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Abstract: We present a model for calculating energy-based carrying capacities for bufflehead (*Bucephala albeola*), a small North American sea duck wintering in coastal and estuarine habitats. Our model uses estimates of the seasonal energy expenditures that incorporate site-specific energetic costs of thermoregulation, along with available prey energy densities to calculate carrying capacities in numbers of birds per winter. The model was used to calculate carrying capacities under several foraging scenarios for bufflehead wintering at three urban and three rural sites in the coastal northeast U.S. We found that energy-based carrying capacities varied from 20 – 320 birds per site per winter (0.38 – 6.22 birds per hectare), and showed a trend towards increasing with prey energy density ($r = 0.53$) and with decreasing average daily energy expenditure ($r^2 = 0.57$, $p = 0.08$). We found greater prey species richness at rural sites, but similar prey biomass and productivity across all sites. Bufflehead density averaged 1.89 ± 2.34 birds per hectare (range 0.38 – 6.22 birds per hectare) across the sites. Bufflehead abundance at urban sites was reduced by an average of 43.7% from that predicted using the relationship between per-hectare carrying capacity and bufflehead abundance at rural sites. This difference may arise from natural or human induced factors that act to limit sea duck populations on wintering habitats.

Keywords: Bufflehead *Bucephala albeola,* Energy-based carrying capacity, Habitat alteration, Narragansett Bay, Wintering waterfowl.

INTRODUCTION

Sea ducks (Anseriformes: Anatidae, tribe Mergini) are a guild of species that breed in northern latitudes and winter primarily in marine habitats. Fifteen sea duck species inhabit North America, and there is currently concern about the conservation status of these species, many of which have shown declines in recent years [1]. While information is needed to help guide conservation efforts little is known of the ecology of North American sea ducks and information is particularly lacking on their wintering habitats. In this study, we develop a model to assess energy-based carrying capacities of sea duck winter habitats using as a model species bufflehead (*Bucephala albeola*), a small sea duck that winters in estuarine habitats in the northeast United States. Information on wintering habitats can help guide management and restoration efforts to support sea duck populations.

The energy-based carrying capacity of a habitat reflects both the energy demands of resident species and the abundance and energy density of their food. These carrying capacities integrate the energetic consequences of the consumption of multiple prey types with differing energy densities and may therefore be particularly useful when the food intake rates of resident populations are not well known, for example for omnivores or species that primarily consume animal material [2,3]. Insights gained from energy-based carrying capacities may help to determine if a population is food-limited in a given habitat, demonstrate the effects of changes in food abundance or quality, and provide insights into the management of habitats for wintering waterfowl populations. In addition, they can provide resource managers with important information for managing wildlife populations and may ultimately lend insights into the effects of human disturbance and habitat degradation on resident species.

A number of theoretical and empirical studies have focused on developing energy-based carrying capacities for ungulates and domestic livestock [4-7]. Recently, this concept has been extended to gallinaceous birds [8]. While assessments of waterfowl habitat carrying capacity for herbivorous or granivorous species often incorporate estimates of true metabolizable energy of vegetation [9-12], there is a lack of information on energy-based carrying capacities for omnivorous waterfowl such as diving ducks (Aythyini) or sea ducks (Mergini). In this study we use measures of the productivity of benthic invertebrate prey and estimates of waterfowl daily energy expenditure to develop energy-based carrying capacities for bufflehead (*Bucephala albeola*), a small sea duck that winters in estuarine habitats in the northeast United States. Particularly on their wintering grounds, bufflehead feed primarily on benthic invertebrates such as crustaceans and mollusks [13-15]. This allows us to use measured abundances of invertebrate prey, published models that link biomass to productivity [16], and energy density values of benthic organisms to estimate the available energy for bufflehead populations at specific habitats.

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We report energy-based carrying capacities for bufflehead wintering at six sites in Narragansett Bay, RI under several foraging scenarios (consumption of all available crustaceans and mollusks, consumption of crustaceans and mollusks in proportion to their abundance at the sites, and consumption of crustaceans and mollusks in proportion to previously reported food habits). To calculate site-specific energy-based carrying capacities, we develop estimates of the seasonal energy expenditures of bufflehead using an activity-based energy expenditure model that incorporates site-specific energetic costs of thermoregulation. We then combine these data with available energy from prey to develop estimates of carrying capacity based on the availability and demand for food energy for six wintering habitats of varying area and prey abundance. Our specific objectives are i) to examine habitat differences and possible environmental and behavioral factors that may be influencing carrying capacity, and ii) to use measured abundances of bufflehead at the habitats to demonstrate how energy-based carrying capacities can be used to assess waterfowl habitat and provide a basis for quantifying differences in bufflehead use of urban and rural habitats.

MATERIALS AND METHODOLOGY

Study Area

Our study sites were six bufflehead wintering sites that are well-defined coves or embayments within the Narragansett Bay estuary. Included were three shallow coves located in near urban centers and had greater than 25% (average 50.1% ± 15.6) residential and commercial land-use within a 200 m radius of their shoreline (Apponaug Cove, Brush Neck Cove, and Watchemoket Cove; Fig. **1**), and those we categorized as urban sites. Three embayments (Coggeshall Cove, Sheffield Cove, and Mackerel Cove) were surrounded by predominantly natural vegetation and sparsely developed lands. These areas averaged 3.0% ± 0.1 residential and commercial land-use within a 200 m radius of their shoreline, and were categorized as rural sites. Cove areas ranged from 18.6 - 86.1 ha, with an average of 42.2 ha.

Daily and Seasonal Energy Expenditure

Estimates of daily and seasonal energy expenditure were developed for each of the sites using an activity-based model described elsewhere [17]. The model incorporates site-specific thermoregulatory costs into estimates of daily energy expenditure (DEE) and consists of i) an estimate of basal metabolic rate (BMR), ii) an estimate of the metabolic heat production required to balance heat loss from the bird to the environment through conduction and convection, and iii) an estimate of the energetic costs of the specific daily activities of wintering bufflehead. These three components are summed to arrive at an estimate of DEE, which we then scale to a seasonal energy expenditure by multiplying by an estimate of the number of days that birds are resident on the wintering grounds (150). The model uses average temperatures and wind speeds at the sites, and can therefore be used to generate DEE for multiple time scales; we report both 24 hour and seasonal energy expenditures. We used an allometric relation derived from BMR reported for 18 North American waterfowl species and summarized in McNab [18] to estimate bufflehead BMR. Wind speeds and temperatures at each of the study sites were obtained from a National Oceanographic and Atmospheric Administration (NOAA) weather buoy located near the center of Narragansett Bay (http://www.co-ops.nos.noaa.gov/PORTS_Archives/PORTS _Data Hist.html) that generated wind speeds and temperatures every six minutes throughout the winter. These data were then corrected for site-specific differences by periodically measuring wind speeds and temperatures at each of the sites coincident with the NOAA buoy data. This was accomplished using an apparatus designed to float on the surface of the water consisting of a wing gauge and temperature sensor connected to a remote data logger (Hobo Corp., Onset, MA USA). Local data were then used to develop site-specific correction factors for temperature and wind speed.

Estimates of the energetic costs of physical activity were developed from bufflehead time-activity budgets obtained from each of the study sites. We used focal animal sampling to quantify behavior and activity of bufflehead during the winters of 2001-2002 and 2002-2003 [19,20]. A total of 965 observations were completed on individual birds resulting in over 80 hours of activity budget data. Observations were randomly distributed over sample sites and time of day throughout the winter period when ducks were present (November through March). Activity data were recorded using an observational software program installed on a laptop computer (J Watcher, Animal Behavior Laboratory, Macquarie University, Australia). Individual ducks were chosen at random and observed through a 32-60 x spotting scope or through 10 x 50 binoculars for 5 minutes, and behaviors were categorized as dive, surface, look (i.e., peering through the water at the cove bottom), courtship, agonistic, swim, fly, preen, alert, and rest. Gender for each individual was identified when possible. Energetic costs of each activity were calculated as multiples of BMR using published conversion factors [21-24]. Data were averaged across the entire period when ducks were present (November – April). Since our estimates were generated using diurnal measures of bufflehead activity, DEE values would tend to underestimate energy expenditure if birds were engaging in any nocturnal activity at the sites. Details of DEE calculations are provided in Appendix **1**. We used simple linear regression analysis to investigate the relationship between bufflehead abundance and energy-based carrying capacity.

Benthic Prey Analysis

We used grab sampling to measure the abundance of benthic invertebrates at each site. Sub-tidal sample locations within the sites were chosen at random using a probability-based random sampling protocol [25]. A total of ten samples were obtained from each site using a Ponar grab sampler, which samples the sediment surface down to a depth of 2-5 cm. Samples were passed through a 0.5 mm sieve and immediately sorted, counted, and measured. Abundances were calculated as the average of ten grabs. Biomass of available soft tissue for each prey species in grams of tissue wet weight per m^2 was calculated using existing allometric length-weight relationships [26]. We calculated productivity at each site using known productivity to biomass relationships [27], and used these values along with species-specific

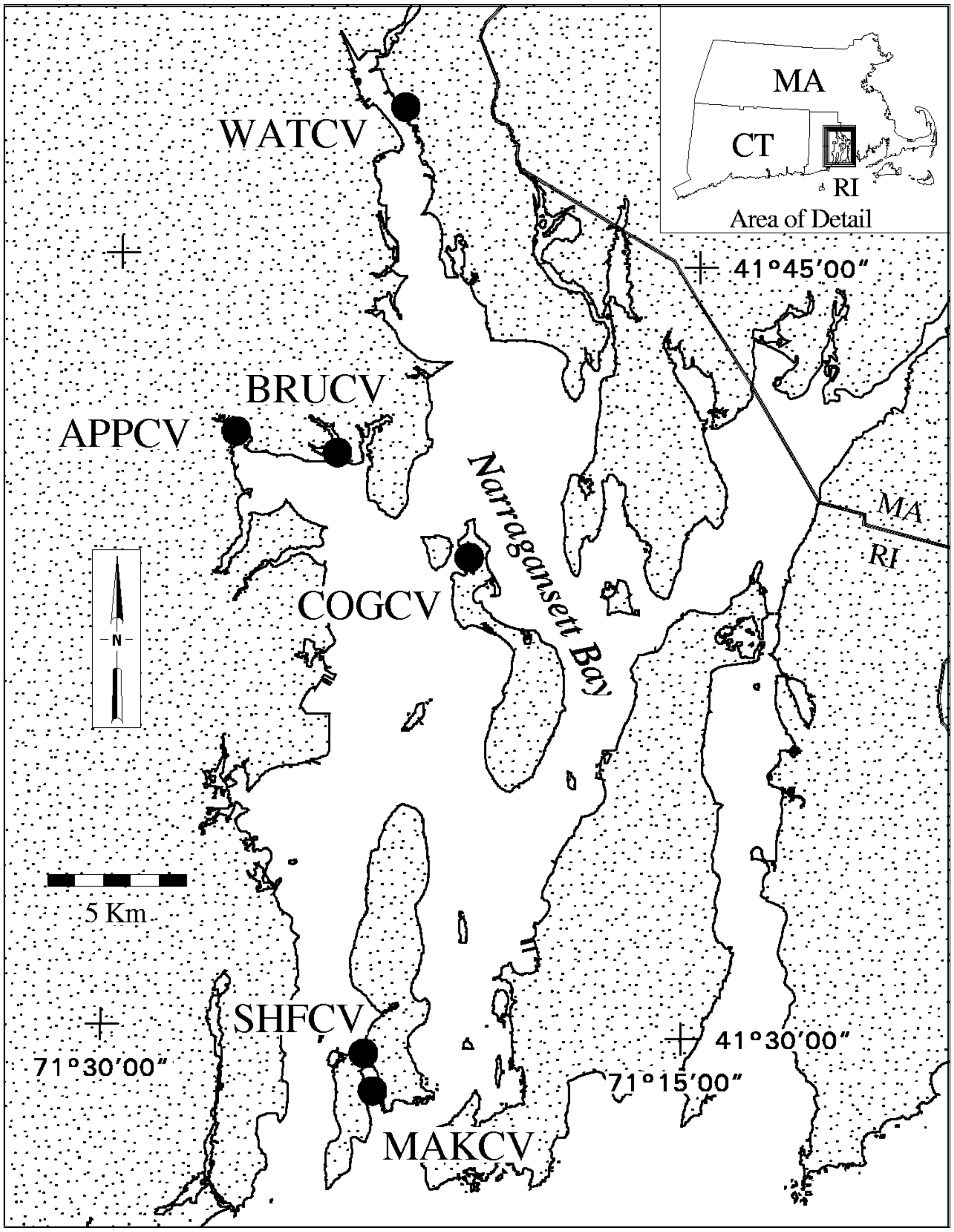

Fig. (1). Location of study sites in Narragansett Bay, RI. APPCV = Apponaug Cove, BRUCV = Brush Neck Cove, COGCV = Coggeshall Cove, MAKCV = Mackerel Cove, SHFCV = Sheffield Cove, WATCV = Watchemoket Cove.

tissue energy densities to estimate the energy density at the sites in kcal per m^2 [26,28,29].

Energy-Based Carrying Capacities

Energy-based carrying capacities were estimated by first calculating the energy density of relevant prey (for bufflehead, crustaceans and molluscs; [15]), multiplying energy density of prey by habitat size to arrive at the total available energy, and then dividing total available energy by the required average site-specific energy expenditure of a bufflehead during the winter. We developed estimates for three foraging scenarios: i) assuming that all available prey (crustaceans and molluscs) were entirely consumed, ii) assuming that prey were consumed in proportion to their abundance at the sites (e.g., Brush Neck Cove, 87.8% molluscs, 12.2% crustaceans), and iii) assuming that bufflehead consumed prey in proportion to previously reported food habits (22.6% molluscs, 77.4% crustaceans; [13-15]). For scenarios ii) and iii), the total available energy was determined by the limiting prey, which in the case of energy-based carrying capacity based on food abundance was usually mollusks, and for food habits crustaceans. There was therefore residual, unused energy at the sites for each of these limiting scenarios versus the scenario involving total consumption of available prey.

Bufflehead Abundance

Census data were collected using instantaneous scan sampling during which the number, species, and if possible gender of waterfowl present at the sites was recorded [19, 20]. Bimonthly censuses at each site were performed on randomly chosen days and at randomly chosen times of day. Bufflehead abundances were calculated by averaging data from November through March of both years.

Landscape Characteristics

Sites were categorized using land use within a 200 m radius of the shoreline of each site delineated with 15 minute (1:24,000) scale United States Geological Survey topographic maps. Then geographic information system (GIS) data (e.g., land use and land cover) obtained from the Rhode Island Geographic Information System were overlaid and used to calculate the proportion of land use within each zone. Data were processed using Environmental Systems Research Institute ARC GIS software (Redlands, CA). To categorize the sites, we assessed the proportion of residential development at a density greater than two houses per hectare and all commercial and industrial development within the zone.

RESULTS

Daily and Seasonal Energy Expenditure

Daily energy expenditures for bufflehead were higher in mid-winter that in early or late winter across all sites for both males and females (males: $t_5 = 2.26$, $p = 0.004$, females $t_5 = 2.31$, $p = 0.01$; Table **1**). Seasonal changes in DEE generally tracked changes in the average monthly temperature (Fig. **2**), but there were also differences in DEE between sites. Overall DEE at the sites ranged from 199 – 227 kcal day^{-1}, and there were no significant differences in DEE between males and females. Bufflehead at Apponaug Cove and Brush Neck Cove consistently had the lowest DEE, and those at Coggeshall Cove the highest. Average corrected wind speeds ranged from 2.6 – 5.2 m sec^{-1}, and were lowest for Apponaug and Brush Neck coves and highest for Coggeshall Cove (Table **1**).

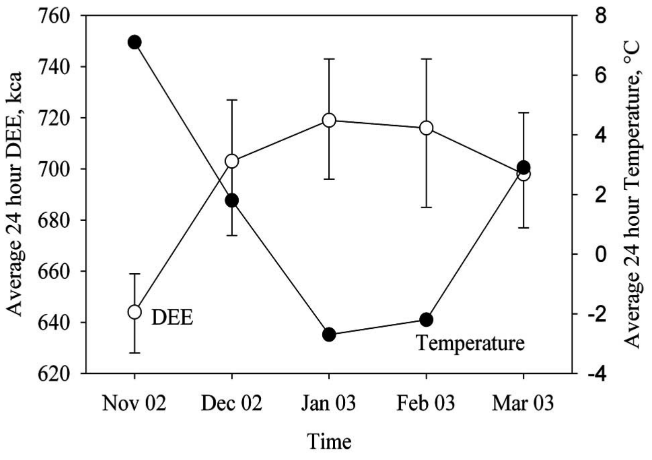

Fig. (2). Average 24 hr temperature and daily energy expenditure (DEE, kcal) of bufflehead wintering at Apponaug Cove from November, 2002 to March 2003.

Table 1. a) Average Corrected Wind Speed and b) Average (± SE) 24 hour daily energy expenditures (DEE, kcal day-1) for bufflehead wintering at six Narragansett Bay sites during the winters of 2001 -2002 and 2002 - 2003

a)

	Corrected Wind Speed, m sec^{-1}		
Study Site	**Early**[a]	**Mid**	**Late**
Apponaug Cove	2.6	2.3	2.9
Brush Neck Cove	2.6	2.5	2.8
Watchemoket Cove	3.0	2.8	3.1
Coggeshal Cove	5.2	5.1	5.3
Mackeral Cove	5.0	4.8	5.2
Sheffield Cove	5.1	4.8	2.8

[a] Early = November - December, Mid = January - February, Late = March – April

b)

	Daily Energy Expenditure, kcal day^{-1}		
Study Site	**Early**	**Mid**	**Late**
Apponaug Cove	190 ± 0.3	208 ± 2.3	199 ± 7.1
Brush Neck Cove	189 ± 4.7	208 ± 0.02	203 ± 2.4
Watchemoket Cove	202 ± 3.8	222 ± 1.7	210 ± 1.14
Coggeshal Cove	208 ± 2.1	241 ± 7.1	232 ± 2.3
Mackeral Cove	208 ± 2.2	224 ± 4.9	213 ± 7.0
Sheffield Cove	201 ± 1.3	229 ± 4.1	215 ± 1.5

[a] Early = November - December, Mid = January - February, Late = March – April

Benthic Prey Analysis

We identified 27 species of benthic invertebrates at the sites, including 7 polychaete, 10 mollusc, and 10 crustacean species (Appendix **2**). The rural sites (Coggeshall Cove, Sheffield Cove, and Mackerel Cove) had higher species richness (11.3 ± 3.3 versus 6.7 ± 2.7; $t_3 = 2.13$, $p = 0.03$) than the urban sites (Apponaug Cove, Brush Neck Cove, Watchemoket Cove), but similar overall average productivity. Prey energy density estimates for crustaceans and mollusks ranged from 8.16 – 22.2 kcal m^{-2}, and did not vary significantly with site area (Table **2**). Overall, the available energy from prey at a site increased almost 5-fold from 211 to 958 kcal, and estimated bufflehead energy expenditures showed a trend towards decreasing as available prey energy increased ($r^2 = 0.31$, $p = 0.24$).

Energy-Based Carrying Capacities

Energy-based carrying capacity (carrying capacity hereafter) ranged from 0.84 – 5.92 birds ha^{-1} $winter^{-1}$across the sites and for each foraging scenario was lowest at Sheffield Cove and highest at Brush Neck Cove (Table **2**). Carrying capacity based on consumption of prey in proportion to relative abundance at the sites (food abundance) was similar to that based on total consumption of all available mollusk and crustacean prey (mollusk and crustacean abundance), and averaged 2-times higher than that based on consumption of prey in proportion to previous bufflehead

Table 2. Prey Energy Density of Mollusks and Crustaceans (± SE) and Energy-Based Carrying Capacities Based on Mollusk and Crustacean Abundance for Bufflehead Wintering at Six Narragansett Bay sites

	Prey Energy	**Energy-Based Carrying**
Study Site	**Density (kcal m^{-2})**	**Capacity (Birds ha^{-1}winter^{-1})**
Apponaug Cove	14.1 ± 6.1	3.42 ± 2.16
Brush Neck Cove	19.1 ± 9.8	4.46 ± 2.74
Watchemoket Cove	19.6 ± 11.4	4.80 ± 3.24
Coggeshal Cove	22.2 ± 12.8	9.86 ± 6.58
Mackeral Cove	9.92 ± 5.24	0.91 ± 0.55
Sheffield Cove	8.16 ± 5.20	4.39 ± 3.15

food habits (Fig. **3**). Carrying capacity based on the proportion of food abundance was correlated both with carrying capacity based on food habits ($r^2 = 0.72$, $p = 0.03$) and based on all available prey ($r^2 = 0.58$, $p = 0.08$). Energy expenditure increased with increasing average wind speed ($r^2 = 0.75$, $p = 0.03$).

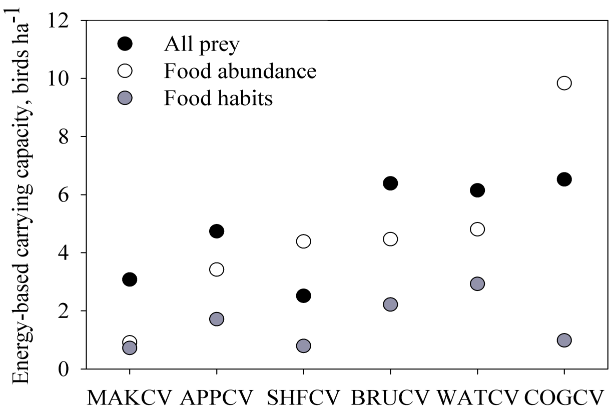

Fig. (3). Energy-based carrying capacities in kcal per site assuming: i) all prey (crustacea and mollusca) are totally consumed, ii) prey are consumed in proportion to their abundance, and iii) prey are consumed in proportion to previously reported bufflehead food preferences. Standard deviations have been omitted for clarity and can be found in Table **2**.

Bufflehead Abundance *vs.* Carrying Capacity

Bufflehead density averaged 1.89 ± 2.34 birds per hectare and ranged from 0.38 – 6.22 birds per hectare. Carrying capacity based on mollusk and crustacean abundance averaged 8 times greater than bufflehead abundance across sites.

We saw a difference in the average carrying capacity based on mollusk and crustacean abundance between urban (4.23 ± 0.72 birds ha^{-1} winter^{-1}) and rural (5.06 ± 4.51 birds per winter) sites. There was also a difference in the magnitude of the difference between carrying capacity and bufflehead abundance at urban (average 10.2 times abundance) versus rural (average 3.5 times abundance) sites. Carrying capacity based on mollusk and crustacean abundance expressed on a per hectare basis was strongly associated with bufflehead density for rural ($r^2 = 0.99$, $p = 0.007$; Fig. **4**) but not for urban sites. Bufflehead density at urban sites was lower by an average of 43.7% from that which would have been predicted using the relationship between per-hectare carrying capacity and bufflehead abundance at rural sites (Density = 6.0 x (per-hectare carrying capacity) + 0.8).

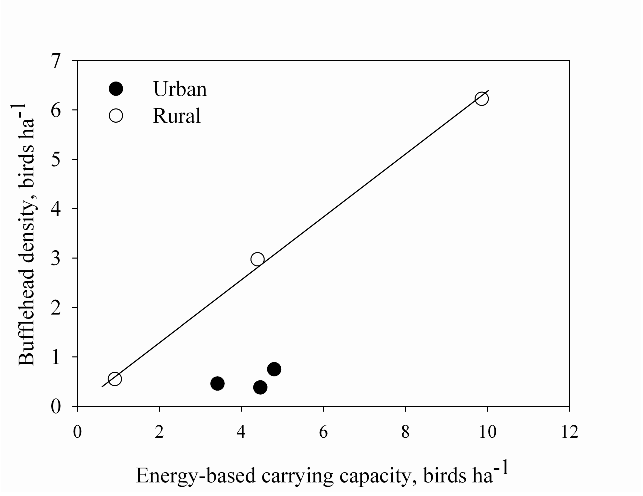

Fig. (4). Wintering bufflehead density in birds per hectare versus per hectare carrying capacity based on mollusk and crustacean abundance for urban and rural habitats in Narragansett Bay. Standard deviations have been omitted for clarity and can be found in Table **2**.

DISCUSSION

We saw differences in the range and magnitude of carrying capacities derived under the different feeding scenarios, but the values calculated using all three prey consumption scenarios were correlated. Previous studies have shown that wintering bufflehead in coastal habitats eat primarily crustaceans and mollusks [13-15], and this along with the finding that polychaetes averaged less than 2% of the available prey density at our sites led us to consider only crustaceans and mollusks when calculating carrying capacities for different feeding scenarios. Birds have been shown to maximize foraging efficiency by shifting to the consumption of more common or regularly distributed foods, even if the energy required in processing of these foods is high [30,31]. Molluscs, and particularly gastropods, were more abundant at our sites, followed by crustaceans. Assuming that bufflehead would attempt to maximize foraging efficiency by minimizing foraging effort, and taking into account a previous study of bufflehead food habits where consumption reflected relative abundance of prey species at a habitat [14], we predicted the predominance of mollusks at the sites should be reflected in bufflehead diets [32-34]. We therefore felt that the carrying capacities developed using the abundance of mollusks and crustaceans at our sites would best represent bufflehead feeding patterns at our sites, and for the balance of this discussion we use these values in comparisons between sites.

Per hectare carrying capacity increased by a facto of ten across our study sites. We would predict an increase in carrying capacity with increasing prey energy density and with decreasing DEE. However, these factors are not independent and will act in concert to determine a habitat's carrying capacity, so it may be difficult to determine which is driving observed differences. Carrying capacity did not vary with site area at our sites, but did show a trend towards increasing with prey energy density and decreasing with increasing bufflehead DEE. Increasing prey energy density would be expected not only to raise carrying capacity by allowing a site to provide the energetic requirements of more birds per unit area, but may also reduce bufflehead DEE by decreasing the foraging effort required to meet their energy needs [33-35].

Differences in environmental conditions across the sites may also affect bufflehead DEE, and therefore carrying capacity. For example, site-specific differences in average wind speeds may lead to increases in the thermoregulatory component of a bufflehead's DEE [36,37]. Bufflehead at more exposed, windier sites may need to alter their activity to offset increased thermoregulatory costs [38,39]. In this study, we saw an increase in bufflehead energy expenditure with average wind speed. Increased energy expenditure may lead to decreased carrying capacity at less protected sites with higher average wind speeds.

Carrying capacity was considerably greater than observed bufflehead abundances at each of the sites. Abundance may be less than carrying capacity as a result of a number of behavioral processes that are not reflected in our carrying capacity estimates. For example, competition with other waterfowl species or aquatic benthivores for invertebrate prey, predation, and density-dependent processes such as dominance or territorial behavior may be limiting the number of bufflehead that will use a habitat [40,41]. Bufflehead abundance may also be largely determined by site fidelity, in which case factors that limit the size of each local population during the breeding season may be influencing abundance at a given habitat [42]. That the average abundances of bufflehead are well below our calculated carrying capacities may be an indication that bufflehead populations are not limited by food on their wintering grounds [43]. In addition, the effects of both direct and indirect human disturbance may also influence the utilization of wintering habitats by waterfowl [44,45]. If human activity is reducing waterfowl abundance at wintering sites, assessments using energy-based carrying capacities may be useful in informing management actions to protect habitat by providing information about the extent and impact of human disturbance on resident populations.

In our study we found a greater difference between the carrying capacity and the density of bufflehead present at urban versus rural sites. The density of bufflehead at rural sites was significantly correlated with per hectare carrying capacity, however; at urban sites there was no correlation between abundance and carrying capacity, and bufflehead abundances fell below the curve defining the carrying capacity – abundance relationship for rural sites. If we consider the relationship between abundance and carrying capacity at rural sites to represent an optimal relationship determined by the ecology of bufflehead wintering in Narragansett Bay habitats (i.e., integrating the effects of predation, intra- and inter-specific competition, resource depletion, social behavior), we can use this relationship to predict the abundance of bufflehead at urban sites under optimal conditions. Doing this, we found that the measured abundances of bufflehead were reduced by an average of 43.7% from predicted values. This reduction in habitat utilization at urban sites may arise from the effects of development or of the close proximity of human activity in these urban sites.

Hunting activity is foremost on the list of direct human disturbance affecting wintering waterfowl populations, but hunting is not allowed at any of the urban sites because of the close proximity of residences to the coves. Hunting is permitted at all three rural sites, but none of these sites, with the possible exception of Coggeshall Cove, has significant hunting activity (C. Allin, RI Division of Fish and Wildlife, personal communication). Other human activities that may affect resident waterfowl populations include increases in pedestrian and vehicular traffic, noise, and pets, and the indirect effects of nutrient enrichment on prey assemblages, increases in contaminants, and introduced species [44-46]. Also, there may be between-site differences in the rates of predation, interspecific competition for food, or the depletion of food resources. Nonetheless, our results demonstrate that energy-based carrying capacities may help to at least alert those responsible for habitat management to the potential for a human disturbance effect on habitat utilization.

Future studies will be needed to further develop the link between human disturbance and habitat use for both waterfowl and other wildlife species. Once these links are established, approaches incorporating the assessment of energy-based carrying capacity will help provide insights into the effects of human disturbance on coastal habitats, and may be useful in determining acceptable levels of impact, setting development thresholds, or setting standards for habitat restoration.

CONFLICT OF INTEREST

None declared.

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Lake, and J. Serbst who provided comments on the manuscript. C. Allin, waterfowl biologist with the Rhode Island Division of Fish and Wildlife, provided insights into waterfowl hunting patterns in Narragansett Bay. Mention of trade names or commercial products does not constitute endorsement or recommendation. Although the research described in this article has been funded wholly by the U.S. Environmental Protection Agency, it has not been subjected to Agency-level review. Therefore, it does not necessarily reflect the views of the Agency. This is the Office of Research and Development, National Health and Environmental Effects Research Laboratory, Atlantic Ecology Division contribution number AED-04-136.

Appendix

Appendix 1. Model and Equations Used for Calculation of Energy Expenditure

We used a model incorporating site-specific thermoregulatory costs to calculate daily energy expenditure (DEE) [1]. The model consisted of a thermoregulatory component or estimate of the metabolic heat production required to balance heat loss from the bird to the environment through conduction and convection, and an activity component to estimate additional energetic costs resulting from specific daily activities expressed as multiples of basal metabolic rate (BMR). We sumed these components to arrive at an estimated DEE in kJ/hr. The model used average temperatures and wind speeds that coincide with activity budget sampling at the sites.

Basal metabolic rates were estimated from those of 16 North American duck species summarized in McNab [2]. A plot of BMR versus body mass for these species gave the relation: $BMR = 4.05M^{0.79}$, where BMR is basal metabolic rate in ml O_2/hr, and M is body mass in g. Estimates of BMR were converted to kJ/hr using a conversion factor of 18.8 kJ/L O_2, derived from the average composition of the bufflehead's winter diet. Body mass was approximated at 450 g for males and 325 g for females.

Before calculating metabolic heat production, we first determined when this component of a bufflehead's DEE is necessary by comparing ambient temperature with their lower critical temperature, or the temperature below which metabolic heat production is required to maintain body temperature [3]. Lower critical temperature (LCT) was estimated by the empirical relation: $LCT = 47.2M^{-0.18}$, where LCT is in ^{o}C, and M is body mass in g [4]. We compared effective ambient temperature (T_{ef} or the ambient temperature corrected for the effect of wind speed) [5] to LCT to determine whether metabolic heat production would be required to maintain the duck's body temperature. If T_{ef} was less than LCT, we assumed that metabolic heat production was required to maintain body temperature; we then calculated this energy requirement and included it in the final DEE. On the other hand, if T_{ef} was greater than the lower critical temperature, we did not include metabolic heat production. Effective temperature was calculated using the relationship derived by Siple and Passel [5]:

$$T_{ef} = T_b - (T_b - T_a) \times (0.474 + 0.239 \times \sqrt{u} - 0.023 \times u),$$

where T_{ef} is the effective temperature (^{o}C) used for comparison with the lower critical temperature, T_b is body temperature (^{o}C), T_a is ambient temperature (^{o}C), and u is wind speed (m/sec).

If T_{ef} was less than LCT, we used an empirical model to estimate metabolic heat production as a function of temperature and wind speed (Goldstein 1983):

$$H_{T+u} = a + b\sqrt{u}\ ,$$

where u is wind speed (m/sec) and H_{T+u} is metabolic heat production (watts). The coefficient b is determined empirically from data summarized by Goldstein [6] on seven species of birds (body size 13.5–3,860 g) by the relation: $b = 0.0092M^{0.66} \times)T^{0.32}$, where M is body weight in g and)T is the difference between lower critical temperature and ambient temperature in ^{o}C. The coefficient a is determined under conditions of free convection ($u = 0.06$ m sec^{-1}) by the relation:

$$a = H_T - b\sqrt{0.06}\ ,$$

where H_T is an adjusted metabolic rate in watts at ambient temperature [6]. We estimated H_T using a heat transfer model proposed by Birkebak [7] that calculates conductive heat loss from different anatomical regions of the bird to the environment using geometrical representations (e.g., head represented as a sphere, body represented as a cylinder) and heat transfer theory (Table **A1**) [7]. Morphological measures of body dimensions were obtained from live captive buffleheads ($n = 4$, obtained from the Connecticut Waterfowl Trust, Farmington, Connecticut) and bufflehead study skins ($n = 16$, obtained from the Harvard Museum of Comparative Zoology, Cambridge, Massachusetts). Equations drawn from Birkebak [7] were used to calculate metabolic heat production. We used heat transfer coefficients (k) of 0.102 cal/cm/^{o}C for the entire body surface and 0.160 cal cm^{-1} ^{o}C^{-1} to calculate heat loss from the ventral body surface to the water. Metabolic heat production was calculated as: $\mathbf{BMR + Q_{head} + Q_{neck} + Q_{breast} + Q_{body} + Q_{ventral\ surface}}$, where BMR is basal metabolic rate and Q is the heat loss term for each body component.

Estimates of additional energetic costs resulting from specific daily activities ($EE_{Activity}$) were calculated by multiplying the proportion of time spent in a particular activity by the energetic cost of that activity. We used previously reported multiples of BMR, summarized in Table **A2**, to calculate the energetic costs of activities by multiplying the proportion of time spent in that activity by the corresponding multiple of BMR. The contribution of physical activity to DEE was then calculated by summing the energetic costs of all activities in which buffleheads engaged.

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Table A1. Variables Used to Calculate Heat Transfer, An Adjusted Metabolic Rate at Ambient Temperature, Using a Heat Transfer Model Proposed by Birkebak (1966). Representative Values are from Repeated Measurements on Live and Preserved Buffleheads from Northeastern Estuaries. Equations are taken from Birkebak (1966); k is the Heat Transfer Coefficient, T is the Difference between Body Temperature (39^{o} C) and Ambient Temperature

Variable	Symbol	Equation	Representative Value (cm ± SD)
Head length	A	---	5.9 ± 0.4
Head height	B	---	5.0 ± 0.8
Head width	C	---	3.2 ± 0.4
Body width	D	---	9.1 ± 0.9
Body length	F	---	18.2 ± 1.1
Body height	G	---	6.3 ± 0.6
Neck length	H	---	2.0 ± 0.3
Neck width	I	---	2.9 ± 0.4
Neck height	J	---	2.9 ± 0.4
Integument depth- body	X_{body}	---	0.4 ± 0.1
Integument depth- head	X_{head}	---	0.7 ± 0.2
Integument depth- neck	X_{neck}	---	0.7 ± 0.2
Inner radius of body	$r_{i\ body}$	$r_{ibody} = \frac{D+G}{4}$	3.9 ± 0.5
Inner radius of head	$r_{i\ head}$	$r_{ihead} = \frac{B+C}{4}$	2.1 ± 0.4
Inner radius of neck	$r_{i\ neck}$	$r_{ineck} = \frac{I+J}{2}$	2.9 ± 0.6
Length of body	L_{body}	$L_{body} = F - \frac{D+G}{2}$	10.5 ± 0.5
Length of neck	L_{neck}	$L_{neck} = H - \frac{I+J}{2}$	0.9 ± 0.1
Inner radius of body	$r_{i\ body}$	$r_{obody} = r_{ibody} + \Delta x_{body}$	4.6 ± 0.8
Inner radius of head	$r_{i\ head}$	$r_{ohead} = r_{ihead} + \Delta x_{head}$	2.8 ± 0.7
Inner radius of neck	$r_{i\ neck}$	$r_{oneck} = r_{ineck} + \Delta x_{neck}$	6.8 ± 1.1
Area of ventral surface	A_{vs}	$A_{vs} = L_{body} \times 2 r_{obody}$	96.0 ± 21.6

Variable	Symbol	Equation	Representative Value (cm ± SD)
Heat loss from head	Q_{head}	$Q_{head} = \frac{2\pi \times r_{Ohead} \times r_{ihead} \times k \times \Delta T}{r_{Ohead} - r_{ihead}}$	---
Heat loss from neck	Q_{neck}	$Q_{neck} = \frac{2\pi \times L_{neck} \times k \times \Delta T}{\ln(\frac{r_{Oneck}}{r_{ineck}})}$	---
Heat loss from breast	Q_{breast}	$Q_{breast} = \frac{2\pi \times r_{Obody} \times r_{ibody} \times k \times \Delta T}{r_{Obody} - r_{ibody}}$	---
Heat loss from body	Q_{body}	$Q_{body} = \frac{2\pi \times L_{body} \times k \times \Delta T}{\ln(\frac{r_{Obody}}{r_{ibody}})}$	---
Heat loss from ventral surface	Q_{vs}	$Q_{vs} = k \times A_{ds} \times (T_b - T_a)$	---
Heat loss from tail	Q_{tail}	$Q_{tail} \cong Q_{breast}$	---

Table A2. Incremental Multiples of Basal Metabolic Rate (BMR0 Used in Calculating Energetic Costs of Activities

Activity	Increment of BMR	Reference
Courtship	2.4	[8]
Dive	5.1	[9]
Preen	2.1	[8]
Fly	12.5	[11]
Rest	1.4	[11]
Surface	3.5	[11]
Aggression	1.8	[11]
Swim	3.5	[10]
Look	1.4	[11]
Roost	1.1	[11]

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Appendix 2. Abundance (organisms m^{-2}), and Annual Productivity (g m^{-2} $year^{-1}$) and Energy Density (kcal m^{-2}) of the Edible Tissue in Benthic Invertebrates at Narragansett Bay Bufflehead Wintering Sites Sample during the Fall of 2001 and 2003. Average Values are Reported ± SE

	Apponaug Cove			Brush Neck Cove		
			Energy			Energy
Species	**Abundance**	**Productivity**	**Density**	**Abundance**	**Productivity**	**Density**
Neiries virens (Poly.)	5.6 ± 1.7	0.93 ± 0.31	0.19 ± 0.08	--	--	--
Glycera spp. (Poly.)	--	--	--	--	--	--
Nephtys incisa (Poly.)	--	--	--	16 ± 5	0.34 ± 0.12	0.07 ± 0.03
Capitella spp. (Poly.)	21 ± 7	1.61 ± 0.53	0.33 ± 0.14	12 ± 7	0.09 ± 0.04	0.33 ± 0.14
Spiochaetoptorus costarum (Poly.)	--	--	--	--	--	--
Clymenella spp. (Poly.)	--	--	--	--	--	--
Unidentified Polychaetes	--	--	--	--	--	--
Nassarius obsoletus (Moll.)	167 ± 35	27.7 ± 9.3	10.2 ± 3.8	200 ± 42	38.2 ± 13.7	14.0 ± 5.6
Littorina littorea (Moll.)	--	--	--	--	--	--
Urosalpinx cinerea (Moll.)	--	--	--	--	--	--
Mitrella spp. (Moll.)	--	--	--	--	--	--
Unidentified Gastropods (Moll.)	--	--	--	--	--	--
Crepidula fornicata (Moll.)	--	--	--	--	--	--
Geukensia demissa (Moll.)	--	--	--	--	--	--
Nucula proxima (Moll.)	--	--	--	--	--	--
Macoma spp. (Moll.)	--	--	--	--	--	--
Unidentified Bivalves (Moll.)	--	--	--	--	--	--
Ampelisca spp. (Crust.)	--	--	--	--	--	--
Gammarus spp. (Crust.)	--	--	--	--	--	--
Ideotea spp. (Crust.)	--	--	--	--	--	--
Palaemonetes pugio (Crust.)	56 ± 41	19.1 ± 16.9	3.37 ± 3.30	27 ± 20	28.5 ± 20.9	5.02 ± 4.16
Crangon septemspinosa (Crust.)	--	--	--	--	--	--
Carcinus maenas (Crust.)	--	--	--	--	--	--
Cancer spp. (Crust.)	--	--	--	--	--	--
Panopeus spp. (Crust.)	8.4 ± 6.1	1.85 ± 1.96	0.47 ± 0.52	--	--	--
Rhithropanopeus harrisii (Crust.)	--	--	--	--	--	--
Pagurus spp. (Crust.)	2.8 ± 2.0	0.44 ± 0.32	0.10 ± 0.08	--	--	--
All Polychaeta	27 ± 8	2.54 ± 0.84	0.52 ± 0.22	28 ± 9	0.43 ± 0.16	0.09 ± 0.04
All Mollusca	167 ± 35	27.7 ± 9.3	10.2 ± 3.8	200 ± 42	38.2 ± 13.7	14.0 ± 5.6
All Crustacea	67 ± 49	21.4 ± 19.2	3.94 ± 3.90	31 ± 23	28.9 ± 21.2	5.11 ± 4.24

[a] Species classification: Poly. = Polychaeta, Moll. = Mollusca, Crust. = Crustacea

	Watchemoket Cove			Coggeshal Cove		
			Energy			Energy
Species	**Abundance**	**Productivity**	**Density**	**Abundance**	**Productivity**	**Density**
Neiries virens (Poly.)	4.9 ± 1.5	1.33 ± 0.41	0.28 ± 0.11	--	--	--
Glycera spp. (Poly.)	3.3 ± 1.0	0.41 ± 0.13	0.08 ± 0.03	6.5 ± 2.0	0.21 ± 0.06	0.04 ± 0.02
Nephtys incisa (Poly.)	--	--	--	--	--	--

	Watchemoket Cove			**Coggeshal Cove**		
Species	**Abundance**	**Productivity**	**Energy Density**	**Abundance**	**Productivity**	**Energy Density**
Capitella spp. (Poly.)	114 ± 35	0.27 ± 0.21	0.06 ± 0.05	38 ± 12	0.63 ± 0.24	0.13 ± 0.06
Spiochaetoptorus costarum (Poly.)	--	--	--	--	--	--
Clymenella spp. (Poly.)	--	--	--	3.3 ± 1.0	0.20 ± 0.06	0.04 ± 0.02
Unidentified Polychaetes	--	--	--	23 ± 7	0.98 ± 0.34	0.20 ± 0.09
Nassarius obsoletus (Moll.)	207 ± 44	32.6 ± 12.5	12.0 ± 5.1	98 ± 21	19.9 ± 6.9	7.31 ± 2.84
Littorina littorea (Moll.)	--	--	--	3.3 ± 0.7	1.58 ± 0.33	0.46 ± 0.13
Urosalpinx cinerea (Moll.)	--	--	--	--	--	--
Mitrella spp. (Moll.)	--	--	--	--	--	--
Unidentified Gastropods (Moll.)	--	--	--	--	-- --	
Crepidula fornicata (Moll.)	36 ± 16	2.60 ± 1.79	0.37 ± 0.29	345 ± 148	81.9 ± 51.4	11.8 ± 8.6
Geukensia demissa (Moll.)	--	--	--	--	--	--
Nucula proxima (Moll.)	--	--	--	--	--	--
Macoma spp. (Moll.)	--	--	--	--	--	--
Unidentified Bivalves (Moll.)	--	--	--	3.3 ± 1.4	0.04 ± 0.02	0.01 ± 0.004
Ampelisca spp. (Crust.)	186 ± 135	9.41 ± 7.47	2.18 ± 1.47	--	-- --	
Gammarus spp. (Crust.)	--	--	--	90 ± 66	4.13 ± 3.24	0.96 ± 0.64
Ideotea spp. (Crust.)	--	--	--	--	--	--
Palaemonetes pugio (Crust.)	3.4 ± 2.4	19.1 ± 14.0	3.36 ± 2.78	28 ± 20	3.06 ± 2.23	0.54 ± 0.44
Crangon septemspinosa (Crust.)	--	--	--	--	--	--
Carcinus maenas (Crust.)	--	--	--	--	-- --	
Cancer spp. (Crust.)	--	--	--	--	--	--
Panopeus spp. (Crust.)	29 ± 22	6.02 ± 6.15	1.54 ± 1.65	--	-- --	
Rhithropanopeus harrisii (Crust.)	--	--	--	49 ± 36	2.39 ± 3.02	0.61 ± 0.80
Pagurus spp. (Crust.)	3.3 ± 2.4	0.42 ± 0.31	0.10 ± 0.08	13 ± 10	2.09 ± 1.68	0.48 ± 0.43
All Polychaeta	122 ± 38	2.01 ± 0.75	0.42 ± 0.19	71 ± 22	2.02 ± 0.70	0.41 ± 0.19
All Mollusca	243 ± 60	35.2 ± 14.3	12.42 ± 5.4	450 ± 172	103 ± 59	19.6 ± 11.5
All Crustacea	222 ± 161	35.0 ± 28.0	7.18 ± 5.98	180 ± 132	11.7 ± 8.2	2.59 ± 2.31

[a] Species classification: Poly. = Polychaeta, Moll. = Mollusca, Crust. = Crustacea

	Mackeral Cove			**Sheffield Cove**		
Species	**Abundance**	**Productivity**	**Energy Density**	**Abundance**	**Productivity**	**Energy Density**
Neiries virens (Poly.)	--	--	--	4.9 ± 0.5	0.42 ± 0.04	0.09 ± 0.02
Glycera spp. (Poly.)	--	--	--	--	--	--
Nephtys incisa (Poly.)	4.9 ± 1.5	0.04 ± 0.01	0.01 ± 0.003	13 ± 4	0.16 ± 0.05	0.03 ± 0.01
Capitella spp. (Poly.)	52 ± 16	0.19 ± 0.13	0.04 ± 0.03	95 ± 29	0.29 ± 0.20	0.06 ± 0.05
Spiochaetoptorus costarum (Poly.)	17 ± 5	0.16 ± 0.05	0.03 ± 0.01	--	--	--
Clymenella spp. (Poly.)	--	--	--	--	--	--
Unidentified Polychaetes	--	--	--	--	--	--
Nassarius obsoletus (Moll.)	--	--	--	5.0 ± 1.0	2.38 ± 0.50	0.87 ± 0.22
Littorina littorea (Moll.)	--	--	--	--	--	--

	Mackeral Cove			**Sheffield Cove**		
			Energy			**Energy**
Species	**Abundance**	**Productivity**	**Density**	**Abundance**	**Productivity**	**Density**
Urosalpinx cinerea (Moll.)	5.7 ± 1.2	1.14 ± 0.24	0.42 ± 0.05	--	--	--
Mitrella spp. (Moll.)	32 ± 8	0.12 ± 0.04	0.08 ± 0.06	--	--	--
Unidentified Gastropods (Moll.)	9.0 ± 1.0	0.14 ± 0.02	0.02 ± 0.02	--	--	--
Crepidula fornicata (Moll.)	--	--	--	144 ± 62	37.2 ± 20.8	5.36 ± 3.52
Geukensia demissa (Moll.)	--	--	--	--	-- --	
Nucula proxima (Moll.)	2.8 ± 1.8	0.01 ± 0.01	0.002 ± 0.001	--	--	--
Macoma spp. (Moll.)	9.1 ± 4.2	0.01 ± 0.01	0.001 ± 0.001	--	--	--
Unidentified Bivalves (Moll.)	--	--	--	4.9 ± 2.1	0.04 ± 0.02	0.01 ± 0.003
Ampelisca spp. (Crust.)	1115 ± 816	26.1 ± 19.3	6.90 ± 4.13	--	--	--
Gammarus spp. (Crust.)	345 ± 242	13.0 ± 10.0	2.13 ± 1.70	84 ± 62	3.77 ± 2.91	0.87 ± 0.58
Ideotea spp. (Crust.)	20 ± 14	1.00 ± 0.73	0.23 ± 0.15	10 ± 7	1.17 ± 0.85	0.21 ± 0.17
Palaemonetes pugio (Crust.)	--	--	--	9.8 ± 7.2	0.40 ± 0.55	0.07 ± 0.10
Crangon septemspinosa (Crust.)	--	--	--	--	--	--
Carcinus maenas (Crust.)	--	--	--	9.3 ± 7.2	5.01 ± 3.66	0.77 ± 0.61
Cancer spp. (Crust.)	--	--	--	--	--	--
Panopeus spp. (Crust.)	--	--	--	--	--	--
Rhithropanopeus harrisii (Crust.)	--	--	--	49 ± 36	2.39 ± 3.02	0.61 ± 0.80
Pagurus spp. (Crust.)	5.7 ± 4.2	0.59 ± 0.43	0.14 ± 0.11	--	--	--
All Polychaeta	74 ± 238	0.39 ± 0.30	0.09 ± 0.05	113 ± 34	0.87 ± 0.29	0.18 ± 0.08
All Mollusca	58 ± 15	1.42 ± 0.31	0.52 ± 0.15	154 ± 65	39.6 ± 21.3	6.24 ± 3.74
All Crustacea	1486 ± 1076	36.2 ± 30.4	9.40 ± 5.09	113 ± 83	10.3 ± 8.0	1.92 ± 1.46

[a] Species classification: Poly. = Polychaeta, Moll. = Mollusca, Crust. = Crustacea

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