 1980 are compared in Table 16. The disparity between measures was greatest in January, whereas in March

Table 16. Two estimates of consumption of six important bufflehead prey species^{a} in *Zostera*, compared to the fall standing crop of these species. Values are means and standard deviations.

	TO 19 JANUARY		TO 19 MARCH		
	1^{b} gAFDW m^{-2}	2 gAFDW m^{-2}	1 gAFDW m^{-2}	2 gAFDW m^{-2}	Fall Standing Crop^{c} gAFDW m^{-2}
Crepidula convexa	0.14 ± 0.111	0.48 ± 0.674	0.30 ± 0.590	0.81 ± 0.429	2.77 ± 0.859
Pyramidellidae	0.05 ± 0.041	0.04 ± 0.052	0.11 ± 0.220	n.s.	0.01 ± 0.013
Astyris lunata	0.08 ± 0.061	0.31 ± 0.314	0.17 ± 0.324	0.28 ± 0.264	0.03 ± 0.038
Bittium varium	0.04 ± 0.028	0.03 ± 0.032	0.08 ± 0.147	0.01 ± 0.309	0.01 ± 0.010
Anadara transversa	0.05 ± 0.041	0.18 ± 0.191	0.11 ± 0.219	0.14 ± 0.197	0.30 ± 0.311
Erichsonella attenuata	0.09 ± 0.066	0.42 ± 0.517	0.18 ± 0.351	0.19 ± 0.349	0.48 ± 0.275
Cons. by buffleheads	0.45 ± 0.348		0.95 ± 1.851		
By total waterfowl^{d}	0.59 ± 0.795	1.46 ± 1.780	1.42 ± 3.617	1.43 ± 1.270	3.10 ± 1.506

---

[a] Polychaetes were not analyzed in January cage experiment, therefore *Nereis succinea* is not included.

[b] Estimate 1 = Bird Density x Daily Intake x Proportion in Diet x Days
Estimate 2 = Caged biomass - Uncaged biomass (n.s. indicates no significant difference between treatments).

[c] From abundance data (van Montfrans 1981).

[d] For estimate 1, refers to buffleheads, scaups, and scoters.

the difference was negligible. Total consumption of six important prey species amounted to approximately 1.46 g and 1.43 g AFDW m^{-2} in January and March respectively by the exclosure method. Based on calculations from bird density, buffleheads, scaup and surf scoters removed 0.59 and 1.42 g of these prey species in January and March respectively, assuming a similar diet within this habitat for all three waterfowl species. Degree of agreement varied for individual prey speceis, and was generally poorer than between combined values.

Consumption estimates calculated for March are cumulative, and should approximate total annual consumption per unit area, for comparison with the fall standing crop of the same species (Table 16). Combined ash-free dry weight biomass was approximately 3.1 g in Zostera in October/November 1979 (data from van Montfrans 1981), or about twice the amount consumed by waterfowl.

DISCUSSION

Patterns of Waterfowl Abundance

Short term fluctuations in waterfowl abundance are difficult to interpret, and may relate to changes in conditions on the breeding or wintering grounds. Absence of Canada geese from the grassbed in the second year of this study, following high abundances in 1978-79, did not simply reflect local changes in wintering populations, as aerial surveys conducted by U.S. Fish and Wildlife Service and the Virginia Commission of Game and Inland Fisheries indicated similar abundances of this species in the Eastern Shore survey zone in both years (F. Settle, pers. comm.). Large flocks of geese rafting directly offshore from the study area in 1979-80 also indicated the presence of a comparable wintering population.

The intense foraging activity exhibited by Canada geese at Vaucluse Shores in 1978-79 is presumably atypical, as the species is primarily field feeding in the Chesapeake Bay (Stewart 1962, Munro and Perry 1981). Factors which influence such short term use of submerged vegetation are not clear, but possibly reflect the availability and accessibility of SAV in a given year. It is likely that when aquatic vegetation is abundant in a localized area, geese may switch from or supplement field feeding. Grain fields on the Eastern Shore of Virginia are often adjacent or very close to beds of submerged vegetation, and thus a temporary transition would not involve a redistribution of the population. This is especially important for Canada geese, as wintering flocks are highly organized socially, and members remain strongly attached to specific feeding and resting sites (Raveling 1979).

Goose foraging may have had a negative impact on SAV in the shallows in 1978-79, discouraging utilization the following year. However, several authors report comparable or more extensive depletion of SAV by waterfowl, yet do not infer a significant impact on vegetation (Kiørboe 1980, Jacobs et al. 1981). Alternatively, Ruppia may have been less abundant in 1980 for reasons unrelated to waterfowl grazing. Comparable biomass data are not available for both years, but researchers in the area noted a visible decline in cover of Ruppia in the shallows, and low abundance of this species was also reported in other areas of the Bay in 1980 (R. J. Orth, pers. comm.). The decrease in numbers and species of non-diving waterfowl as a group in 1979-80 may also reflect depleted SAV resources in the area, as non-divers are restricted to very shallow water for feeding and as a general rule, vegetation is the principle dietary component.

The importance of the bufflehead at Vaucluse Shores in both years of this study is consistent with the findings of Perry et al. (1981) that populations of this diving duck wintering in the Chesapeake Bay appear to be stable over the short term, and have shown a long term increase in proportion to increases in the flyway as a whole. Vegetation comprises a minor portion of the diet of buffleheads, and declines in SAV have not greatly affected its abundance or distribution (Perry et al. 1981). An invertebrate diet increases the range of suitable foraging habitats available to buffleheads, and this flexibility may partially account for the relative stability of wintering populations.

Species historically more dependent on submerged vegetation, such as brant and redheads, were infrequently observed at Vaucluse Shores but were occasionally very abundant. Brant are more typically found in coastal bays rather than estuaries, and now feed primarily on sea lettuce (Ulva latuca). Within the Chesapeake Bay, brant are abundant only where large areas of Zostera still exist (Stewart 1962). Redheads still rely on submerged vegetation, and therefore have declined in the Bay in response to declines in SAV. As with brant, they are concentrated only in areas with considerable coverage of SAV, such as Tangier Sound (Perry et al. 1981). Sporadic use of the study area exhibited by these two species thus reflects a currently patchy distribution throughout the Bay. Whistling swans and wigeon were relatively important in 1978-79 but the following year were nearly absent. Both species are primarily herbivorous, but whistling swans have recently begun field-feeding and include some animal material in the diet, whereas wigeon have not greatly altered food habits (Munro and Perry 1981).

In 1978-79 water depth was found to be important in determining the periodicity (via tide stage) of foraging by Canada geese. This relationship undoubtedly results from the behavior of up-ending rather than diving to obtain food, whereby foraging is restricted to very shallow water. Palmer (1976) states that timing of feeding in brant is governed by tide stage, food being more accessible at low tide. Jacobs et al. (1981) also found a relationship between low tide and numbers of waterfowl foraging in a *Zostera noltii* bed in the Dutch Wadden Sea. The area available to non-diving waterfowl for feeding is greatly increased at low tide, especially where the depth gradient is gradual, as is characteristic of seagrass meadows.

Tide level had little effect on foraging by waterfowl in the second season of study, as the most abundant species were diving ducks, notably buffleheads, redheads and scaup. Buffleheads will feed at all stages of the tide in areas where the preferred feeding depth of 2 to 3 m is not greatly exceeded at high tide (Erskine 1971). Redheads usually feed at depths less than 2 m, including extremely shallow water where they will feed as dabbling ducks if they cannot dive (Palmer 1976). Scaup forage at comparable depths, and are affected by tide level only when feeding grounds are completely exposed at low tide, in which case they cannot feed (Cronan 1957). In the present study the only significant effect of tide on waterfowl numbers in 1979-80 occurred in the inshore *Ruppia* zone, due to the fact that the area was often exposed at low tide or covered by only a few cm of water, which effectively excluded all waterfowl. The maximum depth in the study area at high tide was approximately 2 m, which is well within the preferred range of the above species.

The range of temperatures observed had no effect on waterfowl abundance, as ice formed rarely at the study site. Open water always remained in deeper areas and therefore birds could feed throughout freezing conditions. Time of day was not an important factor influencing numbers of birds present in the study area. Buffleheads moved in and out of the study area in small groups throughout the day, and did not exhibit obvious morning flights to the feeding area typical of many waterfowl species. Johnsgard (1975) notes that, while data are few, local movements of buffleheads on the wintering grounds are probably limited.

Waterfowl generally seek shelter from severe winds, which may account for the observed correlations between wind parameters and waterfowl numbers. At most stages of the tide, the sandbar which encloses the grassbed acts as a buffer to wave action, especially when winds fetch across or down the bay. Shoaling is more extensive at the extensive at the northern end and thus the sandbar offers more protection from NNW winds than from winds with a more westerly component. When winds are from the east or northeast, the entire western shore of the peninsula is equally protected and the study area offers no additional shelter. The presence of greater numbers of birds during strong NNW winds therefore reflects the orientation of the study area and the configuration of the protective sandbar.

Variation in bird density within the habitat in 1979-80 may be related to several factors. Densities were greatest in the *Zostera* zone, which approximates the preferred feeding depth of buffleheads (Erskine 1971) and is also the vegetated area farthest from shore. Avoidance of the inshore sand and *Ruppia* zones can be partially explained in similar terms in that these areas are very shallow and close to shore. Availability of food may be a more important factor. Abundances of epifaunal invertebrates were much lower in *Ruppia* than in the mixed and *Zostera* zones (van Montfrans 1981), possibly due to the shorter growth form and narrower blade width of *Ruppia*, and also its patchy distribution within the grassbed. The bare sand zone contained even lower numbers of invertebrates, with very few species of importance to foraging waterfowl. Nilsson (1969) also found that diving ducks in the Oresund fed over dense *Zostera marina* in preference to mixed areas with patchy cover, and that food resources were less abundant in the latter zones.

Bufflehead Food Habits

The importance of invertebrates in the diet of buffleheads is well documented, and small molluscs and crustaceans are the dominant prey in salt water habitats. Weimeyer (1967) found that buffleheads in the Humboldt Bay region fed primarily on bivalves, crustaceans, fish and gastropods and that the relative contribution of these groups varied between habitats. Erskine (1971) also emphasized the importance of crustaceans (mostly decapods and isopods) and molluscs as bufflehead foods on the wintering grounds. Nereid worms and bryozoans were cited as minor components of the diet. In these and other general accounts of bufflehead food habits (Cottam 1939, Stewart 1962, Munro and Perry 1981), diversity of food items is high, whereas Stott and Olson (1973) found that on the New Hampshire coast, sand shrimp (*Crangon septemspinosa*) comprised 75% of the diet of buffleheads.

Bufflehead gizzard contents analyzed in this study were dominated by species which are also abundant members of the epifaunal communities associated with *Ruppia* and *Zostera*, such as *Crepidula convexa* and *Nereis succinia*, suggesting that buffleheads rely heavily on commonly encountered animals. This agrees with the findings of Madsen (1954), who maintained that the diet of most diving duck species reflects the availability of prey. Stott and Olson (1973) also reported a close relationship between foods utilized by sea ducks and the abundance of these foods in preferred habitats. However, buffleheads in this study exhibited a degree of apparent electivity, with several species eaten in numbers disproportionate to their relative environmental abundances. Foraging behavior in buffleheads is probably similar to the closely related goldeneye (*Bucephala clangula*), which takes food items singly with a forceps action of the bill (Pehrsson 1976). Prey selection is enhanced by such a strategy and is limited only by bill morphology, visual acuity, and energy cost. A major difficulty in demonstrating electivity is that the relationship between numerical abundance and ecological availability is often unknown. Madsen (1954) stated further that among available (i.e. abundant) food items, the most easily obtainable within size limits are preferred. Thus positive selection may indicate real preference or degrees of availability, and for this reason the term apparent electivity is used.

Crepidula convexa was the only species which was apparently selected against by foraging buffleheads, although it was still the dominant prey item. This dark-shelled species lives attached to vegetation or hard substrates which, combined with the extremely small size of overwintering individuals (less than 2 mm average), may make it difficult to collect. Alternatively, some gastropods may move into the rhizome layer in the winter when above-ground vegetation is reduced (Marsh 1976), and may be encountered infrequently rather than avoided by diving ducks.

The gastropod Bittium varium is also dark in color, but is not firmly attached to vegetation and is conical in shape. It should therefore be more easily removed from blades by predators, although size in winter is comparable to Crepidula convexa individuals. The dove shell Astyris lunata and the bivalve Anadara transversa are larger (3-5 mm) and therefore more visible, which could explain the greater importance of these species in the diet relative to environmental abundances. Selection of pyramidellid gastropods is difficult to reconcile with the minute size of individuals (1.6 mm average) and the translucent nature of the shell. However, species of the genus Odostomia are reported to be ectoparasitic on other invertebrates, notably B. varium (Hyman 1967), and this association should increase availability.

Electivity studies inherently assume that the predator has fed in the same area where samples of prey abundance are taken. Because waterfowl are highly mobile, this may not always be true. In the present study, the presence of Ruppia and Zostera fragments in gizzard samples, as well as epifauna characteristic of the habitat, suggest that birds had fed either in the study area or in similar vegetated habitats.

Carbon isotope analysis also indicated the importance of SAV-associated invertebrates in the bufflehead diet. The difference between the mean $\delta^{13}C$ value for bufflehead liver tissue and that predicted from mean composition of gizzard contents and prey $\delta^{13}C$ values was within the 1-2 $^{o}/oo$ variation typically reported for such comparisons. However, the departure was in the negative direction whereas the shift is usually positive, resulting from metabolic processes which conserve ^{13}C (De Niro and Epstein 1978). It is likely that gizzard data used in this study to predict $\delta^{13}C$ values did not accurately reflect the diet, due to inadequate sample size or differential digestion of prey items. Gizzard analyses appear to have underestimated the nutritional contribution of species with more negative $\delta^{13}C$ values (primarily suspension feeders) rather than the softer-bodied polychaetes and crustaceans which had higher $\delta^{13}C$ values. Barnacles and bryozoans may account for most of the discrepancy, as these filter feeders were frequently eaten, but because only shell fragments remained in the gizzard, proportional contribution to total $\delta^{13}C$ could not be calculated.

Intraspecific variability in bufflehead $\delta^{13}C$ values (3.2 $^{o}/oo$ range) exceeded that suggested by Fry et al. (1978) for animals having the same diet (<1.6 $^{o}/oo$). However, the low standard deviation obtained suggests that individuals did not vary widely in food habits, at least with respect to broad trophic groups. The greater variability in $\delta^{13}C$ values of food items and species composition of gizzard contents emphasizes the value of time-integrated data when describing food habits of species with highly mixed diets.

$\delta^{13}C$ analysis confirmed the minor role of submerged vegetation in the diet of buffleheads and most other waterfowl sampled. With few exceptions, waterfowl values were several parts per mil lower than those for *Zostera* and *Ruppia*, with considerable overlap between species having known preferences for vegetation (Canada geese, wigeon, pintails, black ducks) and the remaining species which rely more on animal foods. It is likely that terrestrial sources (especially agricultural grains such as corn and wheat) provide a large portion of vegetation eaten by Canada geese and possibly black ducks, as these plants are highly negative in $\delta^{13}C$ values (De Niro and Epstein 1978). Slightly more positive values exhibited by wigeon and pintails suggest a more substantial contribution by aquatic vegetation. Values for species with predominately animal diets were generally more negative than those for buffleheads, implying greater importance of suspension feeders or planktivorous fish.

Waterfowl Consumption Estimates

Submerged vegetation was an important resource for wintering waterfowl (primarily Canada geese) at Vaucluse Shores in 1978-79. If 80 g AFDW m^{-2} is considered a maximum early winter biomass value for *Ruppia* and stands of mixed *Ruppia* and *Zostera*, (R. J. Orth, unpubl.

data) then waterfowl removed 25% of the standing crop in shallow water at the study site. A comparison of this estimate with those from other studies is attempted in Table 17, by standardizing all reported values to percentages of standing crop biomass, and restricting examples to studies conducted in the non-growing season. From these data, it is evident that the impact of waterfowl grazing varies widely among habitats and with waterfowl species composition and density. At Vaucluse Shores, grazing pressure was moderate in 1978-79 and minimal the following year, relative to previous estimates.

Apart from variable research conditions, a major difficulty with such comparisons is that consumption is often averaged over a large area, ignoring within-habitat variations in resource use. Jacobs et al. (1981) found that grazing pressure by geese and wigeon was not uniform in *Zostera noltii*, and was directly proportional to initial percent cover of vegetation. In the present study, bird densities, and therefore consumption rates, were much higher in the vegetated area than in the total habitat. Foraging by Canada geese was restricted to the shallows, further increasing consumption estimates in those areas. Variable consumption rates within a given habitat have also been reported for wading birds (Wolff et al. 1975) and diving ducks (Nilsson 1969), emphasizing the need to partition consumption within a habitat before attempting to estimate impact on benthic communities.

The results of exclosure experiments carried out in 1979-80 suggest that waterfowl had a significant effect on the abundances of a

Table 17. Reported or calculated estimates of waterfowl grazing pressure (% of standing crop consumed) in SAV habitats.

References	Habitat and Location	Estimated Grazing Pressure
Ranwell and Downing (1959)	*Zostera nana* *Zostera hornemanniana* Scolt Head Is., England	30-75%
Sincock (1962)	Submerged Aquatics Back Bay, VA and Currituck Sound, NC	20%
Steiglitz (1966)	*Halodule wrightii* *Ruppia maritima* Apalachee Bay, FL	32%
Cornelius (1977)	*Halodule beaudettei* Laguna Madre, TX	4%
Jupp and Spence (1977)	*Potamogeton* spp. Loch Leven, Scotland	13%
Verhoeven (1978)	*Ruppia cirrhosa* Texel, Netherlands	21%
Kiørboe (1980)	Submerged Aquatics Ringkøbing Fjord, Denmark	50%
Jacobs et al. (1981)	*Zostera noltii* Dutch Wadden Sea	50%
Wilkins (1982) (This study)	*Ruppia maritima* *Zostera marina* Chesapeake Bay, VA	25%

number of invertebrate species in the Zostera zone. By 19 March, when exclosures were removed, both estimates indicated a consumption of nearly 50% of the combined ash-free dry weight standing crop of six important bufflehead prey species. Qualitative agreement was obtained between the results of caging experiments and bufflehead gizzard analyses, in that species most affected were also important prey items. However, caging results obtained in January are diffcult to interpret on the basis of waterfowl foraging alone, with respect to these dominant prey species. Consumption calculated from exclosure samples was much higher than that based on bird density, and was within 0.03 g of the estimate for March. Waterfowl densities were comparable over the two intervals, and one would expect an increased difference between treatments in proportion to the number of days between sampling periods.

In studies where cages are used to exclude predators, the possibility of an artificial cage effect must always be considered. Larval settlement is enhanced by the current-baffling effect of the cage structure, and has been a major problem in previous caging experiments in soft-bottom habitats (Virnstein 1981). This effect was not demonstrated by sediment analyses in this study, although pipette analysis may not have detected slight changes in the silt and clay fractions. Increased sedimentation would have been expected from the degree of fouling that reduced the effective mesh size of the cages. In this habitat, however, few invertebrates which were significantly more abundant inside exclosures have free-swimming larval stages, and recruitment should not be affected by current velocity. Crepidula *convexa* exhibits direct development of larvae, with individuals hatched as juvenile snails (Ament 1979). The same is probably true for the gastropod *Astyris lunata*, and peracarid crustaceans are known brooders (Barnes 1980).

The prosobranch gastropod *Bittium varium* has a planktonic veliger larva, as does the bivalve *Anadara transversa*, but it is unclear whether reproduction continues into the fall. Marsh (1970) reported egg masses of *B. varium* in May and June in a *Zostera* bed in the lower York River, with juveniles predominant through the late summer and fall. Newly set individuals (0.5-0.7 mm) were not found in field collections at Vaucluse Shores in September 1979 (J. Lunz, pers. comm.) although bufflehead gizzard samples contained some individuals less than 1.0 mm. Information on the reproductive cycle of *A. transversa* was not available, but Marsh (1970) reported peak densities in August possibly indicating larval settlement. High densities of these two species may be related to the effect of the cage structure, but only if recruitment occurred after mid-October when exclosure experiments began. The high abundances of *Mytilus* juveniles in caged samples in March was almost certainly induced by the cage structure, as planktonic larvae are produced in early spring in the Chesapeake Bay, and *Mytilus* was not recorded in gizzard contents. The reverse trend for *Ilyanassa obsoleta* (higher numbers outside cages) may also be an artifact of the experiment, as *I. obsoleta* are attracted to artificial structures in order to deposit egg capsules and would therefore be found at the edges of the cages rather than in the sampled area (R. Orth pers. comm.).

The above comparisons between estimates of waterfowl consumption are made with caution, as confidence intervals on each estimate are very broad and many assumptions are involved in calculations. However, 1979-80 data suggest a range of values for annual consumption of invertebrates of approximately 2-3 g ash-free dry weight m^{-2} in Zostera marina, with lower values for the total habitat.

Few previous studies provide comparable estimates of the impact of waterfowl on invertebrates. Nilsson (1969) calculated that diving ducks consumed 9% of the total standing crop of invertebrates, or 22 g fresh weight m^{-2}, in the most heavily utilized part of the habitat. If this quantity is converted to ash-free dry weight and only the standing crop of prey species considered, the resulting values would probably be within the range obtained in this study.

Consumption by waterfowl at Vaucluse Shores was undoubtedly low relative to total standing crop biomass and annual production of invertebrates, but it was shown that significant cropping of dominant prey species occurred. Given the predominance of very small food items in the diet of buffleheads, this habitat represents an optimal feeding ground for the species, as the density and diversity of invertebrates are higher than in unvegetated areas. This research suggests that the interaction between waterfowl and the benthic fauna of SAV ecosystems is of greater trophic importance than has been previously recognized. Further long-term studies are required to more clearly define the role of non-grazing waterfowl in SAV habitats, and to determine and interpret patterns of direct utilization of submerged vegetation by grazing species.

SUMMARY

1. Canada geese were the dominant waterfowl at Vaucluse Shores in 1978-79, averaging 526 birds per 100 ha. Foraging by this species was influenced by tide level, with greatest activity around low tide. An estimated 21.4 g AFDW m^{-2} of vegetation was removed by grazing waterfowl during the season, if bird density calculations are based on shallow vegetated areas. This represents approximately 25% of the estimated fall standing crop of vegetation.

2. The following year (1979-80), the waterfowl community in the study area was dominated by diving ducks, primarily buffleheads. Canada geese and other non-diving species were nearly absent, although local wintering populations were much the same size as in the previous year. Reasons for this marked contrast are unclear, but intense grazing in 1978-79 may have reduced the availability of vegetation in the shallows, or a decline in *Ruppia* biomass unrelated to waterfowl activity may have discouraged foraging in the study area in 1979-80.

3. In 1979-80, daily patterns of waterfowl abundance were influenced by wind parameters, whereas tide level, temperature, and time of day had little or no effect.

4. Differential waterfowl use of areas within the SAV habitat was found to occur in the 1979-80. Bird densities were greatest in

the *Zostera* and mixed vegetation zones, and minimal in *Ruppia* and bare sand areas. The latter areas are very shallow and contain lower densities of invertebrates, and would therefore be less attractive to foraging buffleheads.

5. Bufflehead gizzard analyses indicated the importance of small gastropods such as *Crepidula convexa*, peracaridan crustaceans such as *Erichsonella attenuata* and the polychaete *Nereis succinea* in the diet of this diving duck. Predominant food items were also abundant members of the grassbed epifauna, although some evidence for selectivity was found. Carbon isotope analysis generally supported conclusions regarding bufflehead diet. Variability in bufflehead $\delta^{13}C$ values was low compared to the range obtained for food items, indicating a similar diet among individuals. These analyses confirmed the minor role of submerged vegetation as a direct food source for buffleheads and other waterfowl in the area in 1979-80.

6. Exclosure experiments yielded estimates of consumption of invertebrates which compared well with calculations based on bird density in March, and annual consumption in *Zostera* was estimated at 2-3 g AFDW m^{-2}. Approximately 50% of the fall standing crop of six important prey species was removed by foraging waterfowl in 1979-80.

7. These data suggest that waterfowl foraging may be an important, if unpredictable, component of energy flow in SAV habitats in winter

months, both from direct consumption of vegetation and predation on associated epifaunal invertebrates.

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