

ABSTRACT

Title of Dissertation: FORAGING VALUES OF *MULINIA LATERALIS* AND *ISCHADIUM RECURVUM*: ENERGETICS EFFECTS OF SURF SCOTERS WINTERING IN THE CHESAPEAKE BAY.

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Surf scoter (*Melanitta perspicillata*) populations wintering in the Chesapeake Bay primarily prey on two food items, the hooked mussel (*Ischadium recurvum*) and dwarf surfclam (*Mulinia lateralis*). The decline of oyster reefs (*Crassostrea virginica*) has decreased availability of mussels inducing surf scoters to switch to a more opportune food item, the dwarf surfclam. The objectives of this study were: 1) to determine the comparative nutrient composition of these prey items; 2) to evaluate the energy assimilated by surf scoters from these prey items; 3) to determine the functional responses of scoters foraging on four different ecologically relevant densities (30, 100, 1000, and 3000 m⁻²) of each prey item; and 4) to model the foraging value (costs – benefits) of both prey items for surf scoters. *I. recurvum* contained higher ash, protein, lipid, and energy per item than *M. lateralis*. Metabolizable energy from each prey item by surf scoters was 83% for *M. lateralis* and 87% for *I. recurvum*. The shell strength of *I. recurvum* was significantly stronger than *M. lateralis*. For scoters foraging in a large diving tank 2 m deep, intake (# s⁻¹) for *M. lateralis* was significantly higher than *I.*

recurvum at high densities, but lower at the low densities. Gross energy intake (kJ s^{-1}) and metabolized energy intake (kJ s^{-1}) were significantly greater for *I. recurvum* than *M. lateralis*. Based on nutrient content, metabolizability, behavior and intake rates, and energy expenditure at naturally occurring densities, the foraging value for *M. lateralis* was significantly lower than *I. recurvum*. Despite higher ash content and harder shell, which would partly offset the apparent energetic advantages of *I. recurvum*, greater foraging value of *I. recurvum* than *M. lateralis* provides a more beneficial prey item for wintering surf scoters. Therefore, wintering surf scoters must adapt in order to maintain their daily energy requirement. If surf scoters are forced to feed primarily on *M. lateralis*, the most advantageous and available prey in the Chesapeake Bay, instead of *I. recurvum*; there may be insufficient energy for them to build fat reserves needed to make migration.

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ENERGETICS EFFECTS OF SURF SCOTERS WINTERING IN THE CHESAPEAKE
BAY

by

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Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2008

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Dedication

I would like to dedicate this dissertation to my family. Without their love and support throughout the past five years I would not have been able to finish this study. Thank you, Dave, for being my rock anytime I felt beaten and for giving me the most beautiful son. Thank you, Mom and Dad, for giving me the thirst for knowledge and the drive and focus to succeed. Also, thanks for being my sounding boards when I was stressed and babysitting whenever needed. Thank you Trevor, Kelly, Marissa, and Brennan for making me laugh as always; it is the best cure for anything. Thank you, Tom and Mary, for babysitting whenever possible and not complaining when I would come home later than expected. Thank you, Dan, Heidi, and Adam for being there whenever I needed a mental break. All of you are wonderful and having you in my life is a true blessing; one which I will never take for granted.

Acknowledgements

I would like to thank Dr. Matthew C. Perry for having the confidence in me and for all his help with every aspect of this study. Without his support this study would not have happened. Dr. Mary Ann Ottinger also deserves my utmost gratitude for her constant support and helping me whenever I was in desperate need. I would also like to thank all the assistants that have helped with the project over the last five years with special thanks to Marie Brady, Michelle Maley, Peter Osenton, Allegra Schafer, and Whitney Walker-Mehrhof. I would also like to thank fellow graduate students, David Kidwell, Diann Prosser, and Moira McKernan, for their invaluable advice and support. My committee deserves many thanks as well. Without their invaluable insight and support; whether it be providing advice or providing assistance, this project would not have come to fruition. Dr. Paynter's lab, Ben Parks, and Woods Hole Marine Laboratory thankfully provided the prey items used for this project. Thank you, Dr. Bruck, Arun Kota, and the rest of the lab, for the use of the force meter and the many hours of help. The USGS Chesapeake Bay Program, Seaduck Joint Venture, and Friends of Patuxent Wildlife Research Center and Research Refuge provided the financial support for this project. Finally, I thank the administrators and staff of Patuxent Wildlife Research Center that provided office space, pen and lab facilities, computer and statistical support, library materials, and the unrelenting support to enable me to pursue my dreams and accomplish my goals.

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Introduction:

Over time, the expanding human population and industry in the Chesapeake Bay watershed have released increasing amounts of sediment, toxic chemicals, sewage, and agricultural runoff (Horton and Eichbaum 1991; Gottlieb and Schweighofer 1996). There has been an increase in the severity, duration, and frequency of anoxic events in the deep areas of the Bay and some of its tributaries (Officer et al. 1984; Seliger et al. 1985; Tuttle et al. 1987), with devastating consequences for benthic organisms (Seliger et al. 1985; Kemp and Boynton 1992). The drastic decline of the American oyster (*Crassostrea virginica*) in the Chesapeake Bay – estimated to be about 1% of its historic abundance (Newell 1988) – may be a major contributing factor to the shift in trophic structure (from benthic to pelagic) and recent anoxic conditions (Dame et al. 1980; Newell 1988; Mann et al. 1991; Ulanowicz and Tuttle 1992; Gottlieb and Schweighofer 1996).

The primary source of hard substrate in the Bay was the oyster beds. However, diseases and overharvesting have caused major declines in the oyster populations so the beds are not regenerating and are being smothered by sedimentation, which reduces hard substrate available for hooked mussel larvae to settle upon (*Ischadium recurvum*; Figure 1). These mussels have declined and, since they are a very important food source to wintering surf scoters (Figure 2; Perry et al. 2007), could directly affect the abundance or occurrence of surf scoters in those areas. Alternatively, the scoters may be forced to feed on another food item, the dwarf surfclam (*Mulinia lateralis*), that may not be as energetically efficient for them. In addition, the alternative food item may not be of similar size to the mussels and, therefore, may require more effort to obtain their daily energy requirement. Conversely, reduced habitat availability for mussels could increase

densities in existing habitats, which could potentially benefit scoters by reducing the effort expended to search for obtainable prey. However, if the energetic value of the mussels declined due to overcrowding then this could influence the foraging response of a scoter. Petersen and Black (1988) reported reduced shell growth, lower survival, and enhanced mortality at higher densities for two suspension feeding bivalves. As Townsend and Hughes (1981) demonstrated, given an array of potential prey (e.g., bivalves) that differ in accessibility (e.g., buried versus attached) or in energy content, there should be an optimal choice of prey that provides the maximum net rate of energy return (energy provided by prey minus energy required to find and eat prey) to a predator (e.g., scoter). The objectives of this study were to 1) to determine the comparative nutrient composition of these prey items; 2) to evaluate the energy assimilated by surf scoters from these prey items; 3) to determine the functional responses of scoters foraging on each prey item; and 4) to model the foraging value (costs – benefits) of each prey item for surf scoters. By estimating the relative foraging values of *I. recurvum* and *M. lateralis* for surf scoters we can determine if the surf scoters may be able to sustain themselves if a drastic shift occurs in the benthos available to them in the Chesapeake Bay. In addition, this research will contribute to the models available to assess impacts of environmental change on wildlife populations.

Background:

The Surf Scoter:



Summary reports of the status of seaducks reveal population declines for some species with increased concern for the status of seaducks in general (Elliot 1997; Kehoe 1994; Petersen and Hogan 1996). Surveys of seaducks wintering on the Atlantic coast (1991-99) have shown major declines for the surf scoter (Caithamer et al. 2000) necessitating further research on this species. Surf scoters are indigenous to North America where they breed across northern Quebec and Alaska. Their primary Atlantic coast wintering area is the Chesapeake Bay (Savard et al. 1998; Figure 3).

An examination of migrational patterns conducted by Perry et al. (2006b) from 2001 to 2005, where surf scoters were implanted with satellite transmitters and monitored for no more than 1 year, represented the first delineation of surf scoter distribution along the Atlantic coast (Kidwell 2007). All scoters, females only, used for this study were collected in late winter on the Chesapeake Bay. They exhibited strong site fidelity, returning to the Chesapeake Bay for winter or at least as a stopover locality the following

year. One scoter traveled south to Pamlico Sound, North Carolina before returning to the Chesapeake Bay and a number of scoters spent time around Cape Cod, Massachusetts and other various locations along the Atlantic coast while migrating to the Bay.

Within the Chesapeake Bay, Perry et al. (2006b) found surf scoters to be widely distributed through the mainstem and major tributaries in both Maryland and Virginia. The majority of satellite telemetry observations occurred in the middle portion of the Bay, between Kent Island and the Rappahannock River, including the Potomac and Choptank Rivers.

Scoters commonly feed in shallow marine coastal waters <10 m deep, usually over substrates of pebbles and sand (Savard et al. 1998). In British Columbia, all 3 species of scoters are found over sand-mud and cobble substrates, but surf scoters are also abundant over rocky substrates and outnumber other scoters along steep rocky shores of fjords (Savard et al. 1998). However, surf scoters near Vancouver Island were positively associated with sandy habitats, where they preyed upon infaunal clams (Žydelis 2006). Stott and Olson (1973) found a preferential use of sandy substrates by surf scoters along the New Hampshire coastline, with decreasing abundance as the percentage of rocky habitat increased. Coastal surveys indicate that the vast majority of scoters (mainly surf scoter) wintering on the Canadian Pacific Coast occur within 1 km of land (Savard et al. 1998). Little is known of wintering habitat preferences of surf scoters on the East Coast, but they commonly occur at depths of 10-25 m in the Chesapeake Bay. Kidwell (2007) found that surf scoters in the Chesapeake Bay select against mud/silt habitats and prefer to forage in hard bottom interspersed with sand or homogenous sandy habitats.

Scoters prey on stationary organisms (mussels, clams) in flocks ranging from a few to several thousand birds. They tear mussels from rocks with their bill, swallow the smaller ones underwater or, if large or in clumps, bring them to the surface and swallow the mussels whole. Surf scoters have been observed with large mussels or clumps of mussels at surface (Savard et al. 1998).

Surf scoters prey upon a variety of marine/estuarine invertebrates, especially bivalves (Cottam 1939; Stott and Olson 1973; Vermeer 1981; Nyström et al. 1991; Bustnes et al. 2000; and Lovvorn et al. 2003). Stomachs collected in each month from U.S. and Canada contained 61% mollusks, 10% crustaceans, 10% insects (during summer), and 12% vegetation (Savard et al. 1998). Individuals (n = 55) collected in winter between Maine and Long I., NY, contained only animal foods: mussels (*Yoldia* spp.) and blue mussels (*Mytilus edulis*) composed 64% of volume (Savard et al. 1998). Along coastal New Hampshire and Massachusetts, mainly clams (60% Arctic wedge clam (*Mesodesma arctatum*), 24% Atlantic razor clam (*Siliqua costata*) and 8% blue mussels; Savard et al. 1998). Individuals collected in coastal waters of Hudson Bay in spring and fall (n = 26) had fed almost exclusively on clams and mussels (99% wet weight), mostly blue mussels (49.4%; average size 15.2 mm ± 6.5 SD, n = 119) and arctic hiatella (*Hiatella arctica* (38.7%); average size 21.6 mm ± 3.6 SD, n = 11; Savard et al. 1998). Molting surf scoters (n = 9) collected in northeast James Bay, near the Bay of Many Islands, fed on blue mussels (67%), northern astarte (*Astarte borealis* (11%)), and *Astarte* spp. (44%), crustaceans (Crustacea (11%); Savard et al. 1998). Perry et al. (2007) found surf scoters also feed on a variety of epifaunal and infaunal invertebrates in the Chesapeake Bay. In their analyses, dwarf surfclam and hooked mussel represented

the most frequently consumed prey (33.50% and 22.36% of their diet, respectively; Figure 2). It was also shown that there were spatial differences in consumption, especially in association with the salinity gradient of the Bay (Figure 4; Kidwell 2007). The hooked mussel was the dominant prey item consumed by scoters in the Choptank River and Herring Bay, whereas dwarf surfclam was consumed primarily in the Tilghman Island area. Scoters collected around Taylor's Island, which is approximately 32 km south, predominantly preyed upon dwarf surfclam, but stout tagelus (*Tagelus plebius*) was consumed in larger quantities. Prey species associated with more high mesohaline and polyhaline waters, such as false angel wing (*Petricola pholadiformis*), Atlantic jackknife clam (*Ensis directis*), and stout tagelus were predominately found in scoters collected around Smith Island. In addition, Kidwell (2007) noticed a significant decline in hooked mussel densities during winter indicating a strong impact of surf scoter predation on mussel availability.

The average length of blue mussels preyed upon by surf scoters at Saltspring I., British Columbia was 16.1 mm \pm 0.4 SE (n = 218); on Fraser Delta, 20.2 mm \pm 0.8 SE (n = 85); and at Jarvis Inlet, 9.4 mm \pm 0.3 SE (n = 197), whereas average length of Manila clams was 1.9 cm \pm 0.2 SE (n = 38; Savard et al. 1998). When foraging over or near clam beds in coastal British Columbia, the surf scoter switches partly from mussels to Manila clams (Savard et al. 1998). Perry et al. (2007) primarily found hooked mussels ranging from 16-24 mm in surf scoter gullets, which corresponded to the size depleted by surf scoters in winter (Kidwell 2007). According to the size of mussels ingested, most appear to be in their first year of life, maybe because large mussels are harder to grind and may block or cut the duck's alimentary system (Savard et al. 1998).

Surf scoter paddle index (square root feet area \div cube root body weight) is third highest among 15 species of ducks (mean 0.97, range 0.92–1.00, n = 5; Savard et al. 1998). This index reflects efficiency of swimming and diving, although some species may use wings as aid in diving. Individuals in flocks tend to dive and surface in highly synchronous fashion and synchrony increases with flock size (Savard et al. 1998). Synchrony may be advantageous in large groups to maintain cohesion during foraging trips, and in the particular case of birds foraging on sessile prey; synchrony may allow individuals to follow one another to localized food patches (Savard et al. 1998). Synchrony may also reduce the amount of energy expended during a dive by reducing the drag coefficient on the individuals following the “leader”. The synchrony with which surf scoters surface is higher when the pauses between dives may be used by the ducks to recover from physiological effects of prolonged diving. The fact that duration of pause in surf scoters tends to oscillate around predicted values supports the idea that such divers foraging on sessile prey complete more of the recovery after each dive than ducks foraging on mobile prey, who occasionally delay repayment of this physiological debt (Savard et al. 1998).

The Chesapeake Bay:

The declining condition of the Chesapeake Bay ecosystem has been the focus of many studies (Gottlieb and Schweighofer 1996). Numerous organisms in the Bay are showing signs of stress. Submerged aquatic vegetation (SAV) was once abundant throughout the Bay, but declined to an all-time low of 24,000 ha (Hurley 1991) due to poor water quality and a reduction in light reaching the plant surfaces (Orth and Moore 1983). These vegetated areas provide nursery areas for fish and invertebrates, are utilized

as food substrate for fish and waterfowl, and provide a stabilizing force for sediment (Heck and Orth 1980). Other indications of stress in the Chesapeake Bay include excessively high levels of nitrogen and phosphorus, declining populations of anadromous and freshwater fish (Flemer et al. 1983), and extraordinarily high levels of bacteria in the water column, as high as 20 million cells ml⁻¹ (Smith et al. 1992; Gottlieb and Schweighofer 1996).

Over time, the expanding human population and industry in the Bay watershed have increased the amounts of sediment, toxic chemicals, sewage, and agricultural runoff (Horton and Eichbaum 1991; Gottlieb and Schweighofer 1996). There has been an increase in the severity, duration, and frequency of anoxic events in the deep areas of the Bay and some of its tributaries (Officer et al. 1984; Seliger et al. 1985; Tuttle et al. 1987), with potentially devastating consequences for benthic organisms (Seliger et al. 1985; Kemp and Boynton 1992). Scientists have observed a dynamic shift in the trophic structure of the ecosystem (Officer et al. 1984; Tuttle et al. 1987) from one dominated by bacterial production (Jonas and Tuttle 1990) to one dominated by predators. Excess nutrient input encourages seasonal blooms of phytoplankton. Research shows that heterotrophic bacterioplankton respond to increased supplies of photosynthetically produced organic food substrate with an increase in biomass. This response indicates bottom-up control of trophic structure (Cole et al. 1982; Malone et al. 1986). Some other responses to excess nutrients include increased production of plankton of little food value to higher trophic levels, a decline of economically important fish species (Officer et al. 1984), and anoxia in additional portions of the Chesapeake Bay (Jonas and Tuttle 1990). A study of the Chesapeake Bay by Malone and others (1986) revealed extended periods

of high bacterial densities, placing the Bay among the most eutrophied estuaries known. The eastern shore experienced a much higher phytoplankton growth rate and lower standing biomass as compared to the western shore, due in part to grazing (Malone et al. 1986). This grazing effect is an example of top-down control. While bottom-up factors in an estuary influence the trophic structure of the system (Ducklow and Shiah 1993), consumer organisms, including bivalve mollusks, can also exert regulatory (top-down) control on nutrient cycling (Kitchell et al. 1979) and trophic structure (Malone et al. 1986; Ulanowicz and Tuttle 1992).

The drastic decline of the American oyster in the Chesapeake Bay – estimated to be about 1% of its historic abundance (Newell 1988) – could be a contributing factor to the shift in trophic structure and recent anoxic conditions (Dame et al. 1980; Newell 1988; Mann et al. 1991; Ulanowicz and Tuttle 1992; Gottlieb and Schweighofer 1996). Over harvesting, pollution, habitat destruction, and disease have all contributed to the deterioration of the American oyster populations in the Bay (Rothschild et al. 1994). Oysters and other benthic bivalves are ecologically important for the reduction of large amounts of phytoplankton in the water column. Phytoplankton blooms can cause extreme fluctuations in the pH and oxygen levels of the water, which in turn may endanger fish and other organisms in the system (Shpigel and Blaylock 1991). The presence of oysters in flow-through aquaculture systems, however, has been shown to stabilize pH and regulate oxygen concentrations of the water, thereby reducing fish mortalities (Shpigel and Blaylock 1991). In addition, benthic bivalves are important for the cycling of nutrients through filtration and excretion, and the transfer of carbon and suspended particles to the sediments (Doering et al. 1986; Dame et al. 1991).

The entire food web is affected by these changes in Bay quality (Gottlieb and Schweighofer 1996). Zooplankton herbivores subsequently dominate and selectively graze large phytoplankton species. On the other hand, zooplankton herbivores are not abundant enough during the spring bloom of phytoplankton to efficiently graze the biomass that was once consumed by oysters and other bivalves. Thus, the unutilized carbon is delivered to the bacterial community, increasing benthic biological oxygen demand and leading to anoxic conditions below the pycnocline (Newell 1988).

Many estuaries depend on filter feeders for control of nutrient cycles and pelagic organisms (Gottlieb and Schweighofer 1996). South San Francisco Bay, a shallow estuary adjacent to a highly urbanized area, receives 70% of the sewage effluents from the San Francisco metropolitan area, and would be expected to exhibit symptoms of eutrophication similar to the Chesapeake Bay (Officer et al. 1982). However, South Bay has a low and relatively static level of phytoplankton biomass, and blooms are generally absent (Cloern 1982). While transport processes occur on too large a time scale to influence phytoplankton population dynamics, empirical and theoretical studies indicate that the healthy condition of the system is maintained by a dense community of benthic filter-feeding organisms, dominated by *Tapes japonica*, a clam, and *Musculus senhousia*, a mussel (Cloern 1982; Officer et al. 1982).

Another example of a benthic bivalve that has been shown to help clear the water column of excess phytoplankton is *Mytilus edulis* in the Netherlands (Riemann et al. 1988; Dame et al. 1991). This mussel is able to remove much of the phytoplankton in the benthic boundary layer, and may be able to lower the levels of phytoplankton throughout the entire water column (Dame et al. 1991). Riemann et al. (1988) found that *M. edulis*

may be able to reduce the chlorophyll *a* concentrations by 10% to 59% in the water. Mussel beds are also a source of ammonium and orthophosphate, while the sediments on which they reside are sources of nitrate and nitrite. Therefore, *M. edulis* not only increases the sedimentation rate through biofiltration, but it also increases the organic content of the sediments, which may stimulate the detritus-based food chain and support greater species diversity in the sediment (Dame et al. 1991).

A recent report by Phelps (1994) assessed the relationship between the invasion of the exotic Asiatic clam, *Corbicula fluminea*, in 1979 and system-level ecological change in the Potomac River Estuary. Phelps provides strong evidence that increases in abundance and diversity of SAV (13 species), fish (31 species), and aquatic birds during 1983-85 corresponded with a flourishing *C. fluminea* population. Furthermore, the early summer clam population was estimated to be capable of filtering 50-100% of the water in the area where it was abundant, and phytoplankton populations decreased 40-60% there in 1980-81.

Although most analyses of Bay benthos occurred after hypoxia became an annual event (Kemp et al. 2005), the effects of hypoxia on benthic communities in the Bay are well known (Kidwell 2007). Throughout the mainstem and major tributaries of the mesohaline Chesapeake Bay, degraded communities of deep-water benthos are strongly related to the recurrence of hypoxia (Dauer et al. 2000). These degraded communities typically contain reduced benthic biomass, species diversity, and altered structure (Holland et al. 1977a; Dauer and Ransinghe 1992; Dauer et al. 2000) and can have implications on the energy flow across trophic levels (Breitburg et al. 1997). Holland et al. (1977b) found benthic fauna in nine meter mud habitat to be in a cyclical pattern of

mortality and recolonization. High faunal mortalities during summer hypoxia were followed by late-summer and fall spawning events preceded summer mortality, a cycle repeated yearly during the multi-year study. Recolonization of deep-water benthos is primarily derived from shallow-water populations, and likely represents a critical compensatory mechanism to mitigate overall population declines. Further, the level of benthic degradation decreases with increasing water depth; with Holland et al. (1977b) finding even more depleted benthic fauna in deeper waters.

Restructured benthic communities due to hypoxia (Diaz and Rosenberg 1995) tend to be composed of large numbers of opportunistic species and a decreased number of equilibrium (larger and long-lived) species (Dauer and Ransinghe 1992). Opportunistic species are characterized by short life cycles (Dauer and Ransinghe 1992), high fecundity, and large recruitment pulses (Holland 1985). Although surf scoters may select dwarf surfclam, the prevalence of this opportunistic species and the relatively low percentage of equilibrium species (e.g., *Mya arenaria* and *Macoma balthica*) in the food habits of surf scoters suggest the possibility that hypoxic events may be affecting prey selection by scoters (Kidwell 2007).

Degradation of the Chesapeake Bay could partly be attributed to declines in the oyster populations, since oysters feed primarily on phytoplankton which frequently blooms in association with eutrophication. In addition to their value as a filter feeder, the tendency for oysters to form bars make them a vital component of the Chesapeake Bay ecosystem. For the above reasons and the economic impacts, a significant amount of research and support has been allocated to oyster restoration. Rodney and Paynter (2006) found that the restored oyster bars were colonized by large densities of sea squirts

(*Mogula* sp.), hooked mussel, barnacle (*Balanus* sp.), small fish, and many other species. The multitude of fauna inhabiting these restored oyster bars may serve as a significant prey source for surf scoters, especially since the hooked mussel densities are vastly different than the densities found on unrestored or other hard substrates in the Bay (3000 m⁻² versus 30 m⁻²; Rodney and Paynter 2006; Kidwell 2007).

The Prey and Predation:

Substrate preference and salinity are the major factors governing the distribution of mollusks in the Chesapeake Bay (Figure 4). The hooked mussel occurs on hard substrates, whereas, the dwarf surfclam occurs in sandy/muddy habitats. The hooked mussel prefers salinities ranging from 5-30 ppt and the dwarf surfclam occurs in salinities ranging from 10-30 ppt (White 1989; Lippson and Lippson 1997). Within these communities, predation is the key determinant of the abundance and size structure of prey populations, as well as the structure and functioning of communities (Seitz et al. 2001). Survival of individuals and persistence of prey species when faced with intense predation pressure derives collectively from antipredator adaptations, environmental conditions, habitat features, and predator prey dynamics (Seitz et al. 2001). Prey patches are selected by predators to maximize fitness or energy intake, within the constraints of predator interference, predation risk, reproductive demands, avoidance of prey, chemical deterrents, and predator behavior (Seitz et al. 2001).

Studies of consumer feeding rates concentrate on encounter rate and handling time, which change with varying prey densities. The predator's "functional response" (FR) relates the quantity of prey consumed per predator to prey density (Seitz et al. 2001; Figure 5). At low prey densities the proportional mortality increases with decreasing

prey density in a type II FR, but decreases with decreasing prey density in the type III FR (Seitz et al. 2001). The form of the predator's FR can indicate whether prey persistence or local extinction would be expected. Because the per capita rate of predation is highest at low densities in the type II FR, it is destabilizing and can lead to local extinction of prey (Seitz et al. 2001). The type III FR has a decreasing risk of mortality at low prey densities, thereby promoting a low-density refuge for prey, which can stabilize prey populations (Seitz et al. 2001). Microhabitat features can protect infaunal bivalves from birds; the tactile penetration of shorebirds can be limited by sediment type so that infaunal prey can achieve refuge at low density (Piersma et al. 1995). Thus, both low density and habitat refuge can promote prey persistence. Living in aggregations is another effective predator-avoidance tactic. For example, marine mussels evade predation by residing in clumps that are difficult for predators to attack, marsh mussels obtain refuge in aggregations, and oysters become less susceptible to predators when residing in clumps (Seitz et al. 2001).

Differential abundance of bivalves by sediment type might be due to physical properties of the sediment, food availability, the geochemical environment, or changes in predator-prey relationships (Seitz et al. 2001). Sediment composition alone can favor survival of one trophic group over another. For instance, clogging of the feeding apparatus in a suspension feeder may preclude its survival in muddy habitats, whereas the facultative deposit feeder can feed in sand or mud, but with differing efficiencies. Differential distributions of these clams can be suggestive of differing refuge properties of each sediment, among other factors (Seitz et al. 2001).

A range of environmental and biotic factors can affect the survival of thin-shelled bivalves. For example, survival may be affected by summer anoxia (Seliger et al. 1985), tropical storms, density-dependent mortality from sedimentation, gradients in salinity and temperature, hydrodynamic processes, growth, recruitment, and predation in general (Seitz et al. 2001). Thus, reduced penetrability of the substrate (i.e., in sand or shell hash), or reduced prey densities, would reduce prey encounter rates. This reduction in encounter rates would lead to a decrease in foraging activity, further diminishing encounter rates or driving the predator from inefficient foraging areas of low prey density (Seitz et al. 2001). Epifaunal sessile prey are usually unable to evade predation and, therefore, must rely on armor, habitat complexity, residence in aggregations, and fast growth to a large size as techniques against predation (Seitz et al. 2001). With armored epifauna, handling time becomes the most important predator foraging concern, thus, an inversely density-dependent predator FR may be characteristic, depending upon settlement location and growth rate. For example, oysters and mussels can avoid predation by initially settling within the interstices of clumps, and then growing fast enough to reach a size unacceptable to predators (Seitz et al. 2001). Alternatively, oyster and mussel larvae that initially settle in vulnerable locations (e.g., the edge of an oyster shell clump) would likely suffer a predator's type II FR and local extinction. In general, a density-dependent (i.e., type III) FR is observed in those predator-prey interactions where encounter rates are reduced through some feature of the habitat or prey behavior (e.g., crabs preying upon clams hidden among cobble or seagrass; Seitz et al. 2001). In contrast, an inversely density-dependent (i.e., type II) FR likely characterizes predator-prey interactions where prey have developed mechanisms that increase the predator's

handling time as an evolutionary tactic (e.g., morphological structures such as a thick shell or heavy ornamentation as found in barnacles or oysters; Seitz et al. 2001). Prey refuges from predation can result from either biological processes or physical factors affected by habitat, including deep burial, seagrass beds, roots and rhizomes, other macrofauna, water depth relative to predation risk of predators, hypoxia, and sediments that impede predator foraging (e.g., shell hash or coarse sediments; Seitz et al. 2001).

Prey, such as mussels and oysters, use shell ornamentation, morphology, and thickness to reduce the handling efficiency of predators (Seitz et al. 2001). These prey species are generally epifaunal or shallow burrowing, and, if solitary or without habitat refuge, they have predators that exhibit an inversely density-dependent (type II) FR. Armor may also provide additional benefits to the organism such as protection from mechanical stress. Furthermore, shell morphology exhibits phenotypic plasticity in response to a mollusk's vulnerability to predation (Seitz et al. 2001). This plasticity suggests that increases in handling time due to armor are not fixed but flexible. These armored bivalves are in "coexistence refugia," since they avoid predators (Seitz et al. 2001).

Foraging Value:

The benthic invertebrate macrofauna are important components in the Chesapeake Bay. Although, other suspension-feeding macrofauna which attach to hard substrates – for instance, oysters, mussels, hydroids, and barnacles – may have been dominant forms of benthic biomass in previous times, they now appear to be of secondary importance because of the generally impoverished oyster beds. The decline in the hooked mussels that utilize these hard substrates would directly affect the abundance or occurrence of

scoters in those areas. They may be forced to feed on another food item, the dwarf surfclam, which may not be as energetically efficient for them. In addition, the alternative food item may not be of similar size to the mussels and, therefore, may require more effort to obtain their daily energy requirement. Conversely, reduced habitat availability for mussels could increase densities in existing habitats, which could potentially benefit scoters. However, if the quality of the mussels declines due to overcrowding then this could influence the foraging response of a scoter. Petersen and Black (1988) reported reduced shell growth, lower survival, and enhanced mortality at higher densities for two suspension feeding bivalves.

Change in intake rate with prey density is a basic component of a number of models of waterbird foraging (Myers et al. 1980; Wanink and Zwarts 1985; Draulans 1987; Piersma et al. 1995; Richman and Lovvorn 2002, 2003). For diving ducks foraging on bivalves it is typical to find a type II FR, where intake rates increase with increasing prey density up to an asymptote where intake is limited by handling time (Takekawa 1987; Giles 1990; Lovvorn and Gillingham 1996; Richman and Lovvorn 2002, 2003). If a food organism is present below a certain density it may no longer be profitable in terms of energy gain for a duck to seek it (Sugden 1971) so it may cause the duck to switch to a more abundant lower energy food source. As the quality and/or quantity of food declines, ducks may travel farther between suitable food items or food patches to maintain adequate energy/nutrient intake. The food taken at any one time depends on both the preferences of the ducks and the availability of the food items. Thus as the availability of any food item changes, the food habits and possibly the relative abundance of the ducks may change, and result in movement into or away from an area. For

example, when the SAV declined in the Bay it directly affected the wintering populations of canvasbacks (*Aythya valisineria*) and redheads (*Aythya americana*). The canvasbacks were able to adapt to the changing food resources and take advantage of the booming populations of Baltic macoma (*Macoma balthica*; Perry and Uhler 1988). In contrast, the redheads moved to less degraded areas and are seen in very small numbers now on the Bay in winter. Based on past food habits data, the primary food item for scoters was mussels; however, in the Bay there may be shift from the hooked mussel to the dwarf surfclam (Perry et al. 2007). The situation for scoters could be similar to that for the canvasback, resulting in the scoters altering their food habits in accordance with the declining availability of the hooked mussel and the abundance of the dwarf surfclam.

Prey depth has been reported to affect the functional responses of crabs, shorebirds, and diving ducks that eat clams (Wanink and Zwarts 1985; Lipcius and Hines 1986; Zwarts and Blomert 1992; Seitz et al. 2001; Richman and Lovvorn 2002, 2003). In this case *M. lateralis* is buried in sand and there would be an additional cost while diving to find them relative to the highly visible *I. recurvum*. Stephenson et al. (1986) found that when tufted ducks (*Aythya fuligula*) swim long horizontal distances underwater for their food, heart rate progressively declines after approximately 15 s so that by approximately 30 s it is significantly below the resting value. During these dives the ducks swim actively to and from the food. However, during normal vertical dives of similar duration heart rate remains elevated above resting. Therefore, increasing search time underwater increases the energetic costs of that dive.

Energetics:

Wild waterfowl are able to balance their diets by foraging on a wide variety of plant and animal foods, with the primary consideration being the availability of sufficient protein, carbohydrates, fats, minerals, and vitamins to form a balanced diet regardless of the sources of these fundamental nutrients (Klasing 1998). Dietary protein is metabolically important because it can supply essential amino acids, and, through intermediary metabolism, it can give rise to glucose, fat, energy, and several vitamins. Protein synthesis requires the presence of all of the essential, semiessential, and nonessential amino acids to be present in the cells of a tissue at adequate concentrations and at the same time (Klasing 1998). Protein synthesis is among the most energetically expensive of any metabolic process. Inadequate consumption of a single amino acid, total protein, or energy decreases the rate of protein synthesis and degradation of skeletal muscle and many other tissues. Nutrition can influence protein synthetic and degradative rates directly, by the supply of amino acids and energy to the tissues, or indirectly, through secondary changes in hormone concentrations. High levels of dietary protein slightly increase protein deposition at levels well above those needed to meet essential amino acid requirements. Diets that maximize the efficiency of energy utilization for growth also minimize the rate of protein degradation.

At maintenance for birds, the requirement for lysine relative to other amino acids is very low and glycine and histidine are not needed. Methionine, arginine, and threonine are required at proportionally high levels (Klasing 1998). The dietary protein requirement (%) increases with the level of protein in a species' customary diet. Faunivores have high rates of endogenous losses, due mostly to high rates of degradation,

and would be predicted to have correspondingly high maintenance protein requirement. A bird's digestive strategy, body size, activity, and endogenous losses of nutrients all affect the relative proportions of protein and energy that must be provided by the diet.

Excess dietary amino acids beyond the need for protein synthesis may be used for the synthesis of metabolites or they may be degraded (Klasing 1998). The first step in the degradation of most amino acids is deamination. The amino group can be channeled to uric acid, either through transamination or through glutamine synthesis. The carbon skeletons may be used for glucose synthesis or fat synthesis or oxidized to provide energy. Endogenous losses of amino acids also occur through the sloughing of skin, in the replacement of damaged feathers, or in protein in the feces. The endogenous fecal losses include unrecovered digestive enzymes, mucus, and sloughed cells. The amount of fecal loss is related to the level of food intake, and the amount of skin and feather loss is environment-dependent. The rates of these endogenous losses have not been accurately quantified in birds.

Amino acid requirements also increase with increasing levels of dietary protein (Klasing 1998). It appears that, in the disposal of excess dietary amino acids, the bird's use of the limiting amino acids becomes less efficient. The limiting amino acids in one food are often compensated by surpluses in another dietary component and the degree to which the two foods correct their respective deficiencies when combined in a diet is referred to as protein complementation. The consumption of foods that have complementary amino acid patterns must occur during the same foraging bout to be most effective.

Excess amino acids in the diet result in the use of amino acids as an energy source (Klasing 1998). Most amino acids are oxidized in the liver or kidney. The branched amino acids can also be transaminated and oxidized in skeletal muscle. The activity of amino acid catabolic enzymes is normally much higher in faunivores than in florivores, reflecting their respective dietary protein levels. When a bird consumes a very low carbohydrate diet, it must synthesize glucose from amino acids. The deamination and catabolism of most of the amino acids provide intermediates of glycolysis or the citric acid cycle, which can be converted to glucose. Gluconeogenesis is particularly active in faunivores, for example, the barn owl (*Tyto alba*) has lost some of its capacity to down regulate gluconeogenesis from amino acids, presumably because of the paucity of glucose from its diet.

With a decrease in body size, the energy needs increase proportionally more than protein needs resulting in a decline in dietary protein requirement (Klasing 1998). This could be due to the ravenous demands for energy drives the high rates of food intake and permits its daily requirements for protein to be met at low dietary concentrations or due to dietary protein requirements decrease with activity levels because high energy needs associated with foraging and thermoregulation drive consumption of greater amounts of food.

The amount of body fat is mostly affected by the level of metabolizable energy intake relative to energy expenditure (Klasing 1998). This relationship depends on appetite and food availability. However, the composition of the diet impacts the amount of fat that is deposited, independent of energy intake. The protein to calorie ratio directly affects fat deposition. A wide ratio (high dietary protein) minimizes fat storage and

enhances muscle deposition, whereas narrow ratios result in more adipose tissue. Fat deposits provide insurance against variability in food supply and ebbs in food-acquisition capabilities due to weather or disease. Counterbalancing these infrequent benefits is a variety of associated costs, including pathological costs, impaired reproduction, and increased susceptibility to predators or injury due to lessened flight capacity and maneuverability.

Birds excrete most of their waste nitrogen as uric acid rather than urea or ammonia (Klasing 1998). Uric acid is a purine synthesized in the liver and to some extent, by the kidney. Amino nitrogen is transaminated to uric acid and eventually to glutamic acid. Mitochondrial glutamine synthetase detoxifies ammonia arising from amino acid catabolism and the glutamine synthesized by this reaction freely diffuses into the cytosol, where uric acid is synthesized. Amidophosphoribosyltransferase is the primary regulatory enzyme in uric acid production and its activity changes directly with dietary protein level. The disposal of excess amino acid nitrogen by the uric acid synthetic pathway by birds results in greater requirements for arginine, methionine, and glycine than mammals. High amounts of arginine are required, even at maintenance, because it is not synthesized due to the lack of a urea cycle. One mole of glycine is consumed in the synthesis of each mole of uric acid. Thus, the metabolic demand for glycine is great and cannot always be met by endogenous synthesis, resulting in a dietary requirement. The consumption of glycine and methionine during uric acid synthesis causes the requirement for these two amino acids to increase directly with increasing dietary protein. Further, uric acid is a relatively reduced molecule and its excretion is accompanied by the loss of more energy than in urea excretion ($3.75 \text{ ATP mol}^{-1}$ of N

versus 2 ATP mol⁻¹ of N). Although uric acid is the most prevalent nitrogenous excretory product, ammonia excretion is relatively high in birds. Chickens fed high protein diet excrete about 25% of their nitrogen as ammonia and this proportion decreases with the dietary protein level. Freshwater ducks excrete large amounts of ammonia since they have access to copious amounts of water and do not have the osmotic necessity to excrete just uric acid (Klasing 1998).

The mineral requirements of species that have digestive strategies that diverge from that of granivorous domestic species will require refinement (Klasing 1998). The digestibility of a mineral, its utilization for specific metabolic processes and rate of endogenous excretion following absorption depend upon the chemical form in which it is found in the diet. Other factors inherent in a food, such as level of fiber, chelators, other minerals, and pH, markedly impact the digestion and metabolism of a mineral. For this reason, the value of food as a mineral source depends upon the concentration and chemical form of the mineral, as well as a wide variety of food specific factors. From a nutritional viewpoint, calcium is the most challenging mineral, because the requirement is extremely variable, depending upon a bird's physiological state, and because many foods are likely to be deficient in calcium. Calcium is one of the most metabolically active minerals and its metabolism is tightly regulated. The primary form of calcium in the shells of these prey items is calcium carbonate, an inorganic form of calcium. This can readily be solubilized by the acid environment of the proventriculus and gizzard.

Nutrient and energy content, as well as digestibility, can vary with both species and size of bivalves (Jorde and Owen 1988; Bustnes and Erikstad 1990; Richman and Lovvorn 2002). Size selection of bivalves has been observed in various organisms, such

as crabs and waterfowl (Draulans 1982, 1984; Bustnes and Erikstad 1990; de leeuw and van Eerden 1992; Ebersole and Kennedy 1994; Bustnes 1998; Hamilton et al. 1999; Richman and Lovvorn 2002, 2003). Size selection was described as a function of differential handling times, meat to shell ratios on nutrient gain relative to passage rates, or avoiding prey that is too large for consumption. Crushing resistance of the shell may also affect the selection of a prey species and size for a predator (Navarro et al. 1989; Richman and Lovvorn 2002, 2003). But the effects of attachment by byssal threads produced by mussels has seldom been studied for diving ducks preying on bivalves attached to hard substrates.

The potential value of a food for supplying energy or a particular nutrient can be determined by chemical analysis, but the actual value of a food to the animal can be arrived at only after allowing for the inevitable losses that occur during digestion, absorption, and metabolism (Hume 2004). The digestibility of an prey item has important implications in studies of nutritional ecology, resource exploitation, and energy flow through ecosystems. As Townsend and Hughes (1981) demonstrated, given an array of potential prey (e.g., bivalves) that differ in accessibility (e.g., capture, buried versus attached) or in energy content, there should be an optimal choice of prey that provides the maximum net rate of energy return (energy provided by prey minus energy required to find and eat prey) to a predator (e.g., scoter).

Purpose of Research:

In this study we measured the nutrient composition, shell strength, and digestibility of *I. recurvum* and *M. lateralis* by surf scoters. We also determined the functional responses of scoters foraging on *I. recurvum* attached to simulated oyster beds

and on *M. lateralis* buried in sand at the bottom of a large dive tank. By combining data on foraging responses, digestibility, and estimated foraging energy expenditure, we created a model to compare the foraging values (costs – benefits) of *I. recurvum* and *M. lateralis*. This comparison provided insights into possible effects of a shift in availability of prey species on the foraging energetics of surf scoters wintering in the Chesapeake Bay.

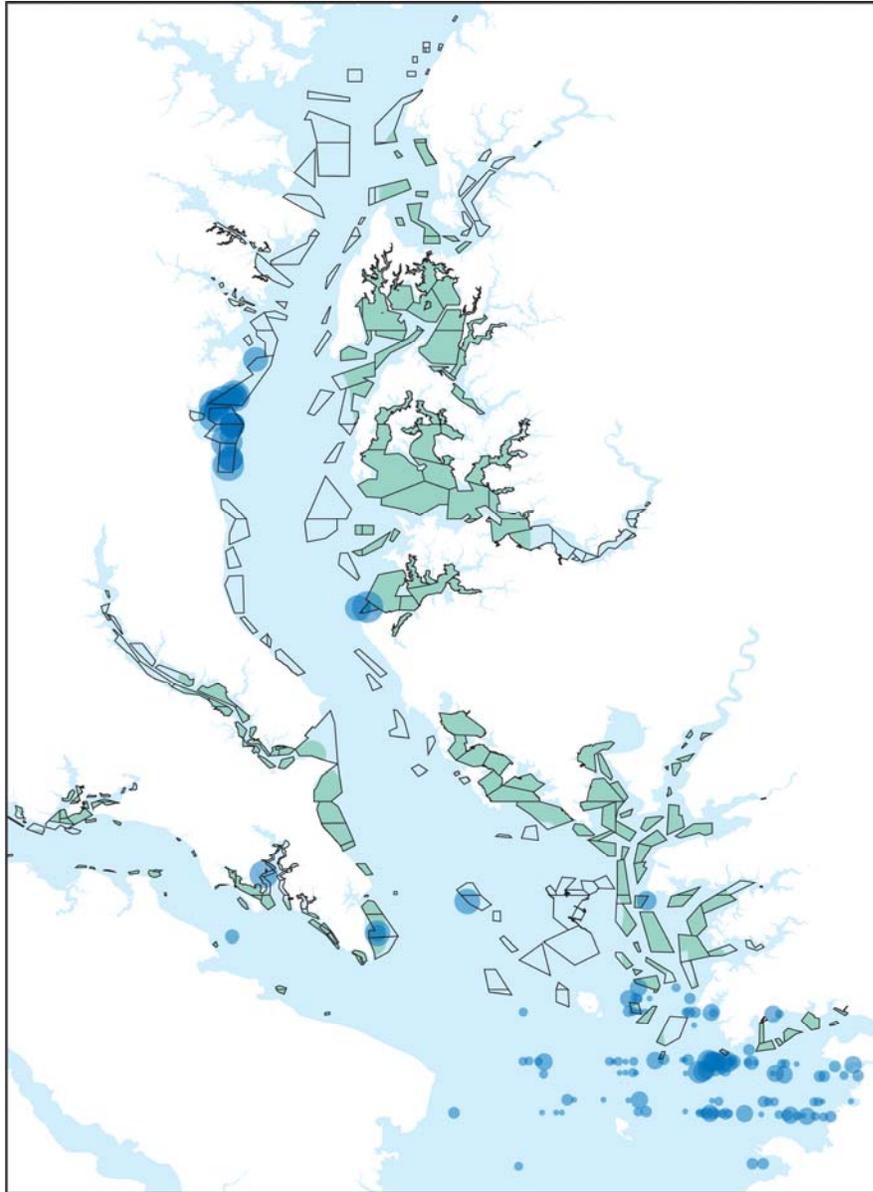


Figure 1. This map portrays the decline in the oyster beds with all the black polygons (MD DNR) representing the historic oyster bars and the black polygons filled in with green areas represent the present oyster bars (adapted from Gottlieb and Schweighofer 1996). The blue dots represent the feeding flocks of surf scoters in winter. The larger and darker blue dots represent a greater number of ducks in that area.

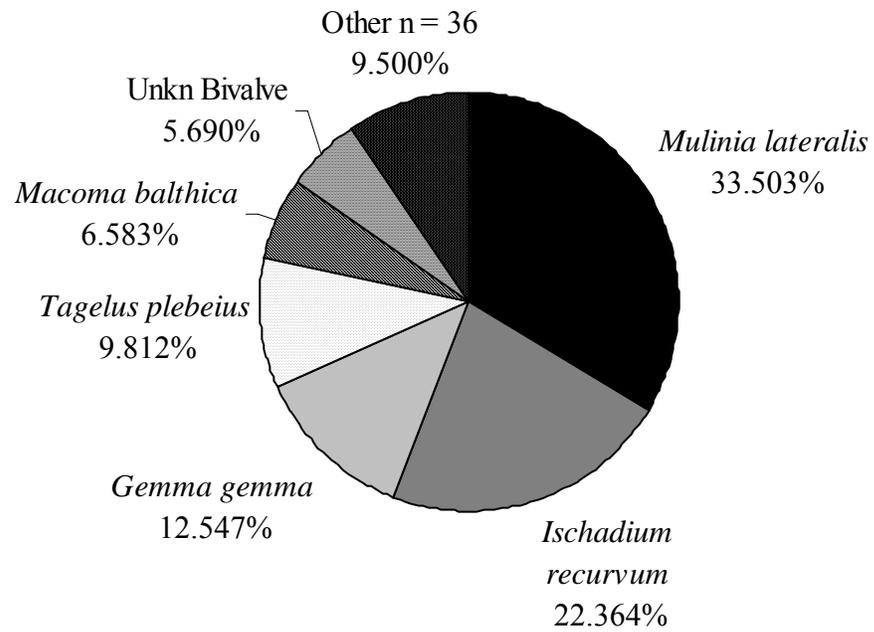


Figure 2. The present food habits for surf scoters wintering in the Chesapeake Bay (n = 278). There are 36 other species of prey that were found in trace amounts and summed to create the “other” category (Perry et al. 2006a).



Figure 3. The distribution of surf scoters in North America. Notice that one of the primary wintering areas on the East coast is the Chesapeake Bay (encircled in red) (Savard et al. 1998).

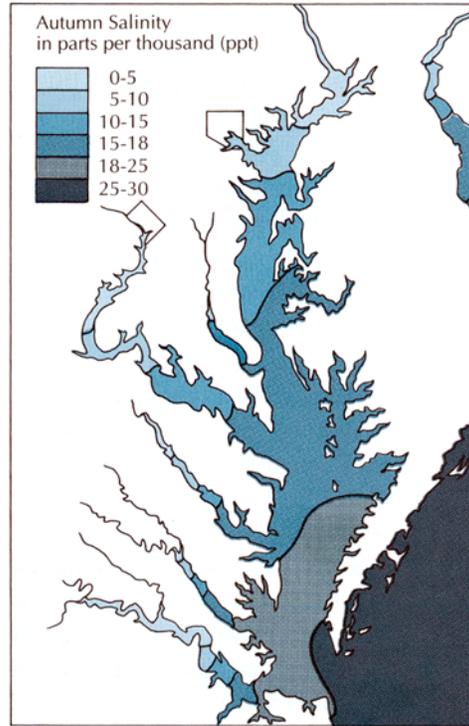


Figure 4. The salinity gradients present in the Chesapeake Bay in autumn (White 1989).

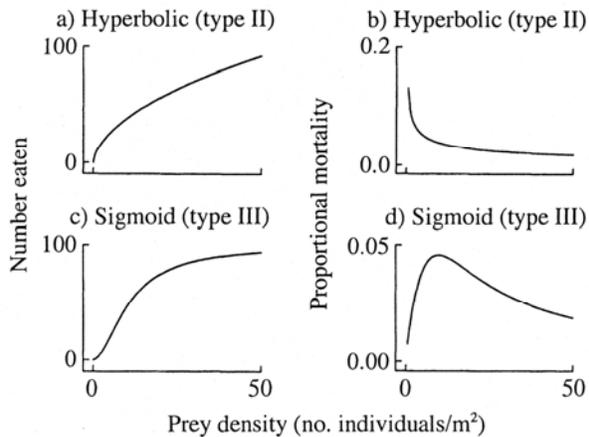


Figure 5. Functional response curves for the number of prey eaten as a function of prey density. Curves were generated with a general model by using different values of β for (a) hyperbolic and (c) sigmoid relationships. (b, d) The first derivative or, as an approximation, Y/X , of the functional response curves depicts the proportional mortality as a function of prey density (Seitz et al. 2001).

Chapter One. Captive management and propagation of surf scoter ducklings and adults.

Abstract:

Declining surf scoter (*Melanitta perspicillata*) populations wintering in the Chesapeake Bay have stimulated research on the factors responsible for causing this decline. A captive colony of surf scoters was established at Patuxent Wildlife Research Center (PWRC) to research foraging energetics as a key factor to scoter survival. Sixteen eggs collected from Lac Malbaie, Quebec, Canada, were transported to PWRC, and incubated at 37.5°C and 70% humidity until pipped. Once the ducklings were hatched, growth measurements including weight (g), culmen length (mm), and tarsus length (mm) were monitored throughout development. As ducklings grew, they were provided access to increasingly deeper water. Ducklings were fed Mazuri Duckling Starter diet until 2 months of age when they were switched to Mazuri Seaduck Diet. The ducklings were also offered mealworms to encourage them to dive for food. Ninety four percent of the eggs hatched, but 40% duckling mortality occurred within the first week after hatch due to an unknown bacterial infection. Duckling weight (g) increased exponentially until it plateaued at approximately 750 g at 45 days after hatch. Duckling culmen length (mm) increased linearly, but no apparent trend was found for tarsus length (mm). All adult ducks were kept in an outdoor pen facility with constantly running fresh water, but to reduce chance of disease, such as aspergillosis, saltwater was offered in bowls; any wet food discarded; and all feed trays and huts were disinfected daily. PWRC is the only site in North America to successfully raise surf scoters in captivity. Here we provide information on duckling growth, management techniques for this species, and

benchmarks for growth and maturation, that were not previously documented. Data from these ducks have provided and will continue to provide researchers with the rare opportunity to learn more about this declining species.

Introduction:

Summary reports of the status of seaducks reveal population declines for some species with increased concern for the status of seaducks in general (Elliot 1997; Kehoe 1994; Petersen and Hogan 1996). Surveys of seaducks wintering on the Atlantic coast (1991-99) have shown major declines for the surf scoter (*Melanitta perspicillata*; Caithamer et al. 2000) necessitating further research on this species.

Surf scoters usually breed in shallow lakes mainly less than 10 ha in size and that are usually saturated in oxygen, clear, and with very little emergent vegetation (Savard et al. 1998). Lac Malbaie, Quebec, Canada harbors about 50-60 breeding pairs of surf scoters, is 664 ha in size, and 54% of its area is less than 2 m deep. They nest usually in a hollow in the ground lined with down and vegetative debris, such as mosses, twigs, needles, and bark.

Research on foraging energetics provided the rare opportunity to raise and observe surf scoters in captivity. This is the only captive colony of surf scoters in North America, and its establishment has enabled the collection of more details about the growth of these ducklings and the management of these ducks. This species breeds in very remote locations and the ability to take repeated measurements in the field is challenging. The purpose of this study was to provide baseline knowledge on raising surf scoters in captivity and to determine the growth trends of surf scoter ducklings raised in captivity.

Methods:

Surf scoters eggs were collected from Lac Malbaie, Quebec, Canada in June 2003, one of the few known breeding areas of surf scoters along the Atlantic flyway that was both readily accessible and well studied. Nests were located on the islands on Lac Malbaie by walking systematic transects across the island and disturbing the underbrush with a stick to flush the female from the nest.

The eggs were candled in the field to determine stage of incubation, marked with a hen and egg number for individual identification, and placed in a portable incubator. The eggs were then transported to Laurel, Maryland, USA where measurements were taken for length (mm), width (mm), and weight (g) prior to placing in an incubator until hatch. The incubator was maintained at 37.5°C and 70% humidity until pipped, the first crack in the shell (G.Q.F. Manufacturing, Inc., model 1502). Once pipped, the eggs were transferred to a different incubator that was maintained at 37.5°C and 80% humidity (G.Q.F. Manufacturing Inc., model 1550). Once the duckling hatched, emerged from the shell, and was completely dry, it was removed from the incubator. The duckling was weighed; culmen and tarsus were measured; and it was web tagged for individual identification. Growth measurements were taken on all ducklings every week. These measurements included weight (g), culmen length (mm), and tarsus length (mm).

After morphometric measurements and tagging, ducklings were placed in a plastic tank with a vinyl-coated wire platform with ramp, gravel, and approximately 2 cm of water. The tank was equipped with a small standpipe that maintained the water level and allowed for fresh water to constantly flow through the tank. All ducklings were fed Mazuri[®] Duckling Starter Diet (number 5641, PMI Nutrition International, Brentwood,

MO; 20% protein) ad libitum until they were 2 months of age, after which they were fed Mazuri[®] Seaduck Diet (number 5681, PMI Nutrition International Brentwood, MO; 21.5% protein) ad libitum. The tank was equipped with a heat lamp to provide added warmth, but the tanks were located in a well ventilated greenhouse type room. This allowed plenty of light and the environment to be controlled. The ducklings were checked every 8 hours, fed, and the tanks were cleaned to reduce chances of disease.

A total of four plastic tanks were setup in this fashion each with a different water level. Once the ducklings were two weeks old, they had acquired their waterproofing and were strong enough to swim in deeper water. Subsequently they were moved to the next tank, which contained 4 cm of water and no gravel. In this tank the ducklings were able to swim and search underwater for food. After one week in this tank they were moved to the next tank, which once again only differed in that it contained approximately 6 cm of water and was a larger tank. This tank allowed the ducklings enough room to dive underwater for food. After another week they were moved to the final tank of the same size that contained 8 cm of water. After another week in this tank they were considered mature enough to go to the larger brood tanks outside.

These tanks were long stainless steel half cylinder ponds that were about 24 cm deep with constantly flowing water. The ducklings remained in these ponds until they were approximately two months old when they were moved to larger ponds where the adult ducks were kept. At this time the web tags were removed and adult bands were placed on the right leg of the females and the left leg of the males. Sex of the ducklings was determined by cloacal examination for a penis. These 11.5 m² pens contained a conical rubber-lined pool (2.1 m diameter, 70-80 cm deep at the center) with constantly

flowing fresh water. To help protect the ducks from airborne diseases, such as aspergillosis, they had access to salt water (35 ppt salinity) prepared by mixing sea salt (Instant Ocean, Aquarium Systems, Mentor, OH) with fresh water in a stainless steel bowl. In addition, all the tanks were cleaned and disinfected everyday and all ponds were cleaned every two weeks. All plastic food trays and huts were disinfected everyday. The pens contain a smooth gravel substrate that allowed for the feces to be washed away whenever it would rain. However, if any feces accumulated during drought conditions the gravel was hosed daily to reduce chances of bumblefoot, a condition caused by bacteria from standing in fecal matter. To monitor the health of the ducks the amount of food fed daily was recorded and the ducks were given health checks every month by the veterinarian at PWRC.

In order to use these ducks in a foraging energetics study they had to be trained to dive in a large tank for natural prey items. This required approximately four months of extensive training. Firstly, the ducks were offered the natural prey items in their food trays without any commercial diet. Once they were readily eating the natural prey item, the food trays were removed from land and suspended over the water to teach the ducks to forage on the water. Once they were familiar with this technique, the trays were slowly lowered into the pond to acclimate them with foraging underwater. After these steps were completed, the ducks were introduced to the dive tanks. The water level in the tanks was lowered to approximately 1 m and groups of individuals that were usually penned together were placed in a tank and left there for 8 hours a day. Mealworms and corn were offered in the study trays in the bottom of the tanks, which taught them that food was available in the bottom of the tank. This process was repeated for several days

until they were accustomed to feeding from the trays. At this point the water level was slowly increased to build up their diving fitness. Once the desired water level was reached, the ducks were offered the natural prey item, mussels (*Ischadium recurvum*) glued to a artificially created oyster bar (*Crassostrea virginica*) using Superglue® or clams (*Mulinia lateralis*) buried in sand. This design was created for a study on surf scoter foraging energetics. The final step was to slowly reduce the number of ducks in the tank at one time. Once there was only one individual regularly foraging in the tank, the official trials began.

Results:

Of the sixteen eggs collected and successfully transported to PWRC, fifteen successfully hatched, but only 9 ducklings survived to adulthood. Four ducklings died within the first week after hatching from unknown causes and one died within the first week from a bacterial infection. Mean egg length was 64.5 ± 3.12 mm (± 1 SD); egg width was 43.9 ± 1.75 mm; and mean egg mass was 64 ± 9 g. Duckling weight (g) increased exponentially up to asymptote at approximately 750 g and 45 days from hatch and culmen length (mm) linearly increased with time (day; Figure 6 and 7). There was no trend detected for tarsus length (mm). Of the four seaduck species present in the Patuxent colony, there have been no adult mortalities from diseases among the surf scoters. All the scoters dove regularly in groups, but only five of the nine individuals were willing to dive alone.

Discussion:

Lesage et al. (1997) measured surf scoter eggs and ducklings at Lac Malbaie, Québec. The average egg breadth/clutch ranged from 41.9 mm ± 0.1 SE in a nest with 8

eggs to $45.8 \text{ mm} \pm 0.1 \text{ SE}$ in a nest with 6 eggs; similarly, average egg length ranged from $58.9 \text{ mm} \pm 0.4 \text{ SE}$ (nest with 7 eggs) to $66.5 \text{ mm} \pm 0.6 \text{ SE}$ (nest with 6 eggs; $n = 22$ clutches). In one nest at Laforge Reservoir, n. Québec, average breadth of 6 eggs was $42.5 \text{ mm} \pm 0.1 \text{ SE}$; average length $61.4 \text{ mm} \pm 0.5 \text{ SE}$ (Savard et al. 1998). Altogether, 160 eggs from 23 clutches in Québec averaged $43.9 \text{ mm} \pm 0.1$ in breadth and $62.4 \text{ mm} \pm 0.2$ in length (Savard et al. 1998). Mean measurements from Western Foundation for Vertebrate Zoology (WFVZ) were 66.2 mm (range 64.4–68.0) x 46.1 mm (range 44.8–47.4; $n = 2$ clutches composed of 6 eggs). Eggs decrease in mass throughout incubation and, therefore, since the eggs collected for this study were previously incubated, mass values could be confounded by this factor. Average egg mass/clutch, from 22 nests at Lake Malbaie, Québec, ranged from $55.9 \text{ g} \pm 0.7 \text{ SE}$ (clutch of 8 eggs) to $78.0 \text{ g} \pm 0.6 \text{ SE}$ (clutch of 6 eggs). Mass of eggs in the heaviest clutch ranged from 76 to 79 g, probably close to mass of fresh eggs. In three clutches examined twice, average egg mass declined by 4.6 g in 12 d ($64.9 \text{ g} \pm 0.8 \text{ SE} - 60.3 \text{ g} \pm 0.9 \text{ SE}$, $n = 7$ eggs) in one clutch, by 1.7 g in 6 d ($61.0 \text{ g} \pm 0.2 \text{ SE} - 59.3 \text{ g} \pm 0.3 \text{ SE}$, $n = 9$ eggs) in another, and by 1.8 g in 6 d ($66.6 \text{ g} \pm 0.7 \text{ SE} - 64.9 \text{ g} \pm 0.7 \text{ SE}$; $n = 8$ eggs) in third clutch (Savard et al. 1998). These data support the measurements obtained from the 16 eggs collected for the establishment of the captive colony.

In addition, the authors observed rapid growth with body mass increasing 18-fold in 55 d, from around 44 g to about 817 g (Lesage et al. 1997, Savard et al. 1998). This directly corresponds with the growth rate found in the surf scoter ducklings raised in this study. Growth began to slow down and level off at approximately 45 to 50 days of age. The measurements obtained for culmen length also corresponded to the values reported

by Lesage et al. (1997). However, the measurements for tarsus length were smaller, but this could be due to the techniques used to obtain these measurements. The tarsus was measured from the middle of the joint of the hock to the middle of the joint at the wrist, which was slightly different from their methods. Combining these data with the previously published data provides an overview and a baseline of surf scoter duckling growth, especially since measurements in this study continued later into development. These data provide a useful baseline for veterinarians and other biologists for management of captive duck populations and are useful to examine the effects of contaminants and other growth deterrents on the development of surf scoters and their eggs.

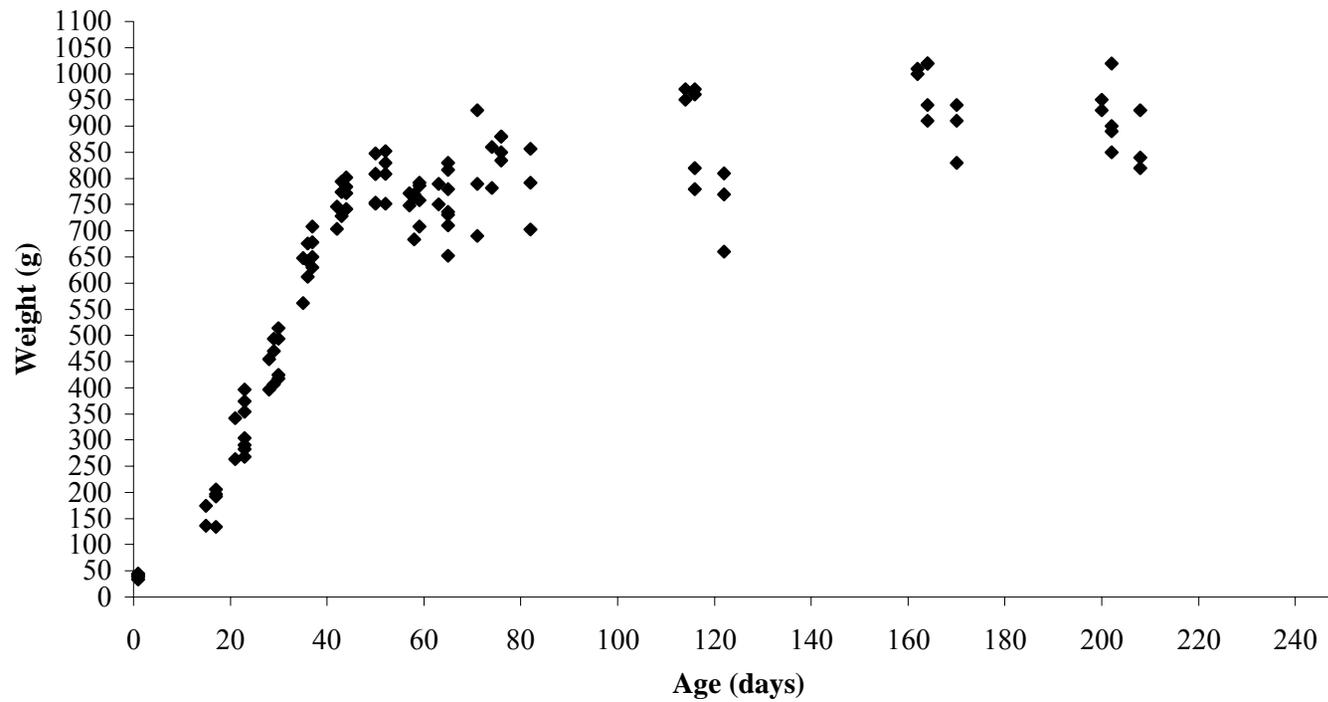


Figure 6. The relationship determined between weights (g) as a function of age (day) for captive surf scoter ducklings raised at Patuxent Wildlife Research Center. Weights were measured weekly from hatch until 7 months of age.

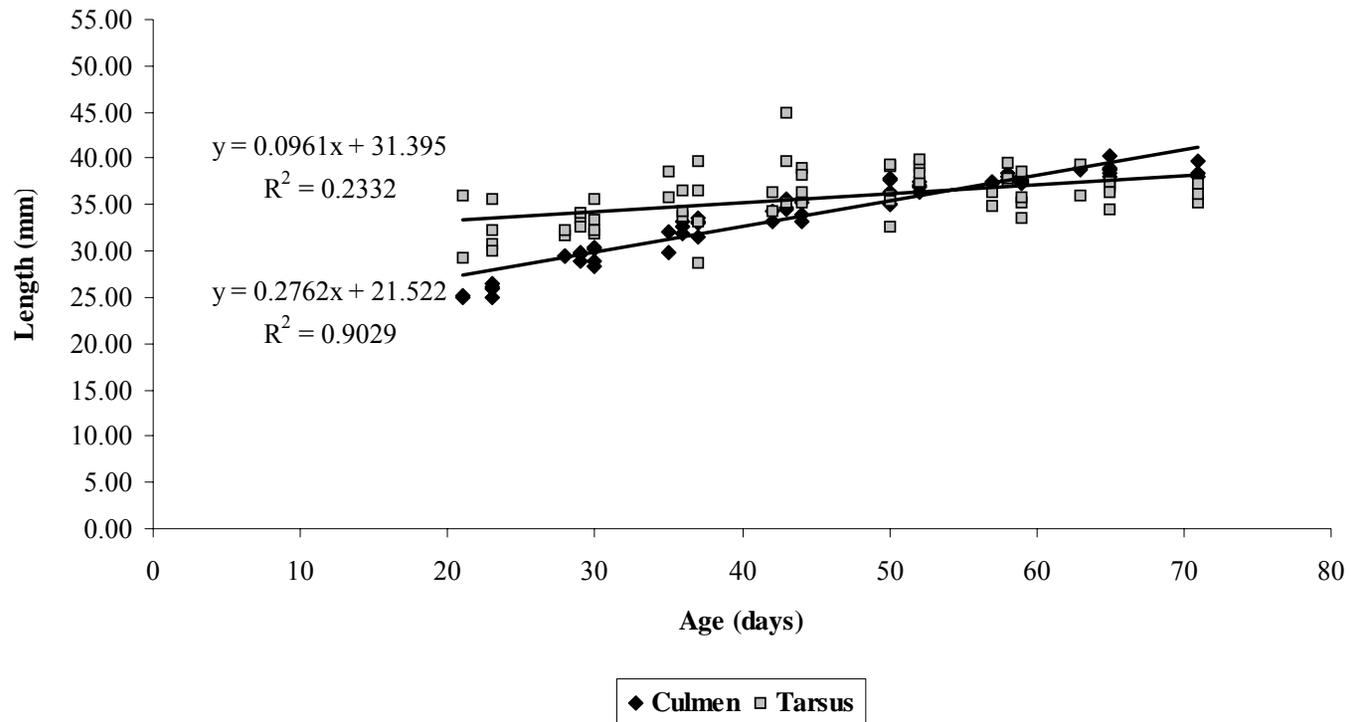


Figure 7. Age-related culmen and tarsus length (mm) of the nine surf scoter ducklings hatched at Patuxent Wildlife Research Center.

Chapter Two. Comparison of the composition, shell strength, and metabolizable energy of *Mulinia lateralis* and *Ischadium recurvum* for wintering surf scoters.

Abstract:

Declines in surf scoter (*Melanitta perspicillata*) populations wintering in the Chesapeake Bay could be due to changes in the availability of benthic bivalves. Over the past 50 years, the Bay has become extremely eutrophied causing drastic changes in the benthos available to surf scoters. The subsequent decline in oyster beds (*Crassostrea virginica*) has reduced the hard substrate needed by the hooked mussel (*Ischadium recurvum*), one of the primary prey items for surf scoters, and induced the surf scoter to switch to a more opportune prey species, the dwarf surfclam (*Mulinia lateralis*). In this study, the composition (macronutrients, minerals, and amino acids), shell strength (N), and metabolizable energy (kJ) of these two prey items was quantified to determine the relative foraging values for wintering scoters. Pooled samples of each prey item were analyzed by CEPS Central Analytical Laboratory at University of Arkansas (CEPS) to determine composition and shell strength (N) was measured at University of Maryland (UM) using a compression test until the shell first cracked. Total collection digestibility trials were completed on eight captive surf scoters at Patuxent Wildlife Research Center (PWRC). For the prey size range commonly consumed by surf scoters (6-12 mm for *M. lateralis* and 18-24 mm for *I. recurvum*), *I. recurvum* contained higher ash, protein, lipid, and energy per individual organism than *M. lateralis*. *M. lateralis* consisted of more potassium, calcium, selenium, and sodium than *I. recurvum*. *M. lateralis* also contained more aspartic acid, asparatine, and arginine (% g) than *I. recurvum*. However, *I. recurvum* contained more glycine than *M. lateralis*. *I. recurvum* required significantly

greater force to crack the shell relative to *M. lateralis*. There was no significant difference in the energy metabolized from each prey item by wintering surf scoters.

Despite *I. recurvum*'s higher ash content and harder shell than *M. lateralis*, wintering surf scoters were able to obtain the same amount of energy from each prey item and would be able to sustain themselves with a shift in prey availability.

Introduction:

Reports of the Atlantic coast surf scoter populations have indicated steady declines (unpub. USFWS survey data) and one of the primary wintering areas for surf scoters along the Atlantic flyway is the Chesapeake Bay. While wintering in the Bay the ducks primarily prey on two food items, the hooked mussel (*Ischadium recurvum*) and dwarf surfclam (*Mulinia lateralis*; Perry et al. 2007). *I. recurvum* is an epifaunal organism that utilizes the oyster beds (*Crassostrea virginica*) in the Bay as its primary habitat. However, disease and over harvesting have caused major declines in the oyster populations, with lack of regeneration of beds, increased sedimentation, and reduced hard substrate. In addition to a loss in available substrate, there has been an increase in the severity, duration, and frequency of anoxic events in the deep areas of the Bay and some of its tributaries (Officer et al. 1984; Seliger et al. 1985; Tuttle et al. 1987). This has potentially devastating consequences for benthic organisms including reduced benthic biomass, species diversity, and altered structure (Holland et al. 1977; Seliger et al. 1985; Dauer and Ransinghe 1992; Kemp and Boyton 1992; Dauer et al. 2000). With the loss of substrate and the increase in anoxic events, the abundance or occurrence of surf scoters in those areas could be negatively affected.

Restructured benthic communities due to hypoxia (Diaz and Rosenberg 1995) tend to be composed of large numbers of opportunistic species and a decreased number of equilibrium (larger and long-lived) species (Dauer and Ransinghe 1992). Opportunistic species are characterized by short life cycles (Dauer and Ransinghe 1992), high fecundity, and large recruitment pulses (Holland 1985). Although surf scoters may select *M. lateralis*, the prevalence of this opportunistic species and the relatively low percentage of equilibrium species (e.g., *Mya arenaria* and *Macoma balthica*) in the food habits of surf scoters suggest the possibility that hypoxic events may be affecting prey selection by scoters (Kidwell 2007). Firstly, the ducks may be induced to feed on another food item, *M. lateralis*, which may not be as energetically efficient for them. In addition, *M. lateralis* may not be available in the same sizes as *I. recurvum* and, therefore, may not provide enough energy on a per dive basis relative to mussels. Secondly, reduced habitat availability for mussels could increase densities in existing habitats, which could potentially benefit scoters. However, as Petersen and Black (1988) reported the energetic value of the mussels may decline due to overcrowding, which could influence the foraging response of a scoter. As Sudgen (1971) stated, there is a minimal density of an organism where it may no longer be profitable for a scoter to seek it. Basically, the net energy gain obtained from that organism is exceeded by the cost associated with obtaining that prey item. Therefore, as the quality and/or quantity of food declines, ducks may travel farther between suitable food items or food patches to maintain adequate energy intake.

Ultimately, surf scoters should select the prey item that provides the maximum net rate of energy return (energy provided by prey minus energy required to find and

consume prey; Townsend and Hughes 1981). Measurements of metabolizable energy are essential in order to define the efficiency of utilization of nutrients within food, to classify the nutritional quality of a food item. For a given prey item, the metabolizability of energy is determined by the prey's chemical makeup and by the digestive physiology of the duck; and measures the sum of activities within the gastrointestinal tract including size reduction, autoenzymatic hydrolysis, alloenzymatic hydrolysis, microbial synthesis, rate of passage, and endogenous losses (Klasing 1998). A duck must choose a foraging strategy that compromises efficiency for low digesta volumes and high total rates of nutrient extraction (Klasing 1998).

The goal of this study was to evaluate the composition (macronutrients, minerals, and amino acids), shell strength (N), and metabolizable energy (kJ) of the top two prey items, *I. recurvum* and *M. lateralis*, for surf scoters in order to determine whether one prey item was more beneficial than the other. This allowed an estimation of whether the surf scoter could maintain their energetic needs if the availability of these two prey items was altered.

Methods:

Dry mass, ash mass, and ash free dry mass:

The dry mass (g), ash mass (g), and ash-free dry mass (g; AFDM) of 30 *I. recurvum* and approximately 25 *M. lateralis* were measured for each size (length) class (6-12, 12-18, 18-24, 24-30, 30-36, 36-42 mm; Table 1). *M. lateralis* samples were not larger than 18 mm so the analyses for this species included only two size classes (6-12, 12-18). In order to examine the seasonal differences in the dry mass (g), ash mass (g), and AFDM (g) of *I. recurvum*, these analyses were completed on 30 individuals per size

class collected throughout the year (January, February, March, May, June, and July). To determine dry mass, all specimens were weighed to the nearest 0.001g and oven dried separately at 50°C to constant mass. Individual whole bivalves were then burned in a muffle furnace at 500°C for 6 hr to yield AFDM.

Nutrient Content:

To determine nutrient content, at least ten pooled bivalves of each size class (20-25 individuals for smallest size classes) collected in winter were sent to CEPS. For *I. recurvum*, additional pooled samples collected in May were analyzed. Protein (%g DM), lipid (%g DM), energy (kJ/g DM), ash (%g DM), dry matter (DM; %g), and mineral content (ppm) of these pooled individuals were determined by CEPS (AOAC 990.03, AOAC 920.39c, ANSI/ASTM D2015-77, AOAC 923.03, AOAC 934.01, and AOAC 968.08). These fractions of protein, lipid, and energy for pooled samples were then converted to absolute amounts (g per individual organism) by multiplying them by the dry mass of each species, size class, and month (January and May) as determined earlier. In addition, to detect any differences in the protein content of these species, amino acid analyses were completed on these pooled samples at CEPS (AOAC 982.30a). The % gram amounts for each amino acid were normalized to lysine to better align differences between profiles of each prey item. The mineral and amino acid analyses were completed on only one pooled sample per size class. It was determined that there was equal contribution by individuals to these data and with the accuracy of 1-2% for these methodologies these single samples were considered representative of the content for these prey species. Therefore, multiple measurements were not performed by CEPS.

Shell Strength:

Shell strength (N) was measured on approximately 20 individuals of each prey species using a compression test at UM. An Imada Force Measurement System was used with a digital force gauge, which monitored the force (lbf) applied to the shell surface and recorded the force at the exact moment the shell cracked. The pressing surfaces of the meter contacted the opposing shells just below the umbo and the force was gradually increased until the shell first cracked.

Metabolizable Energy:

Nine surf scoters (5M: 4F) were raised from eggs collected from Lac Malbaie, Quebec, Canada. All methodologies that involved these ducks were conducted under institutional ACUC approved protocols at the PWRC and UM, College Park committees approved before the experiments were initiated. When not in feeding trials, the scoters were kept in an outdoor pen facility and fed ad libitum Mazuri[®] Seaduck Diet (number 5681, PMI Nutrition International Brentwood, MO; 21.5% protein). Grit was provided ad libitum next to the feed trays. Grit was not supplied for two weeks before and during the trials to prevent variability due to grit in the excreta mass and nutrient analyses.

I. recurvum collected from the Chesapeake Bay in March 2007 were frozen and thawed to room temperature before experiments. We were unable to collect an adequate supply of *M. lateralis* from the Bay; therefore individuals were purchased from Woods Hole Marine Laboratory. The nine surf scoters were randomly placed in individual wire cages with removable trays lined in plastic in May 2007. Each duck was weighed before and after each trial to determine body mass (g) loss. Feeding trials consisted of a 24 hour acclimation period where excreta were collected every 4 hours, a single force feeding of

25 g fresh mass of clams or mussels, and a 48 hour collection period where excreta were collected every 4 hours. Ducks were force fed 25 grams (fresh mass) of 12-18 mm *M. lateralis* and 25 grams (fresh mass) of 18-24 mm for *I. recurvum*, the two size classes that are commonly consumed by scoters, in a cross-over experimental design (Figure 8). Each scoter was fed the randomly assigned test diet by placing thawed bivalves at the back of the throat with a feline pill gun and flushed down the esophagus with water. Any prey regurgitated immediately was once again force fed and flushed with more water. If any was regurgitated overnight this was weighed and deducted from the amount fed. The amounts fed (fresh mass; g; ingesta) were then converted to dry matter (g), ash (g DM), lipid (g DM), and energy (kJ) using values determined earlier in the study. Nitrogen (g) in the ingesta was determined by multiplying the amount fed (g) on a dry matter basis of protein (g DM) and multiplying it by 6.25. Both feces and excretory wastes (excreta) were collected and analyzed together. The excreta were collected into plastic urine cups with a spatula, preserved in 10 ml of 0.1M sulfuric acid, and frozen until analyzed. During analyses, samples were freeze dried and sub samples were ground and homogenized by day for each duck. These homogenized samples were analyzed by CEPS for energy (kJ/g DM), lipid (%g DM), nitrogen (%g DM), and ash (%g DM) content. The excreta mass per day (g/day) were multiplied by the gram DM for ash, lipid, and nitrogen to determine absolute amounts of each nutrient for each duck. In addition, the energy in the excreta (kJ/g) was multiplied by the amount of excreta on a dry matter basis per day per duck. Based on these data the following equations were calculated:

Apparent Digestible Energy (ADE; %) = $[(\text{Gross energy intake} - \text{gross energy excreted}) / \text{Gross energy intake}] * 100\%$

Nitrogen Energy Balance (NEB; kJ) = $(\text{Nitrogen intake} - \text{Nitrogen excreted}) * 36.5$; the 36.5 is the mean energy content (kJ) per gram urine-nitrogen in birds (Titus et al. 1959; Sibald 1982; Richman and Lovvorn 2003).

Metabolizable Energy (%) = $[(\text{Gross energy intake} - (\text{gross energy excreted} + \text{nitrogen balance})) / \text{Gross energy intake}] * 100\%$

The correction for nitrogen balance was needed because the energy in excreta from endogenous sources can otherwise result in underestimates of metabolizable energy (Karasov 1990, Richman and Lovvorn 2003).

Analyses:

Regression analysis was used to predict changes in dry mass, ash mass, and AFDM, and shell strength as a function of size class for each prey species. Based on residual plots, the data were log transformed before analyses when it was appropriate. Bonferroni pairwise comparisons were used to detect differences between means for dry mass, ash mass, ash-free dry mass, macronutrient content and shell strength within each size class by season and by species. For metabolizable energy trials two-tailed t-test were used to detect differences between the two prey items. When a significant difference was detected for the dry matter of ingesta (g) the remaining ingesta factors were weighted for dry matter and analysis of variance was used to test for significance. Due to the possible carry over of nutrients from the commercial diet provided during the acclimation period the results obtained on the day the ducks were force fed were excluded. All tests were

considered significant at the 5% level and all analyses were completed using SAS (Proc Mixed, SAS Institute 2003).

Results:

Dry mass, ash mass, and ash free dry mass:

Dry mass, ash mass, and ash-free dry mass significantly increased nonlinearly with increasing prey length for all seasons and both prey items ($p < 0.0001$; Figure 9, 10, 11). Mean comparison on seasonal differences by size classes for *I. recurvum* indicated that there was a significant difference in AFDM between January, March, and May (spring) mussels 18-24 mm in length ($p = 0.0023$; Table 2). January mussels of this size contained more AFDM than March or spring mussels. There was also a significant difference in dry mass and AFDM between the two prey species within the 6-12 mm size class ($p < 0.0001$ for both, Table 3). But in the 12-18 mm size class, there was no significant difference found between the two prey species for dry mass, ash mass, and AFDM ($p = 0.3255$, $p = 0.0606$, and $p = 0.3239$, respectively).

Nutrient Content:

Macronutrients:

In general, protein, ash, lipid, and energy all increased with increasing length for *I. recurvum* regardless of season (Table 4). Protein (g per individual) contained in spring mussels was significantly higher for all size classes except for the smallest mussels where protein content was significantly lower. Spring lipid content (g per individual) was significantly higher than winter for all the larger size classes, except for 30-36 mm where lipid content in winter was higher than in spring. The lipid content in the smaller size classes was not significantly different between seasons. The energy content in spring

mussels was significantly higher for all size classes than winter mussels. When *M. lateralis* and *I. recurvum* were compared within the same size class (6-18mm) and the same season (winter), *M. lateralis* contained significantly less protein and energy, but similar amounts of lipid as *I. recurvum* (Table 5). When these two prey items were compared based on the size classes commonly consumed by surf scoters, *M. lateralis* contained significantly less protein, lipid, and energy than *I. recurvum*.

Minerals:

M. lateralis contained 82.6% more potassium, 95.6% more calcium, 94.7% more selenium, and 80.2% more sodium than *I. recurvum* (Table 6). *I. recurvum* contained 59.8% more phosphorus, 85.1% more magnesium, 19.6% more iron, 13.0% more manganese, 61.7% more zinc, and 5.0% more copper than *M. lateralis*. *M. lateralis* contained no aluminum unlike *I. recurvum*.

When a seasonal comparison was made by size class on *I. recurvum*, winter mussels consisted of more iron, manganese, zinc, copper, and aluminum than spring mussels for all size classes (Table 6). However, spring mussels contained more potassium and phosphorus than winter mussels. For most of the size classes, winter mussels predominantly contained more magnesium than spring mussels. There did not appear to be any seasonal differences in calcium and selenium. There was no apparent influence of size (length) of the mussel on its mineral content.

Amino Acids:

For convenience, the proportion of each amino acid was expressed relative to the amount of lysine (Figure 12, 13). Lysine was chosen as the standard because it is particularly well studied and metabolically it is not used extensively for purposes other

than protein synthesis. *M. lateralis* contained more aspartic acid and asparagine and more arginine than *I. recurvum* (Figure 12). *I. recurvum* contained slightly more glycine than *M. lateralis*. Seasonally smaller mussels in spring contained more glycine than smaller mussels in winter, however, in the larger mussels this relationship switches with more glycine available in the winter than spring (Figure 13). In the size class commonly consumed by scoters, 18-24 mm, the spring mussels contained more arginine relative to winter mussels. For the rest of the amino acids the winter mussels contained more than the spring mussels.

Shell Strength:

When shell strength was measured, *I. recurvum* was significantly stronger than *M. lateralis* ($F = 61.07$, $p < 0.0001$; Table 7). Shell strength increased nonlinearly with increasing length as well (Figure 14).

Metabolizable Energy:

Scoters lost on average 5% of their body mass during the experiment (Table 8). There was no significant difference in initial body mass, final body mass, or mass loss between prey items ($p = 0.8698$, $p = 0.8569$, and $p = 0.9584$, respectively). Scoters were force fed 25 g fresh mass of each prey item, but some regurgitated some of the prey. This occurred more frequently with the mussels than the clams, and, therefore, there was a significant difference in the amount of food given between prey items ($p = 0.0027$). Ash, lipid, nitrogen, and energy were significantly different between the prey items (Table 8). There were no significant differences between prey items in the mass, ash, lipid, nitrogen, and energy in the excreta. There was no significant difference between the apparent digestible energy (ADE) of each prey item ($p = 0.5733$). There was no significant

difference in the nitrogen energy balance (NEB) between prey species ($p = 0.8110$), in addition, metabolizable energy (ME) was not significantly different between prey items ($p = 0.3474$).

Discussion:

Dry mass, ash mass, ash free dry mass, and macronutrients:

The nutrient content of bivalves changes seasonally due to their reproductive cycle. For *Mytilus edulis*, a close relative (within the same family) to *I. recurvum*, increasing proportion of gonad material in the body through the late summer and autumn increases the oxygen demand of the animal (Bayne 1976). In the summer, gametogenesis is in the “resting stage” and reserves of glycogen are high; the high proportion of metabolically inert material results in a low rate of oxygen consumption per unit weight. Gametogenesis in *Mytilus edulis* is active in the winter, with utilization of glycogen stores are being utilized and the metabolic demand is increased. In the spring, a large mass of developing gametes continues to impose a high demand for oxygen which is only reduced after spawning. Active gametogenesis is in early winter and a mussel retains ripe gametes throughout winter to the spring. During autumn and winter the metabolic demand is high due to gametogenesis and the glycogen reserves fall to a minimum value mid-winter (Jan-Mar; Bayne 1976). The loss of glycogen in female mussels is synchronous with stage II – oogenesis and vitellogenesis – of the gametogenic cycle. Seasonal changes in lipid content show an inverse correlation with the changes in glycogen content. There is an increase in the level of triglycerides and phospholipids during winter – reaching a maximum during stage III of gametogenesis. This increase in lipids in winter was not observed in my results when compared to spring mussels.

However, the lipid level is generally higher in females than males due to fatty reserves of eggs. It is possible that the mussels used for this study were primarily male and therefore the changes in nutrient content were not as apparent. If lipids do increase during winter it is understandable why they would be selected by surf scoters who are trying to rapidly build up their fat reserves in preparation for migration to the breeding grounds.

The lipid level falls rapidly after spawning and then increases again as gametes mature (Bayne 1976). In the middle of summer during the non-reproductive period, the levels of triglycerides and phospholipids remain low. In contrast, in the European oyster the levels of glycogen remain high in winter and there is a positive correlation between the carbohydrate level and the percent of body fat. This suggests that when conditions are good glycogen and lipid accumulate together and when conditions are poor both are lost to a similar degree. There is no case where there is a negative correlation between glycogen and fat content. This difference between oysters and mussels may be related to the form of the reproductive cycle. Gonad development in the European oyster takes place in the spring and summer when food levels are high. Growth and gametogenesis occur at the same time and there is an increase in glycogen and lipid content. During winter there is long period of sexual rest (low metabolic demand) and both carbohydrate and lipid are available as energy reserves. In *Mytilus edulis* glycogen is synthesized in the mantle tissues during the summer and converted into triglyceride reserves in the autumn and early winter (Bayne 1976). The fatty acids are then oxidized and used as energy source during early embryonic development.

Pieters et al (1978) also found that protein and glycogen reserves, built up in summers, decreased rapidly in late autumn and winter and minima are reached next

spring, when lipid contents rise to maximum values. Glycogen reserves, accumulated in summer, are converted into lipids during gametogenesis, which are stored in ripening eggs and will be used subsequently in the larvae as energy reserve during the first life stages. They reported maximal lipid percentages of 16% of dry weight, but on the French coast maximums of 12% for females and 9% for males were found. In all cases the minimum lipid percentages were down to 6% after spawning. Both glycogen and protein seem to be important energy reserves in all tissues of *M. edulis*. In contrast to Bayne (1976), they found none of the variations in storage of energy substrates indicating a possible change-over during winter from glycogen to protein as the main energy reserve. In conclusion, the reproductive cycle can be distinguished in several stages (Pieters et al 1978). In summer the gonads are in a state of rest (stage 0) in which no sexual activity exists. The gonadal development begins in autumn (stage 1) and continues during winter (stage 2) at the expense of body reserves (Dec-Mar). In stage 3, ripening of the gonads has started and, influenced by external factors, release of gametes will be induced. During rest (stage 0) glycogen is stored in the tissues and decreases gradually during gametogenesis (stage 1 and 2), while lipids are produced. Stage 3 (Mar-May) is characterized by minimal glycogen contents and a rapid decrease of lipid and protein. After the spawning period, in which several sheddings can appear, the glycogen content recovers quickly. The results of this study did show higher protein content in the mussels collected in the spring than ones collected in winter.

Larger mussels contain more energy per mussel than smaller ones, so one might expect the scoters to maximize the size of mussels ingested (Richman and Lovvorn 2004). However, a number studies have shown diving ducks selecting small or

intermediate sizes of prey (Draulans 1982, 1984; Bustnes and Erikstad 1990; de Leeuw and van Eerden 1992; Bustnes 1998; Savard et al. 1998; Hamilton et al. 1999; Richman and Lovvorn 2003, 2004). In these studies, size selection has been explained by differential handling times, effects of meat:shell ratio on nutrient gain relative to passage rate, or as a means of avoiding risk of ingesting prey that are too large.

Minerals:

Ring-necked pheasants (*Phasianus colchicus*) quickly pass large limestone particles to their gizzard, where they remain until they are solubilized over time (Klasing 1998). This could be true for the shell of these prey items. Surf scoters use shell fragments as grit to crush other prey items and this digestive strategy may allow for a slow, long-term utilization of the minerals, primarily calcium, provided by the shells of the prey items. The skeleton provides 98% of a bird's calcium, which provides a labile pool of calcium and phosphate (Klasing 1998). The high calcium diet of the surf scoter may allow for depletion of calcium stores when needed, e.g., egg production, without showing much effect on bone density. However, calcium absorption, deposition, and excretion is regulated by the vitamin D endocrine system. Therefore, the utilization of this large amount of available calcium might be limited by the availability of vitamin D. When dietary levels of calcium are in excess, absorption is minimal and most dietary calcium is excreted in the feces. Dietary calcium and phosphorus interact during absorption, metabolism, and excretion. A calcium-to-phosphorus ratio that is optimal for the diet of poultry is 2:1 but 1.4:1 to 4:1 are tolerated if vitamin D is adequate (Klasing 1998). Our ratios are much higher (645:1 for *M. lateralis* and 369:1 for *I. recurvum*), assuming all calcium from the shell can be utilized, which supports the possibility that all

the calcium available in the shell is probably not available all at the same time and is probably broken down slowly over an extended period of time. It would be interesting to look further into the digestibility of calcium and determine the amount of vitamin D available. Klasing (1998) reported calcium-to-phosphorus ratios for oyster meat and snail meat as 0.66 and 4.67 respectively. Assuming that the meat of these two prey items is completely utilized by the ducks, I would expect to find similar values for the ratio for the meat of each prey item. It would be informative to determine the mineral balance of the shell and meat for each prey item separately.

Amino Acids:

The dietary protein requirement increases with the level of protein in a species' customary diet (Klasing 1998). The prey items are very high in protein and scoters probably have high rates of endogenous losses, due mostly to the high rates of degradation, and therefore, would have a correspondingly high dietary requirement (Klasing 1998). The excess dietary amino acids that scoters obtain from these prey items could be used for energy and, therefore, their amino acid catabolic enzyme levels are probably high, as Klasing (1998) reported when faunivores were compared to florivores. When birds consume a very low carbohydrate diet, such as scoters, they must synthesize glucose from amino acids provided by their diet. I would expect that scoters have also lost some of their ability to down regulate gluconeogenesis similar to the barn owl (*Tyto alba*; Klasing 1998).

The disposal of excess amino acid nitrogen by the uric acid synthetic pathway by birds' results in greater requirements for arginine, methionine, and glycine as was observed in these results for both prey items (Klasing 1998). The high amount of

arginine observed was needed because it was not synthesized due to the lack of a urea cycle. The metabolic demand for glycine was great and could not always be met by endogenous synthesis, resulting in a dietary requirement. The consumption of glycine and methionine during uric acid synthesis caused the requirement for these two amino acids to increase directly with increasing dietary protein. The seasonal fluctuations in these results in glycine were interesting and deserve further research (Klasing 1998). This is probably caused by the life cycles of the prey items themselves, but the switch depending on the size of the mussel was puzzling. Ultimately, a bird's digestive strategy, body size, activity, and endogenous losses all affect the relative proportions of protein and energy that must be provided by the diet.

Shell Strength:

In this case, *I. recurvum* had significantly harder shells than *M. lateralis* and this is due to the fact that they are not buried in the sand like the clam and has adapted to have thicker shells and reside in large clumps as a way to reduce predation pressure from scoters and crabs. Seitz et al. (2001) noted that epifaunal sessile prey are usually unable to evade predation and, therefore, must rely on armor, habitat complexity, residence in aggregations, and fast growth to a large size as techniques against predation. Ultimately, *I. recurvum* contained more energy and protein than *M. lateralis*; which should make it a more beneficial prey item, but the increased ash content and harder shell decreased the amount of energy that can be metabolized from it when compared to *M. lateralis*.

Metabolizable Energy:

Hard-shelled prey contain a high fraction of indigestible matter that can restrict available feeding time by limiting storage of food in the digestive tract (Kenward and

Sibly 1977; Zwarts and Blomert 1990). The meat of bivalves is highly digestible (Hockey 1984). However, their large bulk of calcium carbonate shell may limit nutrient assimilation by mechanically restricting access of digestive enzymes to the ash-free food component, by raising the pH in the gut above the optimal range for enzyme function, or by reducing diffusion of nutrients from the lumen to the gut wall (Speakman 1987, Klasing 1998). In black ducks (*Anas rubripes*), Jorde and Owen (1988) found higher digestibility for *Mytilus edulis* than for soft-shelled clams (*Mya arenaria*) when the ash content was approximately 12% lower. Richman and Lovvorn (2004) reported that even though the ash content was 78-100% higher in *Potamocorbula amurensis* than *Macoma balthica*, the assimilation efficiency by lesser scaup (*Aythya affinis*) was 24% higher. Even though *I. recurvum* was 63% higher in ash than *M. lateralis*, the assimilation efficiency was only 1% higher than *M. lateralis*.

The composition of food has a greater impact on apparent metabolizable energy coefficient (*MEC) than the species of bird consuming it (Klasing 1998). Among foods of animal origin, the primary factor was the amount of chitin, bones, scales, fur, feathers, or shells. Mollusks were low in chitin, but the calcium carbonate shells makes up a large percent of their weight. The need for a strong gizzard and high digesta weight relative to body weight impacts the flying capacity of the duck. When oystercatchers (*Haematopus ostralegus* L.) removed mussels from their shells, they obtained an *MEC of 82% from the flesh. However, when oystercatchers consume snails without removing the shell, the *MEC of the flesh was only 64%. Apparently the higher ash content (59%) physically limits access of digestive enzymes and interferes with digestion (Speakman 1987).

Because birds usually eat a quantity of food necessary to satisfy their energy needs, their food intake fluctuates with environmental temperature, activity level, and the energy concentration in the diet (Klasing 1998). Karasov (1990) reported *MEC values for black African oystercatcher (*Haematopus moquini*) fed polychaetes (*Pseudonereis variegata*) and rock mussels (*Choromytilus meridionalis*) as 72%, black African oystercatcher fed limpet (*Patella granularis*) as 73%, lesser scaup (*Aythya affinis*) fed shrimp (*Gammarus* sp.) as 87%, and canvasback (*Aythya valisineria*) fed wild celery buds (*Vallisneria americana*) as 79%. These results were in a similar range as the above reported values (87% *I. recurvum* and 83% *M. lateralis*).

Food energy may be lost from a bird by excretion in urine and feces and through heat of metabolism (Klasing 1998). We assumed that the energy lost in gases (e.g., methane) produced by scoters during the fermentation of prey items was insignificant, and a correction of the digestive energy for these losses was omitted.

The primary factor that explains the metabolizable energy level was the amount and type of fiber and protein content (Klasing 1998). Diets contained so much indigestible bulk or water as to surpass the capacity of the bird's digestive system to process sufficient quantities of food to meet its daily energy requirement. Higher bulk of calcium carbonate shell might limit nutrient assimilation by mechanically restricting access of digestive enzymes to the ash-free component, by raising the pH in the gut above the optimal range for enzyme function, or by reducing diffusion of nutrients from the lumen to the gut wall (Speakman 1987, Richman & Lovvorn 2003). In this case, *I. recurvum* contains more ash than *M. lateralis* which suggested that the digestibility of *I. recurvum* should be lower than *M. lateralis*. However, Karasov (1990) hypothesized that

most noncuticular protein and fat in arthropods can be digested and absorbed, as well as a fraction of the cuticle. If this was the case then it could be possible that even with the higher ash content it could still be digested efficiently. There was no significant difference in metabolizable energy suggesting that the higher ash content must not play a significant role in the digestibility of these two prey items by surf scoters.

There is a minimal dietary metabolizable energy concentration that is necessary for a bird to be able to consume enough food to meet its daily energy requirement (Klasing 1998). Energy is unique among the nutrients in that its acquisition requires high amounts of its expenditure, such as diving up to 5 m to obtain the prey item. Much of the energy in easily obtainable abundant foods cannot be digested and the rewards of consumption are low. Conversely animal prey, such as these bivalves, was fairly digestible (87% and 83%) and is a rich source of energy. But they are often widely dispersed throughout the Bay and require relatively high levels of activity to obtain. It seems reasonable that a scoter would adopt a strategy that best balances the energetic demands of foraging relative to the energetic rewards of consuming various foods.

The food taken at any one time depends on both the preferences of the ducks and the availability of the food items. Thus as the availability of any food item changes, the food habits and possibly the relative abundance of the ducks may change, and result in movement into or away from an area (Sudgen 1971). For example, when the submerged aquatic vegetation declined in the Bay it directly affected canvasbacks and redheads (*Aythya americana*) that wintered there. The canvasbacks were able to adapt to the changing food resources and take advantage of the prolific populations of Baltic macoma (*Macoma balthica*; Perry and Uhler 1988). In contrast, the redheads moved to less

degraded areas and are seen in very small numbers now on the Bay in winter. As Townsend and Hughes (1981) demonstrated, given an array of potential prey (e.g., bivalves) that differ in accessibility (e.g., capture, buried versus attached) or in energy content, there should be an optimal choice of prey that provides the maximum net rate of energy return (energy provided by prey minus energy required to find and eat prey) to a predator (e.g., scoter). To further understand this balance between intake and expenditure the intake rates and expenditures of obtaining the prey by surf scoters needs to be quantified.

Two assumptions made during the metabolizable energy trials were that 1) there was no carry over of nutrients from artificial diet and 2) that they excreted all the prey items in the collection time frame. Grandy (1972) reported that 95% of *Mytilus edulis* fed to black ducks was passed after 50 minutes and Malone (1965) reported that crayfish fed to mallards (*Anas platyrhynchos*) was 5% passed in 66 minutes and 50% passed in 86 minutes. To ensure that there was no carry over from the artificial diet the day the prey item was force fed (9 and 15 May) was excluded from analyses. Figure 13 plots excreta dry matter, ash, lipid, energy, and nitrogen by day. There was a spike in the ash content on 10 May probably due to shell being passed by the scoters; however, this trend did not show up again on 16 May. These results could be confounded by the ducks being stressed, pacing back and forth in the cages or hitting the sides of the cages when the feces were collected. This stress level could have enhanced their metabolism where they quickly utilized the energy from the prey and then were utilizing their endogenous reserves. The slight increase in lipid, nitrogen, and energy by the third day of collection could be due to an increase in endogenous losses, such as unrecovered digestive

enzymes, mucus, and sloughed cells. Endogenous losses of amino acids could occur through loss of protein or nitrogen in the feces. This increase in endogenous losses could also be due to the fact that the ducks were force fed a hard-shelled prey item without becoming physiologically acclimated to digesting that prey item prior to the experiment. Karasov (1990) noted that the digestive physiology of a bird can alter depending on the type of food source it was utilizing, such as switching from seeds to insects. In this study, it was decided that a 48 hour collection was sufficient for following reasons: 1) ducks in cage environment for a long time experience extreme stress so reaching steady state was not possible, 2) there were insufficient quantities of prey items to offer ducks food everyday until they reached steady state or acclimate them to the prey item prior to the experiment, and 3) ducks could not be fasted for an extended period of time before as they would lose too much body weight and become ill. It is recommended to create a method that would allow for the measurement of metabolism without having to alter their behavior in such drastic measures.

In addition, the calcium carbonate in the shells can lower measurements of energy content in bomb calorimeters (Paine 1966). Therefore, the energy value for just meat was used to determine the amount of energy metabolized. It was assumed that all the meat would be metabolized and since the shells contained no energetic value that these results were reliable estimates of the amount of energy metabolized from both prey items by surf scoters.

Summary:

This study revealed that even though *I. recurvum* was higher in ash and contained a harder shell, it contained more lipid, protein, and energy than *M. lateralis*. Therefore, *I.*

recurvum would be a more beneficial prey item for surf scoters wintering in the Chesapeake Bay. However, the amount of energy metabolized by surf scoters was not significantly different between the two prey items. The higher ash content and harder shell of *I. recurvum* does not limit its digestibility by surf scoters. Alternative methodologies that reduce the stress of the ducks are needed to achieve more accurate digestibility results. Ultimately, the foraging values of these prey items, the rate of intake of prey, and the relative expenditures need to be quantified.

Table 1. Pooled samples of *Ischadium recurvum* and *Mulinia lateralis* were sent to CEPS Central Analytical Laboratory, University of Arkansas for macronutrient, mineral, and amino acid analyses. Additional 30 individuals of *I. recurvum* and *M. lateralis* per size class (6-12, 12-18, 18-24, 24-30, 30-36, 36-42 mm) were analyzed at Patuxent Wildlife Research Center to determine dry mass (g/ind), ash mass (g/ind), and ash free dry mass (g/ind). Another 20 individuals per size class were used in a compression test to determine shell strength (N) for both prey items.

	Macronutrient, mineral, and amino acid analyses Pooled samples	Dry mass, ash mass, and ash free dry mass analyses Sample size	Shell strength Sample size
<i>I. recurvum</i>		Per month*	
6-12	25	30	20
12-18	25	30	20
18-24	20	30	20
24-30	10	30	20
30-36	10	30	20
36-42	10	30	20
<i>M. lateralis</i>		One month**	
6-12	30	24	30
12-18		5	NA

* January, February, March, May, June, and July.

** January only.

Table 2. Seasonal differences (mean \pm 1 SD) found in dry mass (g/ind), ash mass (g/ind), and ash-free dry mass (AFDM; g/ind) for each size class (6-12, 12-18, 18-24, 24-30, 30-36, 36-42 mm) of *Ischadium recurvum*, the most common prey item of wintering surf scoters, collected from the Chesapeake Bay in January, February, March, May, and June/July 2007. Values followed by the same letter were not significantly different ($p < 0.05$).

Size Class (mm)	n	Dry Mass (g/ind)	Ash Mass (g/ind)	AFDM (g/ind)
January (Winter)				
6-12	30	0.073 \pm 0.033a	0.038 \pm 0.017a	0.035 \pm 0.016b
12-18	30	0.234 \pm 0.078ac	0.177 \pm 0.063a	0.057 \pm 0.020a
18-24	30	0.721 \pm 0.142a	0.523 \pm 0.120a	0.199 \pm 0.056a
24-30	30	1.141 \pm 0.216a	0.774 \pm 0.168b	0.367 \pm 0.066a
30-36	30	1.753 \pm 0.400b	1.300 \pm 0.328b	0.453 \pm 0.131b
36-42	60	2.677 \pm 0.966b	2.181 \pm 0.867b	0.496 \pm 0.159b
February (Winter)				
6-12	13	0.073 \pm 0.031a	0.048 \pm 0.028a	0.024 \pm 0.008a
12-18	30	0.229 \pm 0.116cb	0.158 \pm 0.088b	0.070 \pm 0.039a
18-24	NA	NA	NA	NA
24-30	NA	NA	NA	NA
30-36	30	1.822 \pm 0.426b	1.370 \pm 0.339b	0.452 \pm 0.218b
36-42	30	2.978 \pm 1.117b	2.096 \pm 0.921b	0.882 \pm 0.655a
March (Winter)				
6-12	30	0.077 \pm 0.031a	0.039 \pm 0.029a	0.038 \pm 0.026ab
12-18	30	0.293 \pm 0.089ac	0.187 \pm 0.060a	0.107 \pm 0.040b
18-24	9	0.569 \pm 0.122b	0.434 \pm 0.900a	0.135 \pm 0.048a
24-30	60	1.325 \pm 0.344b	0.995 \pm 0.273a	0.331 \pm 0.162b
30-36	60	2.448 \pm 0.587a	1.833 \pm 0.451a	0.615 \pm 0.290ab
36-42	31	4.795 \pm 1.660a	3.763 \pm 1.448a	1.032 \pm 0.554b
May (Spring)				
6-12	27	0.059 \pm 0.322a	0.032 \pm 0.195a	0.027 \pm 0.147b
12-18	29	0.301 \pm 0.972a	0.200 \pm 0.777b	0.101 \pm 0.327a
18-24	19	0.697 \pm 1.539ab	0.537 \pm 1.203a	0.160 \pm 0.451a
24-30	30	1.347 \pm 0.284a	1.073 \pm 0.237a	0.274 \pm 0.058a
30-36	30	2.196 \pm 4.246a	1.630 \pm 3.281a	0.566 \pm 1.298b
36-42	30	4.320 \pm 10.47a	3.465 \pm 8.703a	0.855 \pm 2.604b
June & July (Summer)				
6-12	16	0.078 \pm 0.293a	0.048 \pm 0.244a	0.030 \pm 0.158a
12-18	60	0.212 \pm 0.795bc	0.143 \pm 0.699a	0.069 \pm 0.283a
18-24	NA	NA	NA	NA
24-30	41	1.155 \pm 3.156b	0.826 \pm 1.794b	0.329 \pm 2.215b
30-36	59	1.741 \pm 3.043b	1.419 \pm 2.669b	0.322 \pm 1.027a
36-42	59	3.049 \pm 9.716b	2.490 \pm 8.429b	0.598 \pm 1.868b

Table 3. The difference found (mean \pm 1 SD) in dry mass (g/ind), ash mass (g/ind), and ash-free dry mass (AFDM; g/ind) between comparable size classes (6-12 and 12-18 mm) of the top two prey items commonly consumed by wintering surf scoters in the Chesapeake Bay, *Ischadium recurvum* and *Mulinia lateralis*. Values followed by the same letter were not significantly different ($p < 0.05$).

Size Class (mm)	n	Dry Mass (g/ind)	Ash Mass (g/ind)	AFDM (g/ind)
<i>I. recurvum</i>				
6-12	71	0.075 \pm 0.030a	0.043 \pm 0.021a	0.032 \pm 0.014a
12-18	90	0.252 \pm 0.099a	0.174 \pm 0.072a	0.078 \pm 0.040a
<i>M. lateralis</i>				
6-12	24	0.048 \pm 0.022b	0.036 \pm 0.017a	0.011 \pm 0.006b
12-18	5	0.296 \pm 0.050a	0.236 \pm 0.055a	0.060 \pm 0.008a

Table 4. The mean amounts (± 1 SD) of protein (g DM/individual), lipid (g DM/individual), and energy (kJ/individual) found for each size class (6-12, 12-18, 18-24, 24-30, 30-36, 36-42 mm) of *Ischadium recurvum* collected from the Chesapeake Bay in January and May 2007. Values followed by the same letter were not significantly different ($p < 0.05$).

Size Class (mm)	n	Protein (g/ind)	Lipid (g/ind)	Energy (kJ/ind)
January (Winter)				
6-12	30	0.007 \pm 0.003a	0.004 \pm 0.0002	NA
12-18	30	0.018 \pm 0.006a	0.002 \pm 0.0008a	0.468 \pm 0.156a
18-24	30	0.046 \pm 0.009a	0.004 \pm 0.0009a	1.878 \pm 0.370a
24-30	30	0.083 \pm 0.016a	0.015 \pm 0.003a	2.814 \pm 0.532a
30-36	30	0.138 \pm 0.030a	0.010 \pm 0.002a	4.990 \pm 1.086a
36-42	60	0.208 \pm 0.053a	0.020 \pm 0.005a	6.422 \pm 1.623a
May (Spring)				
6-12	27	0.005 \pm 0.003b	NA	0.097 \pm 0.053
12-18	29	0.027 \pm 0.009b	0.003 \pm 0.001a	0.744 \pm 0.240b
18-24	19	0.061 \pm 0.014b	0.005 \pm 0.001a	2.205 \pm 0.487b
24-30	30	0.114 \pm 0.024b	0.011 \pm 0.002b	4.612 \pm 0.971b
30-36	30	0.171 \pm 0.033b	0.018 \pm 0.003b	7.546 \pm 1.459b
36-42	30	0.562 \pm 0.136b	0.026 \pm 0.006b	11.37 \pm 2.757b

Table 5. The mean amounts (± 1 SD) of protein (g DM/individual), lipid (g DM/individual), and energy (kJ/individual) found for *Ischadium recurvum* and *Mulinia lateralis*, the top two prey items consumed by wintering surf scoters in the Chesapeake Bay. Values followed by the same letter were not significantly different ($p < 0.05$).

Size Class (mm)	n	Protein (g/ind.)	Lipid (g/ind.)	Energy (kJ/ind.)
<i>I. recurvum</i>				
6-18	60	0.012 \pm 0.008b	0.001 \pm 0.001b	0.468 \pm 0.156b
18-24	30	0.046 \pm 0.009a	0.004 \pm 0.0009a	1.878 \pm 0.370a
<i>M. lateralis</i>				
6-18	29	0.003 \pm 0.003c	0.001 \pm 0.001b	0.015 \pm 0.016c

Table 6. The mineral content (ppm) determined for 6-18 mm *Ischadium recurvum* and *Mulinia lateralis* collected in winter from the Chesapeake Bay and for *I. recurvum* collected from the Bay in winter and spring by size class (6-12, 12-18, 18-24, 24-30, 30-36, 36-42 mm).

Species	Season	Size	P	K	Ca	Mg	S	Na	Fe	Mn	Zn	Cu	Al
ppm													
<i>Mulinia lateralis</i>	Winter	6-18	540	2436	348413	598	7382	6240	103	18.1	11.9	0.94	0
<i>Ischadium recurvum</i>	Winter	6-18	903	2011	333198	703	6987	5006	526	140	19	19	294
<i>Ischadium recurvum</i>	Winter	6-12	916	1906	335136	703	7038	5069	511	126	19.5	21.3	286
<i>Ischadium recurvum</i>	Spring	6-12	750	1982	328735	547	6735	5000	291	86.0	14.2	8.42	175
<i>Ischadium recurvum</i>	Winter	12-18	890	2116	331260	703	6937	4942	540	154	19.1	16.1	301
<i>Ischadium recurvum</i>	Spring	12-18	1095	2897	336866	603	7150	5238	287	59.4	13.8	6.10	167
<i>Ischadium recurvum</i>	Winter	18-24	1162	2696	331900	977	7550	5538	997	209	22.4	9.12	588
<i>Ischadium recurvum</i>	Spring	18-24	1134	3160	327615	678	7087	5001	312	57.8	13.0	5.06	185
<i>Ischadium recurvum</i>	Winter	24-30	963	2515	312664	930	6970	5318	1191	285	19.2	9.53	713
<i>Ischadium recurvum</i>	Spring	24-30	1610	4541	293973	899	6904	5545	640	67.8	16.3	7.25	415
<i>Ischadium recurvum</i>	Winter	30-36	1112	3370	282631	1073	6520	5727	1022	310	28.8	28.6	601
<i>Ischadium recurvum</i>	Spring	30-36	1230	3803	315862	923	7081	5493	499	79.1	12.9	5.51	322
<i>Ischadium recurvum</i>	Winter	36-42	976	3050	300079	1037	6806	5949	938	350	24.7	17.7	544
<i>Ischadium recurvum</i>	Spring	36-42	1055	3573	321770	1077	7207	5932	650	91.8	19.8	5.59	421

Table 7. The shell strength (N; mean \pm 1 SD) measured for the top two prey items commonly consumed by wintering surf scoters in the Chesapeake Bay, *Ischadium recurvum* and *Mulinia lateralis*. *I. recurvum* was measured in groups based on six size classes (6-12, 12-18, 18-24, 24-30, 30-36, 36-42 mm) and *M. lateralis* was measured for one size class (6-12 mm), which were based on the sizes available to scoters in the Bay. Values followed by the same letter were not significantly different ($p < 0.05$).

Size Class (mm)	n	Shell Strength (N)
<i>I. recurvum</i>		
6-12	20	21.24 \pm 9.61a
12-18	20	32.85 \pm 8.94
18-24	20	47.33 \pm 18.66
24-30	20	82.94 \pm 29.42
30-36	20	109.63 \pm 37.23
36-42	20	114.65 \pm 47.06
<i>M. lateralis</i>		
6-12	30	5.49 \pm 4.50b

Table 8. Means (± 1 SD) of surf scoter body mass before and after trials; of food (dry mass), ash (g DM), lipid (g DM), nitrogen (g DM), and energy (kJ) ingested; of guano (dry mass), ash (g DM), lipid (g DM), nitrogen (g DM), and energy (kJ) excreted; and of apparent digestible energy (ADE; %kJ), nitrogen energy balance (NEB; kJ), and metabolizable energy (ME; %kJ) determined for surf scoters fed 25 g fresh mass (whole bivalves) of the hooked mussel (*Ischadium recurvum*) and dwarf surfclam (*Mulinia lateralis*), the top two prey items consumed by wintering surf scoters in the Chesapeake Bay.

		<i>I. recurvum</i> n = 8	<i>M. lateralis</i> n = 8	<i>p-value</i>
Body Mass	Initial Mass (g)	783 \pm 97	775 \pm 82	0.8698
	Final Mass (g)	705 \pm 60	700 \pm 48	0.8569
	Mass Loss (%)	5.0 \pm 2.9	5.0 \pm 2.4	0.9584
Ingesta (DM)	Food (g)	9.460 \pm 2.780	13.85 \pm 0.591	0.0027
	Ash (g)	7.930 \pm 2.332	12.73 \pm 0.543	< 0.0001
	Lipid (g)	0.058 \pm 0.017	0.101 \pm 0.004	< 0.0001
	Nitrogen (g)	0.010 \pm 0.003	0.072 \pm 0.003	< 0.0001
	Energy (kJ) whole	47.33 \pm 13.91	2.260 \pm 0.096	< 0.0001
	Energy (kJ) meat	185.0 \pm 54.38	147.4 \pm 6.288	0.0075
Excreta (DM)	Guano (g)	8.598 \pm 4.720	8.721 \pm 5.502	0.9623
	Ash (g)	4.014 \pm 3.020	3.964 \pm 3.873	0.9772
	Lipid (g)	0.067 \pm 0.035	0.074 \pm 0.051	0.7294
	Nitrogen (g)	0.989 \pm 0.418	0.987 \pm 0.609	0.9952
	Energy (kJ)	58.09 \pm 26.09	58.13 \pm 30.48	0.9978
Assimilation	ADE (%)*	65.69 \pm 17.11	59.82 \pm 23.07	0.5733
	NB (kJ)	-35.75 \pm 15.26	-33.41 \pm 22.31	0.8110
	ME (%)*	86.74 \pm 8.09	83.04 \pm 7.07	0.3474

* Based on energy value of meat only.

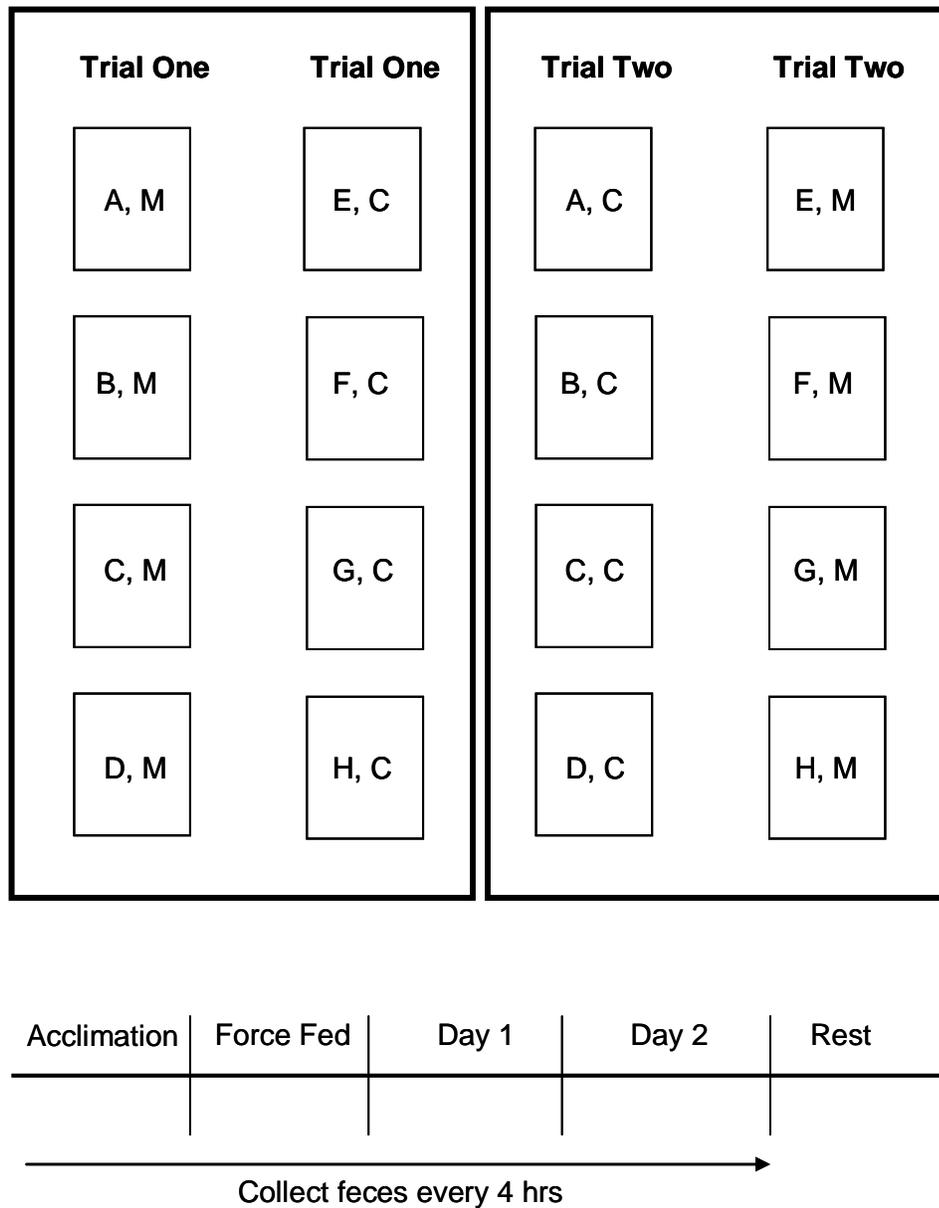


Figure 8. A visual representation of the experimental cross-over design used to determine metabolizable energy obtained by eight captive surf scoters (A-H) feeding on two prey items, *Ischadium recurvum* (M) and *Mulinia lateralis* (C). Feeding trials (one and two) consisted of a 24 hr acclimation period, a single force feeding of 25 g fresh mass of the appropriately assigned prey item, and a 48 hr collection period where excreta were collected every 4 hrs throughout the entire experiment.

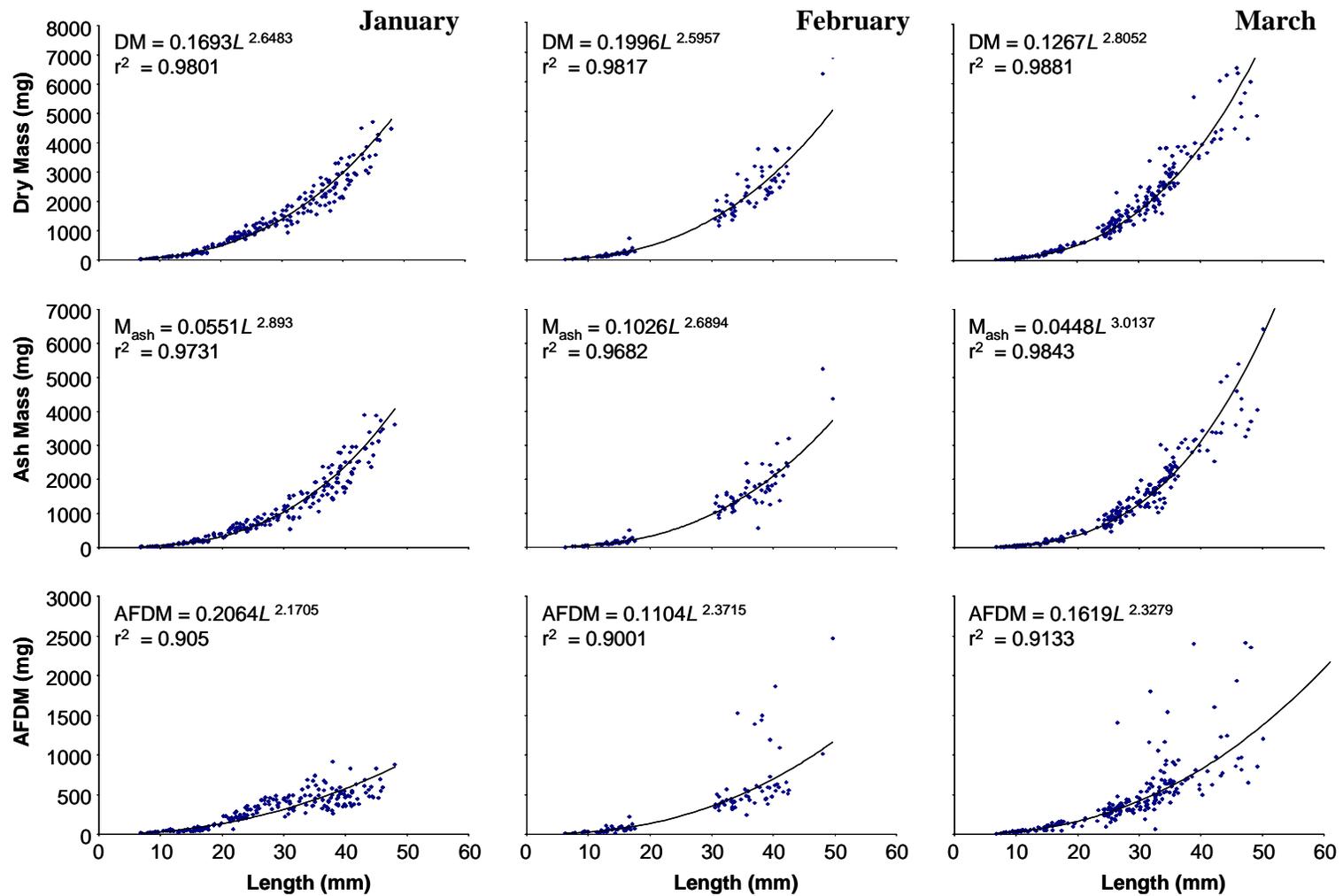


Figure 9. Dry mass (DM; mg), ash mass (M_{ash} ; mg), and ash-free dry mass (AFDM; mg) of *Ischadium recurvum* (including shell) as a function of length (mm) collected from the Chesapeake Bay in January, February, and March 2007. All regressions were significant at the 5% level ($p < 0.0001$).

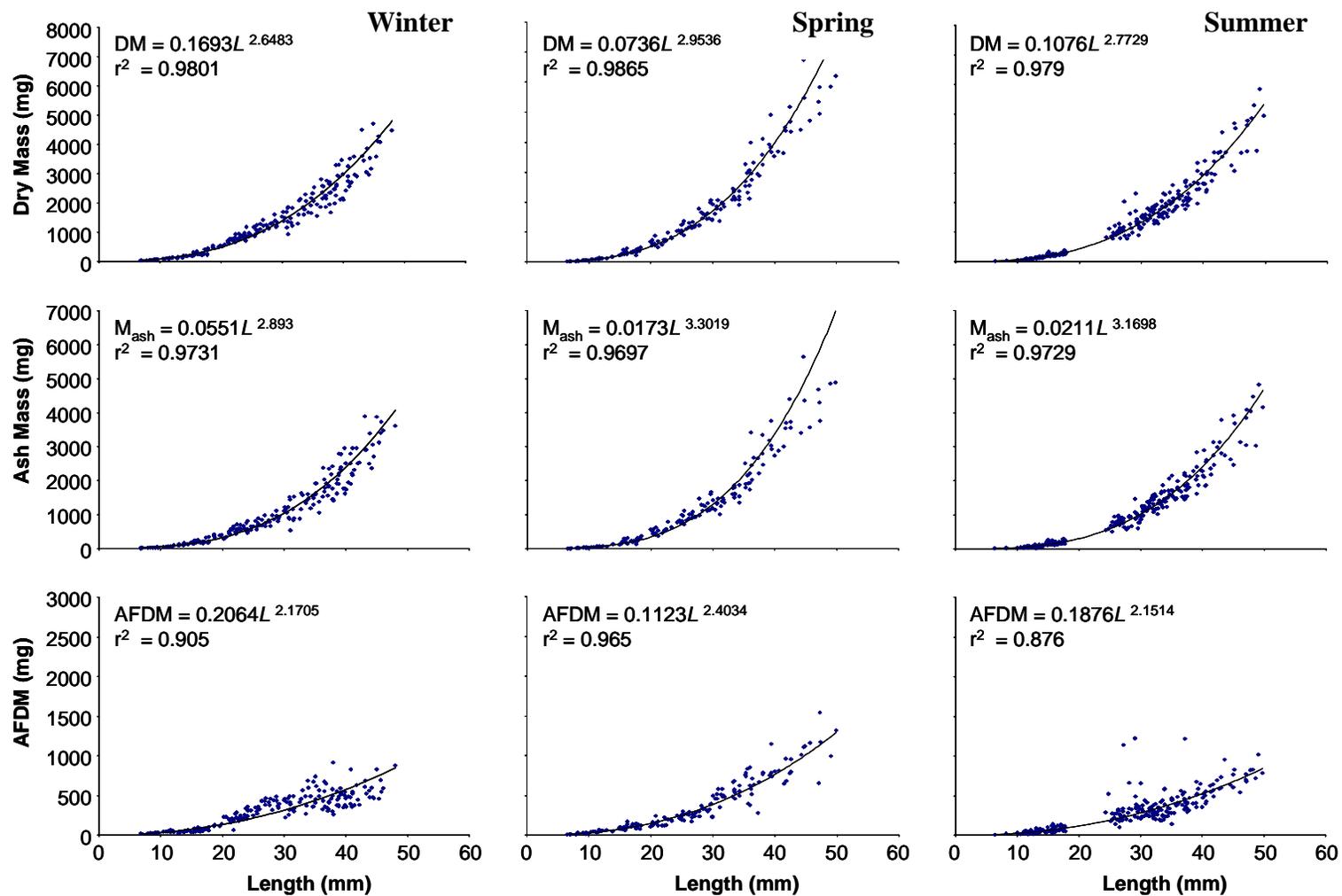


Figure 10. Dry mass (DM; mg), ash mass (M_{ash} ; mg), and ash-free dry mass (AFDM; mg) of *Ischadium recurvum* (including shell) as a function of length (mm) collected from the Chesapeake Bay in winter, spring, and summer. All regressions were significant at the 5% level ($p < 0.0001$).

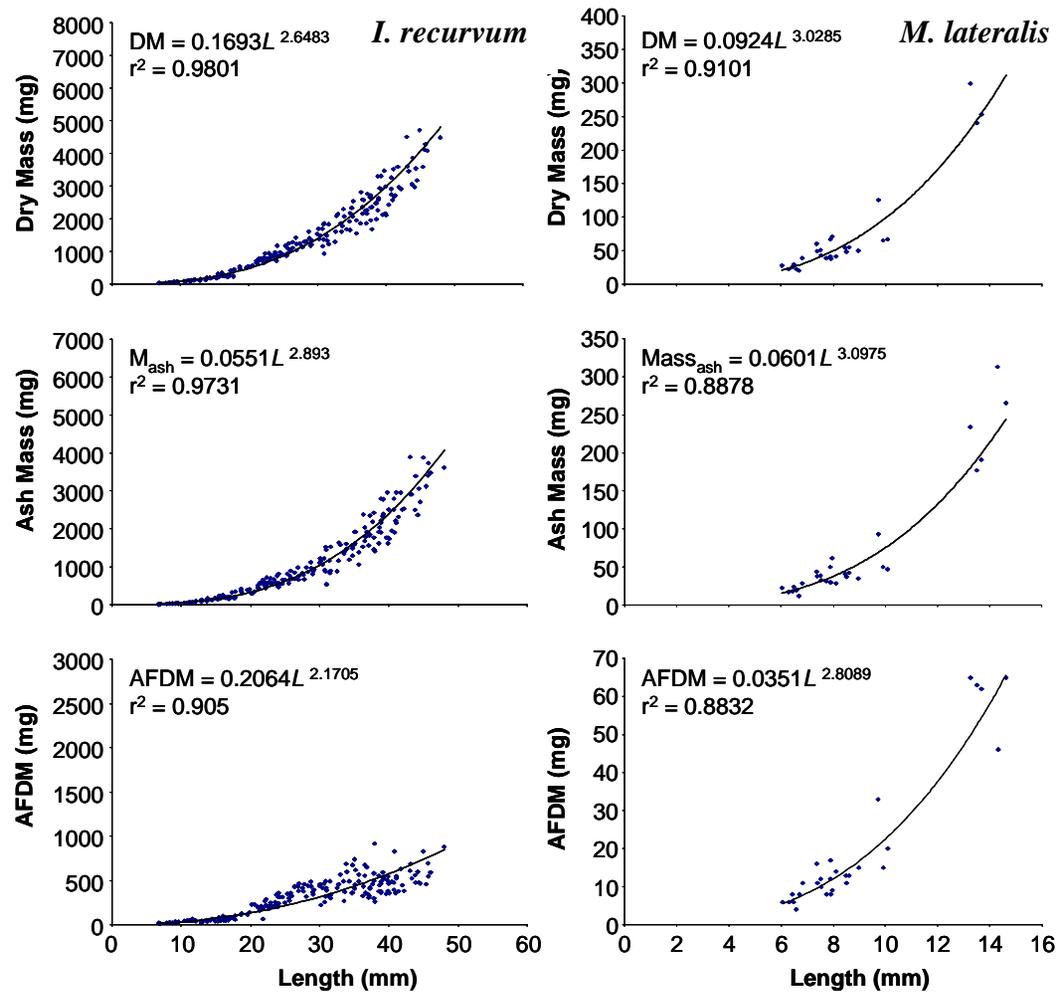


Figure 11. Dry mass (DM; mg), ash mass (M_{ash} ; mg), and ash-free dry mass (AFDM; mg) of *Ischadium recurvum* and *Mulinia lateralis* (including shell) as a function of length (mm). All regressions were significant at the 5% level ($p < 0.0001$).

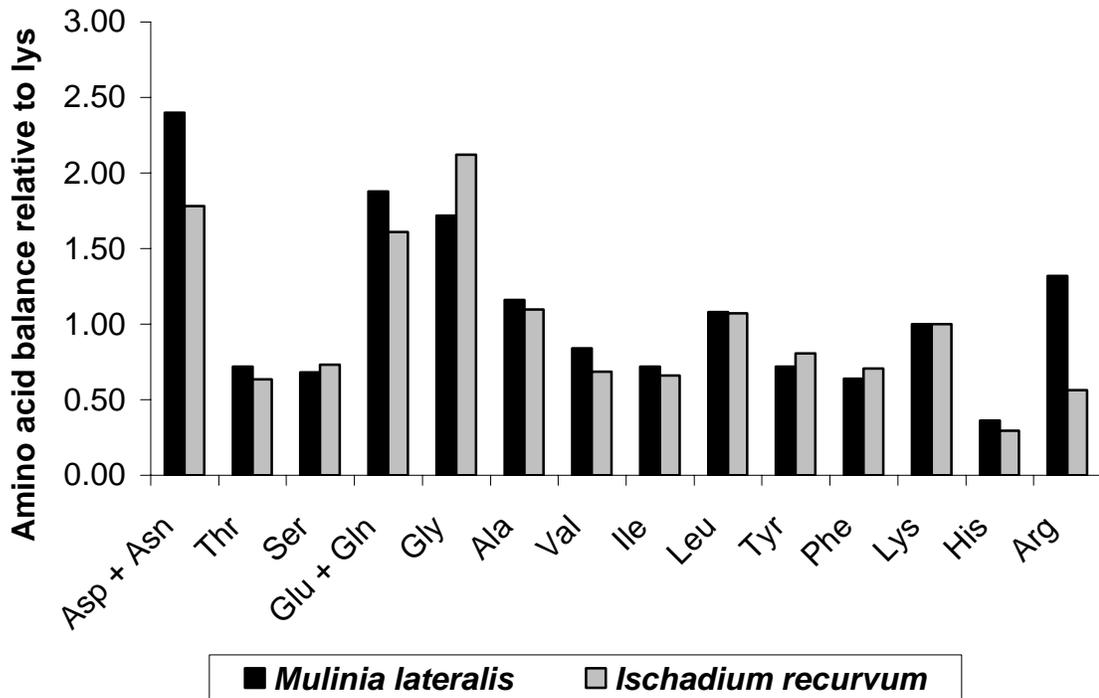


Figure 12. The amino acid balance relative to lysine for *Mulinia lateralis* and *Ischadium recurvum* collected in winter from the Chesapeake Bay. Asp = Aspartic acid; Asn = Asparagine; Thr = Threonine; Ser = Serine; Glu = Glutamic acid; Gln = Glutamine; Gly = Glycine; Ala = Alanine; Val = Valine; Ile = Isoleucine; Leu = Leucine; Tyr = Tyrosine; Phe = Phenylalanine; Lys = Lysine; His = Histidine; and Arg = Arginine.

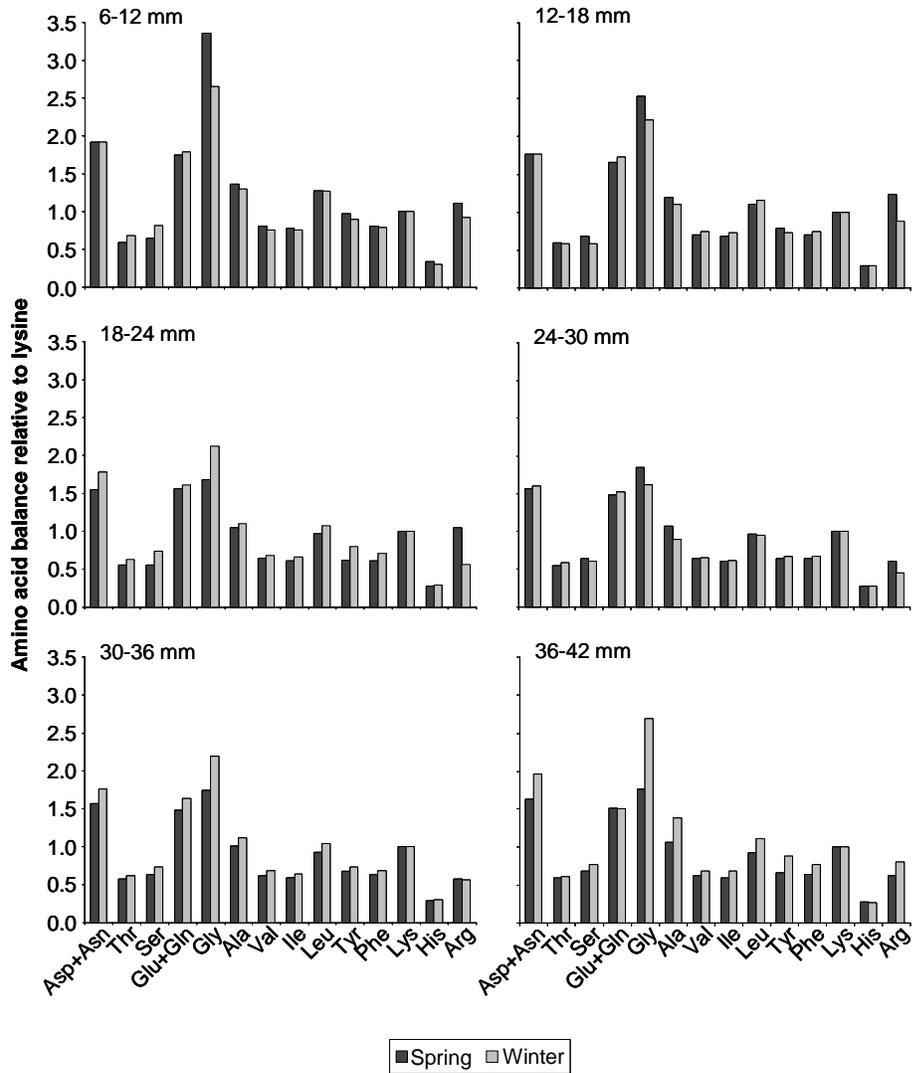


Figure 13. Amino acid balances relative to Lysine for each size class (6-12, 12-18, 18-24, 24-30, 30-36, 36-42 mm) of *Ischadium recurvum* collected from the Chesapeake Bay in spring and winter 2007. Asp = Aspartic acid; Asn = Asparagine; Thr = Threonine; Ser = Serine; Glu = Glutamic acid; Gln = Glutamine; Gly = Glycine; Ala = Alanine; Val = Valine; Ile = Isoleucine; Leu = Leucine; Tyr = Tyrosine; Phe = Phenylalanine; Lys = Lysine; His = Histidine; and Arg = Arginine.

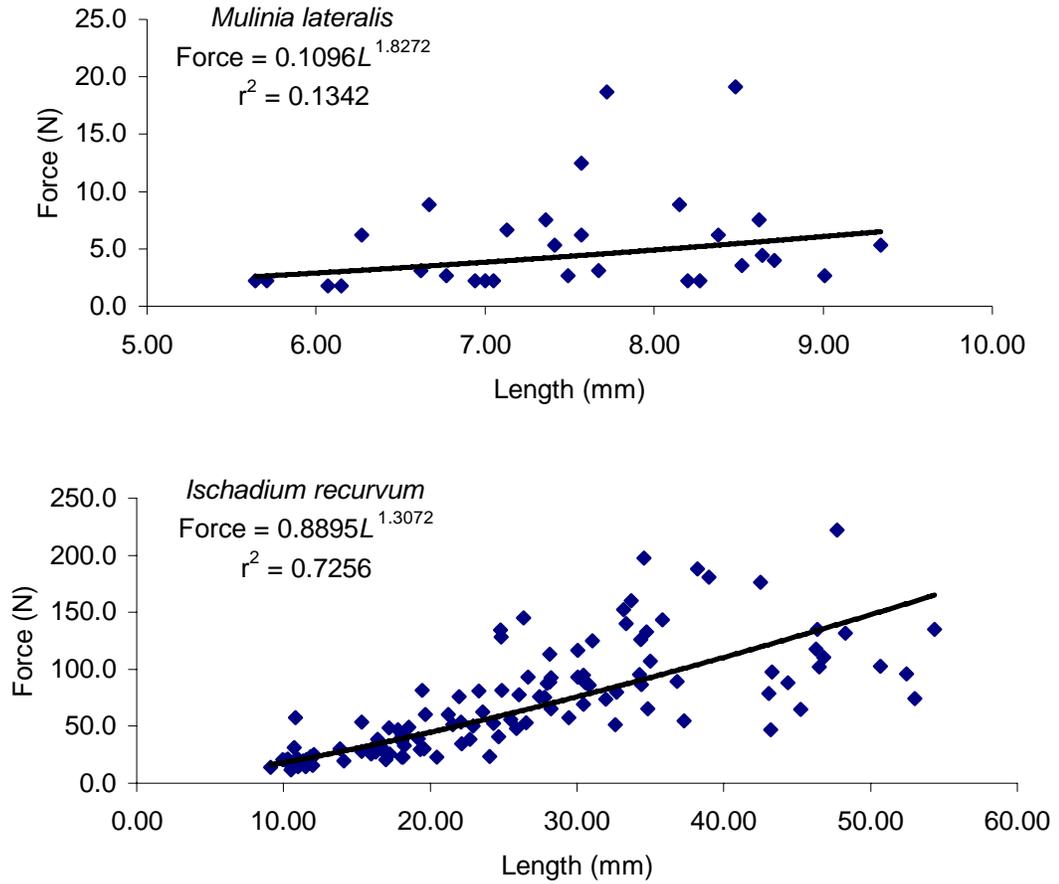


Figure 14. Shell strength, measured as the amount of force (N) needed to crack the shell, as a function of length (mm) for *Ischadium recurvum* and *Mulinia lateralis*, two common prey items consumed by wintering surf scoters on the Chesapeake Bay.

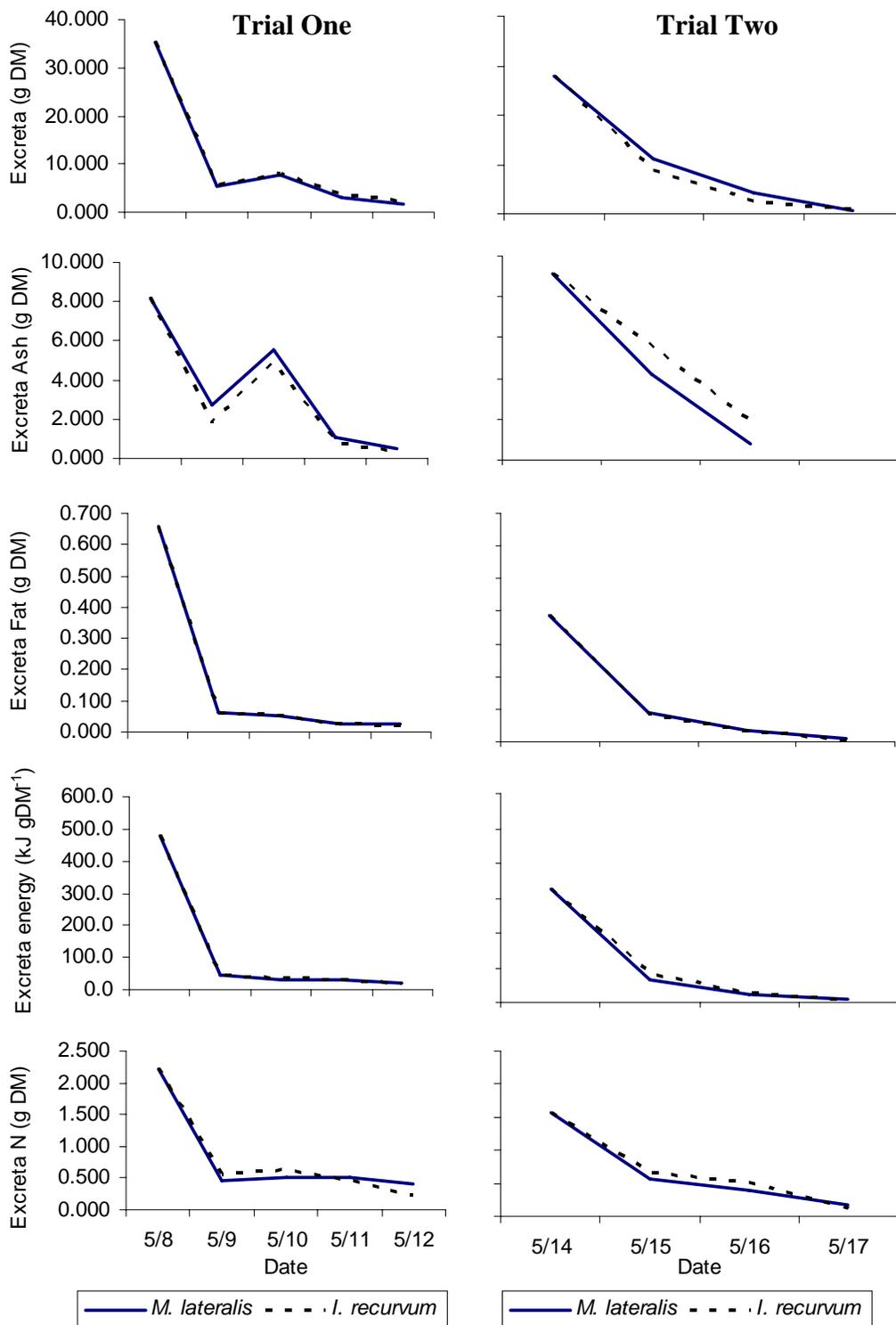


Figure 15. The amount so excreta dry mass (g), ash (g DM), fat (g DM), nitrogen (g DM), and energy (kJ gDM⁻¹) produced each day during feeding trials on eight captive surf scoters fed *Mulinia lateralis* and *Ischadium recurvum*, the top two prey items obtained by wintering surf scoters in the Chesapeake Bay.

Chapter Three. Functional responses of surf scoters foraging on two different prey items: *Mulinia lateralis* and *Ischadium recurvum*.

Abstract:

The decline in availability of *Ischadium recurvum* due to the significant losses in hard substrate, the oyster beds (*Crassostrea virginica*), has possibly induced a switch in the food habits of wintering surf scoters (*Melanitta perspicillata*) in the Chesapeake Bay to a more prolific food item, *Mulinia lateralis*. For scoters foraging in a large diving tank 2.13 m deep, intake (number s⁻¹) of prey either buried in sand or attached to hard substrate increased with increasing prey density up to at least 1000 to 2000 prey m⁻². At low densities the functional response for *I. recurvum* was higher than the functional response for *M. lateralis*; however, the reverse was found at the higher densities. Gross energy intake (kJ s⁻¹) and metabolized energy intake (kJ s⁻¹) for *I. recurvum* were significantly higher than for *M. lateralis*. Even though the harder shell and higher ash content may partly offset the apparent energetic advantages of *I. recurvum*, the larger size commonly consumed compared to *M. lateralis* provides the scoters with more energy and protein per dive. Due to this energetic difference the scoters were forced to increase their intake of *M. lateralis* to obtain their daily energy requirement. It appears that *I. recurvum* was the more beneficial prey item with its higher nutrient advantage and greater visibility which reduced search effort. Therefore, with a steady decline in mussels in the Bay there could be drastic changes in the surf scoter populations wintering in the Chesapeake Bay.

Introduction:

Predation is the key determinant of the abundance and size structure of prey populations, as well as the structure and functioning of these communities (Seitz et al.

2001). Prey patches are selected by predators to maximize fitness or energy intake, within the constraints of predator interference, predation risk, reproductive demands, avoidance of prey, chemical deterrents, and predator behavior (Seitz et al. 2001). Studies of consumer feeding rates concentrate on encounter rate and handling time, which change with varying prey densities. The predator's "functional response" (FR) relates the quantity of prey consumed per predator to prey density (Seitz et al. 2001, Figure 4). Change in intake rate with prey density is a basic component of a number of models of waterbird foraging (Myers et al. 1980; Wanink and Zwarts 1985; Draulans 1987; Piersma et al. 1995; Richman and Lovvorn 2002, 2003). For diving ducks foraging on bivalves, it is typical to find a type II functional response, where intake rates increase with increasing prey density up to an asymptote where intake is limited by handling time (Takekawa 1987; Giles 1990; Lovvorn and Gillingham 1996; Richman and Lovvorn 2002, 2003).

Microhabitat features can protect infaunal bivalves from birds; the tactile penetration of shorebirds can be limited by sediment type so that infaunal prey can achieve refuge at low density (Piersma et al. 1995). Thus, both low density and habitat refuge can promote prey persistence and reduce prey encounter rates. This reduction in encounter rates would lead to a decrease in foraging activity, further diminishing encounter rates or driving the predator from inefficient foraging areas of low prey density (Seitz et al. 2001).

If a prey item is present below a critical density it may no longer be energetically profitable for a duck and the duck may switch to a more abundant lower energy food source to meet its daily requirement (Sugden 1971). The food taken at any one time depends on both the preferences of the ducks and the availability of the food items. Thus

as the availability of any food item changes, the food habits and possibly the relative abundance of the ducks may change, and result in movement into or away from an area. For example, when the submerged aquatic vegetation declined in the Bay it directly affected wintering canvasbacks (*Aythya valisineria*) and redheads (*Aythya americana*). The canvasbacks were able to adapt to the changing food resources and take advantage of the prolific populations of Baltic macoma (*Macoma balthica*; Perry and Uhler 1988). In contrast, the redheads moved to less degraded areas and are seen in very small numbers now on the Bay in winter. Based on food habits data, scoters prefer mussels, however, changes in the Bay ecosystem have altered the availability of the mussels so there may be shift from the hooked mussel (*I. recurvum*) to the dwarf surfclam (*M. lateralis*; Figure 1; Perry et al. 2007). The situation for scoters could be similar to that for the canvasback, where the scoters are altering their food habits in accordance with the declining availability of *I. recurvum* and the abundance of the opportunistic, *M. lateralis*.

M. lateralis is buried in substrate, which could increase search time, thereby increasing the cost associated with diving to obtain this prey. Prey substrate depth has been reported to affect the functional responses of crabs, shorebirds, and diving ducks that eat clams (Wanink and Zwarts 1985; Lipcius and Hines 1986; Zwarts and Blomert 1992; Seitz et al. 2001; Richman and Lovvorn 2002, 2003). Stephenson et al. (1986) found that when tufted ducks (*Aythya fuligula*) swam long horizontal distances underwater for their food, heart rate progressively declined after approximately 15 s so that by approximately 30 s it was significantly below the resting value. During these dives the ducks were observed to swim actively to and from the food. However, during normal vertical dives of similar duration, heart rate remained elevated above resting.

Therefore, increasing search time underwater appeared to increase the energetic costs of that dive. In contrast, *I. recurvum* is highly visible so it may have a reduced search time, but must be removed from the hard substrate, with the energy expenditure needed to break the byssal threads of the mussel. Therefore, retrieving this prey would also have an associated cost.

The purpose of this study was to determine the functional responses, of surf scoters preying on different densities of *I. recurvum* and *M. lateralis*. In addition to determining the amount energy scoters can obtain in a foraging bout, quantifying the change in foraging as a function of density allowed me to determine how changes in prey availability affected the foraging behavior of wintering surf scoters.

Methods:

The Equipment:

Two large concrete tanks (2.44m x 1.83m x 2.44m) were constructed at Patuxent Wildlife Research Center (PWRC; Figure 16). Once they were installed, a two story building was built to provide a controlled environment. There were numerous windows to allow natural light and a HVAC unit to control the temperature. Once the building was completed, the inside of the tanks were painted with multi-purpose epoxy paint (Sherwin Williams Dura-Plate 235). Each tank contained 2 side windows (0.61m x 0.91m) and one end window (0.91m x 0.61m). Four square wood trays (50.8 x 50.8 x 15.24 cm) were fabricated to create a 2 x 2 square meter grid in the bottom of the tank. A large crane was installed to place or remove the trays from each tank. A large framework was created from PVC[®] pipe and covered in soft netting over each tank to contain the ducks in the tanks and still allow for easy manipulation of the trays.

Training:

The ducks had to be trained to eat the natural prey items and to dive for their food. Firstly, the ducks were offered the natural prey items in their food trays without any commercial diet. Once they were readily eating the natural prey item, the food trays were removed from land and suspended over the water to teach the ducks to forage on the water. Once they were familiar with this technique, the trays were slowly lowered into the pond in order to acclimate them with foraging underwater. After these steps were completed the ducks were introduced to the dive tanks. The water level in the tanks was lowered to approximately 1.5 m and groups of individuals that were usually penned together were placed in a tank and left there for 8 hours a day. Mealworms and corn were offered in the study trays in the bottom of the tanks which taught them that there was food available in the bottom of the tank. This process was repeated for several days until they were accustomed to feeding from the trays. At this point the water level was slowly increased to build up their fitness. Once the desired water level was reached, the ducks were offered the natural prey item, mussels or clams. The final step was to slowly reduce the number of ducks in the tank at one time. Once there was only one individual regularly foraging in the tank, the official trials began.

Mussel Trials:

Due to difficulty in obtaining *I. recurvum* in the large numbers needed for the high densities these trials were completed in June, whereas, the lower density trials were completed in February. Concrete plates (48.26 x 48.26 x 2.54 cm) that have cleaned oyster shell systematically placed on the surface were created to simulate an oyster bed for the trials on live *I. recurvum* (Figure 16). The five surf scoters (3 M: 2 F) foraged for

18-24 mm size mussels at 4 densities (30, 100, 1000, and 3000 m⁻²). Before a trial each duck was fasted for 24 hours to ensure there was no effect of the commercial diet on the intake rate of the natural prey item. A partially randomized design was used to determine the tank, prey density, and which duck dove in which tank. Due to the large time investment in the setup of these high density trials, they were completed all in one timeframe and, therefore, day was not randomly determined, but which duck and which tank were randomly determined. Throughout the trials if any prey item died it was removed and replaced with a live individual. The mussels were evenly distributed on the plates and attached by their byssal threads using Superglue®. After the mussels were glued in the appropriate density the four trays were lowered to the bottom in the middle of the tank. After a foraging bout by an individual surf scoter, the trays were raised and the remaining mussels were counted. The number of mussels consumed was calculated by subtraction. The bottom of the tank was inspected for any mussels detached but not consumed. The time spent foraging was measured from video footage from an underwater camera as the time the bill entered and left the mussels. A stopwatch was used to measure the foraging time in a trial. When the scoter's bill entered the mussels the watch was started and was not stopped until the duck stopped foraging. Each dive time was recorded and the number of dives and total foraging time was determined for each duck at each density.

Clam Trials:

These trials were completed in March and April. The same five surf scoters (3 M: 2 F) also foraged for one size class of *M. lateralis* (12-18 mm) at 4 densities (30, 100, 1000, and 3000 m⁻²). Before a trial each duck was fasted for 24 hours to ensure there was

no effect of the commercial diet on the intake rate of the natural prey item. A completely randomized design was used to assign tank number, duck number, prey density, and date for the experiment. Clean sand was obtained and placed in the trays for the dwarf surfclam foraging trials. These clams were purchased alive from Woods Hole Marine Laboratory and maintained in a large aquarium with appropriate salinity until used in trials. Fresh clams were counted and uniformly distributed on the bottom of the tray and covered with 2.54 cm of sand. The sand depth was established by leveling and measuring the sand with a ruler. The four trays were lowered to the bottom in the middle of the tank and, after the foraging bout, the remaining clams were counted after washing the sand through a 2 mm mesh sieve. The number of clams consumed was determined by subtraction. Time spent foraging was measured from video footage from an underwater camera as the time the bill entered and left the sand using the same criteria as stated for the mussel trials.

Analyses:

Bonferroni pairwise comparison was used to detect differences in number of dives and number consumed between each prey item for each density. Intake rates (number consumed per second) of scoters feeding were fitted with Michaelis-Menten equation using the Marquardt method (Proc NLIN, SAS Institute 2003). This method applied the data obtained to the following equation and determined values for the handling time coefficient and the search time coefficient for the four densities tested. In the equation, $I = aX / (b + X)$, I was the number of prey consumed per second at the bottom, X was the number of prey m^{-2} , a was the handling time coefficient or the maximum rate at which

the prey can be consumed independent of density, and b was the search time coefficient or the prey density at an intake rate of $0.5a$.

Please note that accounting for satiation effects, as in other recent functional response models (Jeschke et al. 2002), is not appropriate in this study because intake during a single dive rarely ever reached satiation (filling of esophagus and proventriculus). Dive bouts usually alter cyclically between preening and resting periods (Guillemette 1994). Because of the high energy cost of diving (de Leeuw 1996, Kaseloo 2002), a scoter should consume as many prey as possible in the shortest amount of time spent underwater, with foraging bouts of a series of dives simply being terminated upon satiation (Lovvorn and Gillingham 1996, Richman and Lovvorn 2003). Digestion appears to occur mainly during a resting period after a dive bout, when costs of floating on the water surface are far less than during dives (Kaseloo 2002, Richman and Lovvorn 2003).

Differences between functional response curves were tested using analysis of covariance (ANCOVA). Based on the plots of the residuals the data were log transformed before ANCOVA analyses were performed. All tests were considered significant at the 5% level and all analyses were completed using SAS (Proc Mixed, SAS Institute 2003).

Results:

Possible seasonal effects were tested and there was no significant effect of season on intake rate ($F = 0.38$, $p = 0.5471$). There was no difference in intake rates based on sex so all data were combined for further analyses ($F = 0.36$, $p = 0.5593$). Scoters feeding on low densities of *M. lateralis* dove significantly more than scoters feeding on

low densities of *I. recurvum* ($p = 0.0007$ & $p = <0.0001$; Table 9). There was no significant difference in the number of dives detected between high densities of prey items ($p = 0.2117$ & $p = 0.2526$). There was no significant difference in the number of prey consumed between prey items for all densities ($p = 0.0848$, $p = 0.0515$, $p = 0.5145$, & $p = 0.1152$). At the same water depth, approximately 2 m with the two different substrate types and two different size classes, scoters had significantly different intake rates ($F = 60.60$, $p = <0.0001$). For *M. lateralis*, the functional response was $I = 0.8291X / (-640.8 + X)$; $r^2 = 0.5532$, $p = 0.0022$. For *I. recurvum*, the functional response was $I = 0.5525X / (101.4 + X)$; $r^2 = 0.9732$, $p < 0.0001$ (Figure 15). The functional response at low densities for *I. recurvum* was higher than the functional response for *M. lateralis*, however, the reverse was found at the higher densities. At low densities a negative intake rate was produced for *M. lateralis*. In many cases at the low densities the ducks would forage without finding any of the clams to consume.

Based on the data in Table 10, functional response curves were converted from number of prey consumed per second to ingestion rates of nitrogen (grams per second), gross energy (GE, in kilojoules per second), and metabolized energy (GE x Metabolizable Energy (ME) kilojoules per second) for each prey item (Figure 16). Digestibility of protein in flesh has been estimated at 83% (Zwarts & Blomert 1990); however, I did not determine the digestibility of nitrogen so it was not accounted for in determining the rate of ingestion for nitrogen. *M. lateralis* yielded a higher nitrogen intake, but lower gross energy intake and lower metabolized energy intake than *I. recurvum*. *M. lateralis* was significantly higher in nitrogen intake than *I. recurvum* ($F = 38.95$, $p = <0.0001$). However, *I. recurvum* was significantly higher than *M. lateralis* for

gross energy intake and metabolized energy ($F = 19.25$, $p = 0.0002$ and $F = 12.01$, $p = <0.0001$, respectively).

Discussion:

Prey Size Effects:

Richman and Lovvorn (2003) reported a significant effect on intake rates by prey size and by depth in the substrate. This study did not adjust for these differences because I was interested in a comparison that was based on the ecology of scoters and the prey items themselves. This was apparent in the field when Kidwell (2007) noted a decline in the biomass of 18-24 mm mussels over winter. The mussel beds may be foraged upon when the scoters energetic needs are very high, such as when they first arrive to the Bay in November. Richman and Lovvorn (2003) did note that the relative foraging value depends strongly on the size structure of the prey populations. As Seitz et al. (2001) noted mussels can avoid predation by growing fast enough to reach a size that is unacceptable and by settling in the interstices of clumps. Work on the foraging responses of surf scoters preying upon mussel clumps will occur in the near future and will be invaluable in teasing apart the foraging behavior of scoters. In addition, Kidwell (2007) noted that the most common size of *M. lateralis* in the Bay in the fall was 12 mm, but decreased in the spring to 8 mm. The size difference in the two prey species as Richman and Lovvorn (2003) observed affected the metabolizable energy rate between the two prey items. This also justified the intake rate of *M. lateralis* being higher than the intake rate of *I. recurvum*; the scoters must consume more of them to meet their daily energy requirement.

Density Effects:

The densities that were chosen for this study were based on actual densities of mussels found in the Chesapeake Bay. Kidwell (2007) recorded densities around 30 per square meter in unrestored oyster beds, whereas, Rodney and Paynter (2006) reported densities of 3,000 per square meter on restored oyster beds. This density was high enough that the scoters were no longer limited by handling time, which ensured that scoter predation on the mussels could not deplete the mussel population. However, if the proportion of this density that is in the preferred size class is depleted over winter, as Kidwell (2007) illustrated, then the scoters would be forced to switch to *M. lateralis*. If an increase in area available to mussels induces optimal densities per patch for the ducks foraging, then the restoration effort would benefit the scoter populations wintering on the Bay. Quantifying the potential benefits of restored oyster populations on scoter numbers in the Bay will have to be evaluated further as more data become available for these duck populations.

For comparative reasons, the same densities were used for *M. lateralis*, but this species was largely absent from summer and fall samples, averaging 4.6 per square meter with a maximum density of 56 per square meter (Kidwell 2007). However, after a winter larval settlement a maximum density of 511 per square meter and an average of 75.9 per square meter were noted. My low density results for *M. lateralis* indicated that these densities (30 and 100) were below that critical density and the scoter would have to move to a denser foraging area where prey encounter rates and, therefore, intake rates would be higher. Based on these results, the critical density needed for intake to be beneficial is 641 (number m⁻²), therefore, Kidwell's (2007) densities may be underestimating the

actual maximum density available in winter. If a significant predation effect by scoters occurs on the *M. lateralis* populations in winter Kidwell's (2007) data could be underestimating the actual densities in winter. Benthic samples collected in winter are needed to get a more accurate assessment of the densities available to foraging scoters.

Locations of dense concentrations of *M. lateralis* shift from year to year (pers. comm. V. Kennedy). One might find a dense concentration in a location one year and in the next year in the same location only find a few individuals. Finding these new "hot beds" of clams on a yearly basis could be an extra cost associated with obtaining this prey item. This would support the idea that the scoters immediately forage on the dense mussel beds when they arrive in November in the Bay. After they have refueled and possibly depleted the optimal size of mussels then they might go in search of the high density clam beds. It would be interesting to learn more about this settlement behavior by *M. lateralis* larvae; do they have an infinite number of possible locations within its salinity and substrate range or are they further limited and there are only a few areas able to sustain them. If this were the case then once a scoter learned where these areas were every year it could search them to find the "hot bed".

Why not other more abundant opportunistic clams?

Soil characteristics have been shown as a potentially important environmental element affecting both the intake rate and the energetic costs (Brown 1988, Nolet 2001). Price and Heinz (1984) and Van Eerden and Munsterman (1997) showed that intake rate decreased with soil particle size. Van Eerden et al. (1997) considered pit digging and tuber extraction by swans to be less energetically costly in sandy sediments than in clayey soils. Kidwell (2007) showed that *Macoma balthica* occurred in more clayey sediments,

which may explain why they appear in only small amounts in the food habits of surf scoters wintering in the Chesapeake Bay (Figure 2). In addition, if scoters rely on sight to locate their prey items, especially buried prey, the sediment stirred up during foraging in clayey soils could reduce their visibility, and therefore, search time and the resultant foraging effort would be increased.

Gemma gemma was another prey item consumed by surf scoters and it commonly occurs in sandy habitats, but its largest size is approximately 2 mm and usually occurs in very dense concentrations (Kidwell 2007). The scoters would have to consume more *Gemma gemma* in order to obtain enough energy from this prey item, however, this has the added cost of diving more often. However, since this prey item occurs in such dense concentrations and potentially hundreds could be consumed per dive, it is possible for the energy balance between costs and benefits to be positive. This most likely explains why it appears as the third highest prey item fed upon by scoters in the Bay, but relative to the top two prey items requires more effort to obtain

Physiological Effects:

If the scoters do switch during the end of winter before migration to prey more on the clam, a thinner shelled prey item, than the mussel this could be attributed to the physiological constraints of flying. Dekinga et al. (2001) found that red knots (*Calidris canutus*) increased their gizzard mass 147% when they switched from soft food to hard shelled food. In addition, reversible changes in gut length in response to changes in the diet have been reported to occur in ducks within five days (Drobney 1984, Kehoe et al. 1988). Internal organ mass may directly affect flying performance of birds. Because the costs of flight increase with body mass (Kvist et al. 2001) and maneuverability may be

impaired at heavier masses (Kullberg et al. 1996, Metcalfe and Ure 1995), minimizing digestive organ mass may be an important consideration. Sedinger (1997) suggested that the small ceca in waterfowl reflect a balance between costs of flight for waterfowl and the benefits of the ceca for nutrient balance. In addition, reducing the size of the digestive organs would also increase the space available for fat deposition just before departure on migratory flights. Therefore, there may be a physiological advantage for the surf scoters foraging on a lower ash and thinner shelled bivalve even if they have to increase their intake rate to obtain the necessary energy requirement.

One consideration that was not accounted for was variation in gizzard size of the five ducks used for this study. Van Gils et al. (2003) noticed that hungry red knots with reduced gizzards had significantly lower intake rates than birds with large gizzards. In fact, the maximal sustained intake rate of hard shelled prey was directly proportional to gizzard size. This variation may have biased my results, but since both prey items were treated the same way the relative difference should still be similar and the variance associated with this was included in the variance of the model.

In summary, these results indicate that in spite of the higher ash content and harder shells, the higher protein, higher energy content, and increased visibility (decreased search effort) of the mussel makes it more energetically efficient for the surf scoter especially at low densities. In addition, *M. lateralis* densities would have to be greater than 641 (number m⁻²) for this prey item to be profitable to surf scoters and handling time became independent of density for *I. recurvum* at approximately 101 (number m⁻²) mussels. To estimate the true foraging value (costs – benefits) of these prey items the expenditures associated with each prey would have to be considered.

Table 9. The number of dives and number of prey consumed during foraging trials of five captive surf scoters offered four different densities (30, 100, 1000, 3000 m⁻²) of *Mulinia lateralis* and *Ischadium recurvum* in a large dive tank (2.44m x 1.83m x 2.44m). Values followed by the same letter are not significantly different at the 5% level.

Density	n	# of Dives	# Consumed
<i>Mulinia lateralis</i>			
30	3	2 ± 2a	0 ± 1a
100	3	15 ± 11a	8 ± 8a
1000	5	16 ± 18a	193 ± 272a
3000	4	28 ± 18a	159 ± 227a
<i>Ischadium recurvum</i>			
30	5	27 ± 21a	23 ± 9b
100	5	112 ± 66a	89 ± 22b
1000	5	25 ± 28a	28 ± 6a
3000	5	13 ± 5a	34 ± 18a

Table 10. Parameters used for converting functional response curves of captive surf scoters feeding on *Mulinia lateralis* and *Ischadium recurvum* in a large dive tank (2.44m x 1.83m x 2.44m).

	Nitrogen (g)	Gross Energy (kJ)	Metabolizable Energy (%)
<i>Mulinia lateralis</i>	0.528	0.968	83.04
<i>Ischadium recurvum</i>	0.736	14.11	86.74

Table 11. Fitted parameters used for the functional responses in Figure 18 for surf scoters feeding on *Mulinia lateralis* and *Ischadium recurvum*.

Species	Nitrogen (g/s)			Gross Energy (kJ/s)			Metabolizable Energy (kJ/s)		
	<i>a</i>	<i>b</i>	<i>r</i> ²	<i>a</i>	<i>b</i>	<i>r</i> ²	<i>a</i>	<i>b</i>	<i>r</i> ²
<i>M. lateralis</i>	0.4390	-640.2	0.4998	0.8025	-640.8	0.4992	0.666	-640.8	0.4992
p-value		0.0022			0.0022			0.0022	
<i>I. recurvum</i>	0.3860	104.2	0.9742	7.376	101.4	0.9732	6.398	101.4	0.9732
p-value		<0.0001			<0.0001			<0.0001	



Figure 16. *Clockwise starting at top left picture.* The soft netting used over the tanks to contain the ducks; a side view of one of the large tanks used for diving trials; the simulated oyster bed created for the mussel diving trials; the large aquarium used to hold the prey items during trials; and a male surf scoter foraging on mussels during a trial.

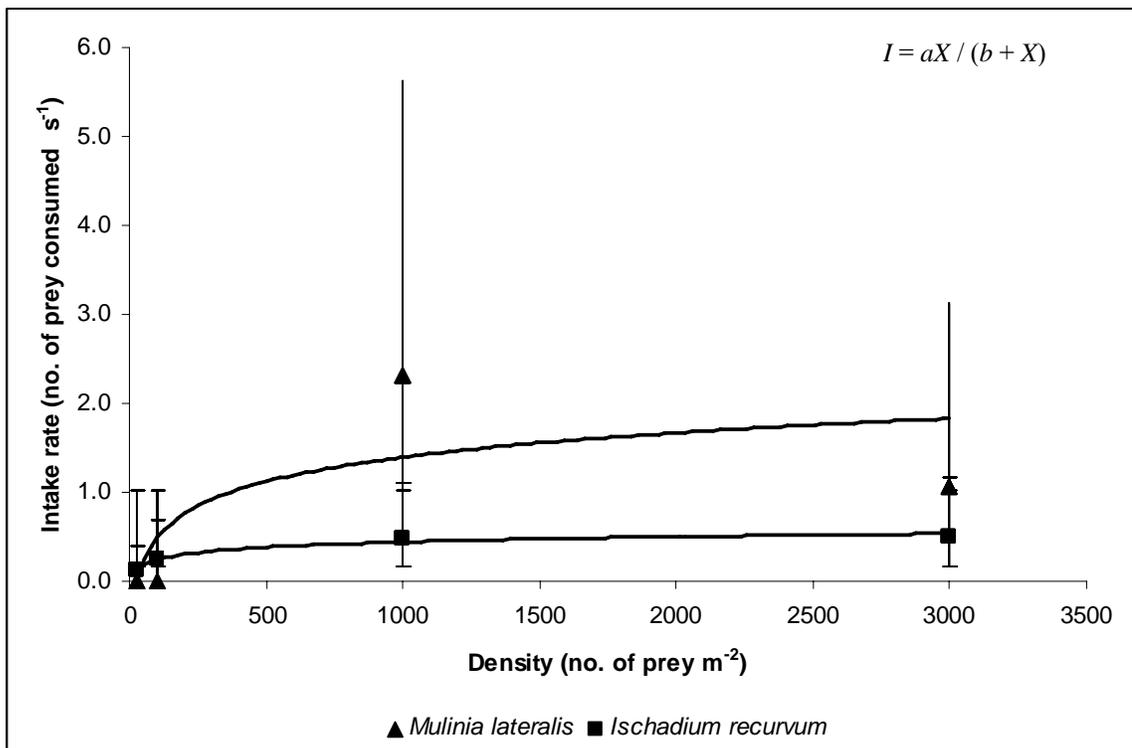


Figure 17. Functional responses determined for surf scoters diving 2 m to feed on *Mulinia lateralis* and *Ischadium recurvum*. The model was $I = aX / (b + X)$, where I was the number of prey consumed per second at the bottom, X was the number of prey m⁻², a was the handling time coefficient or the maximum rate at which the prey can be consumed independent of density, and b was the search time coefficient or the prey density at an intake rate of $0.5a$.

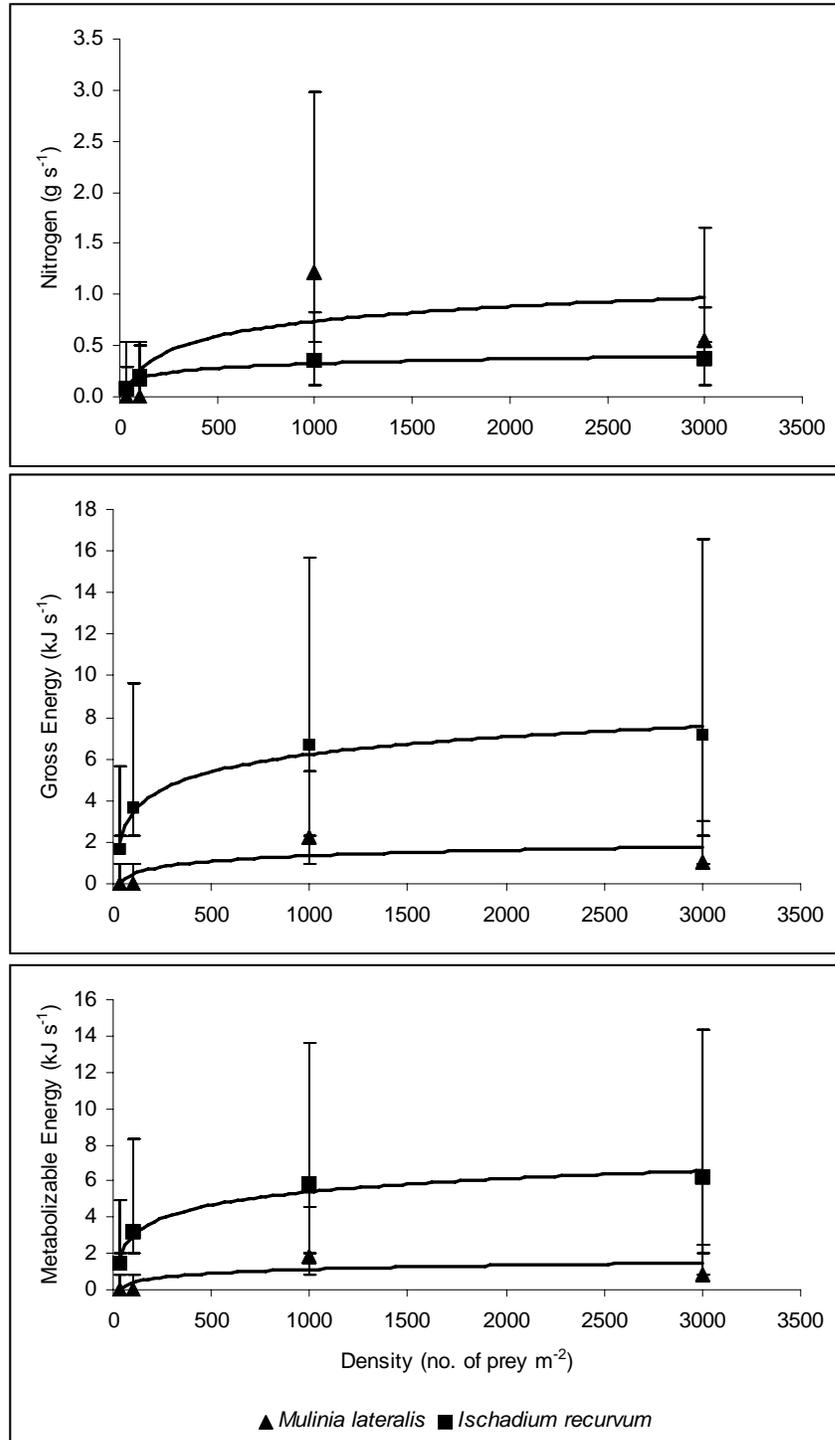


Figure 18. Calculated functional responses determined for surf scoters diving 2 m and feeding on *Mulinia lateralis* and *Ischadium recurvum* in a large dive tank (2.44m x 1.83m x 2.44 m) in terms of nitrogen, gross energy (GE), and metabolizable energy (GE x metabolizable energy (ME)).

Chapter Four. Foraging energetics model for surf scoters wintering on the Chesapeake Bay.

Abstract:

Declines in surf scoter (*Melanitta perspicillata*) populations wintering in the Chesapeake Bay have necessitated further research on possible factors causing this decline. Over the past 50 years, the Bay has become extremely eutrophied causing drastic changes in the benthos available to surf scoters. The subsequent decline in oyster beds has reduced the hard substrate needed by the hooked mussel (*Ischadium recurvum*) one of the primary prey items for surf scoters. This has induced the surf scoter to switch to a more opportune prey species, the dwarf surfclam (*Mulinia lateralis*). In this study we created an energetics model to quantify the relative foraging values (costs – benefits) of these two prey items to surf scoters wintering on the Bay. The difference in expenditure due to attachment by mussels does not affect the overall foraging expenditure. The energy intake drove the difference in foraging value of these two prey items. *I. recurvum* contained more energy and protein per item and resulted in greater intake of metabolizable energy, and, therefore, was more valuable to scoters than *M. lateralis*. Based on these results, *M. lateralis* costs more to obtain than was beneficial for surf scoters in the Chesapeake Bay. Therefore, *I. recurvum* was a key prey item for wintering scoters; successful implementation of oyster restoration in the Chesapeake Bay would benefit the surf scoter populations that winter there.

Introduction:

There has been an increase in the severity, duration, and frequency of anoxic events in the deep areas of the Chesapeake Bay and some of its tributaries (Officer et al.

1984; Seliger et al. 1985; Tuttle et al. 1987), with potentially devastating consequences for benthic organisms (Seliger et al. 1985; Kemp and Boynton 1992), such as reduced benthic biomass, species diversity, and altered structure (Holland et al. 1977; Dauer and Ransinghe 1992; Dauer et al. 2000). The decline of the American oyster (*Crassostrea virginica*) in the Chesapeake Bay – estimated to be about 1% of its historic abundance (Newell 1988) – may be a major factor contributing to the recent anoxic conditions (Dame et al. 1980; Newell 1988; Mann et al. 1991; Ulanowicz and Tuttle 1992; Gottlieb and Schweighofer 1996) and a reduction in the availability of hard substrates to epifaunal organisms.

One organism affected, the hooked mussel (*Ischadium recurvum*), is a very important food source to wintering surf scoters (*Melanitta perspicillata*; Perry et al. 2007). Therefore, the abundance or occurrence of surf scoters in those areas also becomes impacted. Firstly, the scoters may be forced to feed on another prey item, the dwarf surfclam (*Mulinia lateralis*), that is not as energetically efficient for them. In addition, *M. lateralis* is not available in the same sizes as the mussels therefore it does not provide as much energy on a per dive basis relative to the mussels. Secondly, the reduction in habitat availability for the mussels could increase densities in the existing habitats, which could potentially benefit scoters by reducing the costs associated with searching. However, as Petersen and Black (1988) reported if the energetic value of the mussels declines due to overcrowding, this could negatively influence the foraging response of scoters.

Mulinia lateralis occurs in approximately 2 cm of sand in salinities ranging from 10-30 ppt (Figure 2; White 1989, Lippson and Lippson 1997), whereas, *Ischadium*

recurvum attaches to hard substrates, primarily oyster beds, by its byssal threads in salinities ranging from 5-30 ppt. For the size classes commonly consumed by scoters (18-24 mm for *I. recurvum* and 6-18 mm for *M. lateralis*), *I. recurvum* contains a higher ash, lipid, protein, and energy content than *M. lateralis*. For scoters diving 2 m deep in an experimental dive tank to obtain each prey item intake rate increased with prey density up to 1000 per square meter for *M. lateralis* and 2000 per square meter for *I. recurvum*. The assimilated energy functional response for *I. recurvum* was significantly greater than for *M. lateralis*. It appeared that the added cost of removing an attached prey and increased ash content due to significantly stronger shells apparently did not outweigh the added profitability of energy and protein provided by *I. recurvum*. However, the increased cost of searching for dense concentrations of *M. lateralis* every year and the wide distribution within these patches may outweigh any potential benefit to the scoter.

It seems reasonable that a scoter would adopt a foraging strategy that best balances the energetic demands of foraging relative to the energetic rewards of consuming each prey item (Klasing 1998). Optimal solutions to this cost-benefit relationship form the basis of optimal foraging theory. According to the concept, a scoter's morphological, physiological, and behavioral traits have been shaped by evolutionary pressures in a way that maximizes net energy acquisition. Ultimately, surf scoters should select the prey item that provides the maximum net rate of energy return (energy provided by prey minus energy required to find and consume prey; Townsend and Hughes 1981). By estimating the relative foraging values (costs – benefits) of *I. recurvum* and *M. lateralis* for surf scoters we can determine if they are able to sustain

themselves if a drastic shift occurs in the benthos available to them in the Chesapeake Bay.

Considerable data and methodology have been developed that model and measure both energy costs of free existence of animals (Nagy 1987, Costa 1988, Goldstein 1988, Birt-Friesen et al. 1989) and their foraging strategies (Tome 1988, Beauchamp et al. 1992, Houston and Carbone 1992, Kooyman et al. 1992, Nolet et al. 1992, Ball 1994, Halsey et al. 2003, van Gils et al. 2003, Piersma et al. 2003, Hansen and Ricklefs 2004, Green et al. 2005). Managers usually are interested in the habitat capacity needed to support a population of animals and the strong predation influence by scoters requires wintering areas to maintain substantial and stable bivalve populations. Past studies have calculated the average energy requirements of birds and then compared these estimates to total food biomass present to infer sustainable population levels, impacts on the food base, or competition with other species (Lovvorn and Gillingham 1996). However, food dispersion affects the biomass that can be fed upon profitably and thus the fraction of food organisms subject to predation (Lovvorn 1994, Lovvorn and Gillingham 1996). In addition, models using parameters averaged over entire populations might yield different results from individually based models that simulate the foraging energetics of many individuals (Houston et al. 1988, Lovvorn and Gillingham 1996). Models are needed to analyze how changes in prey resources influence the numbers and distribution of surf scoters wintering on the Bay to better understand the influence of environmental and anthropogenic factors on wintering surf scoters.

From this paper, a model of foraging energetics of surf scoters (*Melanitta perspicillata*) was developed to determine the effect of drastic changes in the benthos on

surf scoter energetics. These results have important implications for estimating energy balance, effects of restoration efforts on energy balance, and quality of habitat needed to sustain surf scoter populations during winter on the Chesapeake Bay.

Methods:

The model determines the amount of energy obtained for two primary bivalves (dwarf surf clam (DSC; *Mulinia lateralis*) and hooked mussel (HM; *Ischadium recurvum*) fed upon by surf scoters in winter in the Chesapeake Bay. The metabolizable energy intake (kJ s^{-1}) was previously determined and it was multiplied by the amount of time that is available for foraging in a day.

$$\text{Intake}_{\text{Mulinia}} (I_M) = [(0.666 * \text{Density}) / (-640.8 + \text{Density})]$$

$$\text{Intake}_{\text{Ischadium}} (I_I) = [(6.398 * \text{Density}) / (101.4 + \text{Density})]$$

The above two equations were combined in the following formula to determine amount of energy assimilated:

$$\text{Total Metabolizable Energy Intake (kJ)} = I_{M \text{ or } I} (\text{kJ/s}) * \text{Foraging duration (s)}$$

The energy expended during diving, cost of diving, was determined by Richman and Lovvorn (2008) for white-winged scoters (*Melanitta fusca*), a close congener of surf scoters, and adapted for surf scoters. The cost of diving was the summation of the cost during descent to the prey items at the bottom and the cost associated with staying at the bottom while foraging. Richman and Lovvorn (2008) provide more details on the derivation of the following formulas.

$$\text{Cost of Diving (kJ)} = [\text{cost of decent} + \text{cost at the bottom}] * \text{Foraging duration (s)}$$

$$\text{Cost of Descent (kJ/s)} = [[(0.52 * W) / t_{\text{descent}}] * 20.1 \text{ J/ml O}_2] / 1000 (\text{kJ/J})$$

$$\text{Cost at Bottom (kJ/s)} = [[(0.48 * W) / t_{\text{bottomt}}] * 20.1 \text{ J/ml O}_2] / 1000 (\text{kJ/J})$$

$$\text{Work of Stroking (W)}(\text{ml O}_2) = [\text{MR (ml O}_2/\text{s)} * t_{\text{dive}}(\text{s})] - [\text{RMR (ml O}_2/\text{s)} * t_{\text{ascent}}(\text{s})]$$

where MR was the duck's metabolic rate during diving and RMR was the duck's metabolic rate at rest.

For activity costs of pauses between foraging bouts and surface activities we used mass-specific respirometry data for tufted ducks (*Aythya fuligula*), the relation between aerobic energy cost of resting on the surface (P_r , in watts per kilogram) and water temperature (T_w °C) was

$$P_r = 12.67 - 0.3069T_w$$

(Bevan and Butler 1992, Lovvorn and Gillingham 1996).

This energy cost was prorated for the body weight of scoters and the amount of time spent resting which was estimated based on activity budgets reported in Savard et al. (1998).

$$\text{Resting cost (kJ)} = (P_r \text{ (J/s kg)} * \text{body weight (kg)} * \text{resting time (s)}) / 1000 \text{ (kJ/J)}$$

We assumed the costs of sleeping, alert behavior, comfort movements, dive recovery, and heat increment of digestion were equal to that for resting at given water temperatures (Lovvorn and Gillingham 1996). Aerobic cost of surface swimming was determined by Richman and Lovvorn (2007) for white-winged scoters to be 7.86 W/kg which was determined to be appropriate for surf scoters as well. This was prorated for time spent swimming (Savard et al. 1998) and body weight of surf scoters.

$$\text{Swimming cost} = (11.48 \text{ (J/s kg)} * \text{Swimming time (s)} * \text{body weight (kg)}) / 1000 \text{ (kJ/J)}$$

Lovvorn and Gillingham (1996) determined for canvasbacks that the aerobic power of flying was 230 W at the maximum range speed (V_{mr}) of 23 m/s for the mean (± 1 SD) body mass (1.395 ± 0.128 kg) and wingspan (0.873 ± 0.029 m). At this time we are

using this value in our model until further measurements can be obtained specifically for surf scoters.

$$\text{Flying cost (kJ)} = (230 \text{ (J/s)} * \text{flying time (s)}) / 1000 \text{ (kJ/J)}$$

Detachment work was calculated by using the break energy (J/thread) for *Mytilus edulis*, the blue mussel, and multiplying it by the estimated number of threads for an 18-24 mm mussel (30 threads; Smeathers and Vincent 1979).

$$\text{Detachment work (kJ)} = \text{break energy (kJ/thread)} * \text{number of threads}$$

Piersma et al. (2003) estimated the crushing power of the gizzard for a mollusk foraging shorebird to be -0.045 J/s. Since this is based on a shorebird, we adjusted this value for the average size of a surf scoter gizzard determined by Perry et al. (2007). This assumed that there was a direct relationship between the crushing power of the gizzard and the size of the gizzard. This was also prorated based on the relative difference in the strength of the shells of these two prey items. Guillemette (1994) reported the gizzard working capacity for common eiders (*Somateria mollissima*) as 2.4 g/min which converts to 0.04 g/s. The gizzard energy was calculated by dividing these two factors and multiplying by the mean fresh mass consumed in a foraging bout which was estimated as 196 g/day prorated to g/s (Vermeer 1981) and the estimated amount of time in a day spent by the gizzard crushing food.

$$\text{Gizzard work (kJ)} = ((\text{Amt consumed (g/s)} * \text{Gizzard crushing power (kJ/s)}) / \text{Gizzard working capacity (g/s)}) * \text{Gizzard crushing time (s)}$$

The above water costs including physiological costs were added to the work done underwater for comparison with energy intake during foraging in a day.

$$\text{Energy Balance (kJ)} = (\text{Metabolized Energy Intake Total} - \text{Total Energy Expenditure})$$

We evaluated effects of variation in the parameters on model estimates of mean balance of energy per day of foraging (Table 14, 15). Sensitivity analyses considered ranges of values likely to occur in the Bay (Table 12). Each driving variable was altered based on minimum and maximum values observed in the field. The effects of these changes on the energy balance were examined to determine what variables influenced the final outcome the most.

Results:

The most significant expenditure for scoters was the cost associated with flying followed by diving for both prey items (Table 13). The energy balance for *I. recurvum* remained positive even when all the minimum values of each parameter were applied unlike *M. lateralis*. Metabolizable energy intake total drove the energy balance in this model. Within this total, handling time contributed most when the maximum values were used for *I. recurvum*, but at the lower values search time provided the most influence. Search time also contributed the most to energy intake for *M. lateralis*. Sensitivity analyses reinforced that energy intake contributed most to the variation in the model for *I. recurvum*, but gizzard work contributed the most for *M. lateralis* (Table 14, 15). When each driving variable in the model was increased energy intake and flying cost were integral for *M. lateralis*. When each driving variable in the model was decreased, flying cost also contributed to the variation for *I. recurvum*; energy intake, dive work, and flying cost respectively contributed to the variation for *M. lateralis*. The additional cost associated with attachment strength did not significantly impact the energy balance for *I. recurvum*.

Discussion:

To increase the accuracy of the model, energy expenditure needs to be measured for surf scoters rather than estimated. For example, Savard et al. (1998) reported that surf scoters have the second highest wing area relative to body weight of the nine other diving duck species. This means that they could be more efficient at flying than canvasbacks and, thereby, having a lower overhead work expenditure. In addition, Savard et al. (1998) found that surf scoters have the third highest paddle index among the 15 species of seaducks which signifies their efficiency at swimming and diving. Overall, the model probably overestimates these costs, but further information is needed to determine the true values for the costs associated with these activities.

The fact that gizzard work influenced the variation in the model for *Mulinia lateralis* could have significant implications on the energy balance for surf scoters. Apparently, a softer shelled and lower ash content prey item was more energetically efficient, based on the costs associated with obtaining the prey. However, the amount of energy obtained from the prey could not counterbalance the expenditures; therefore, *M. lateralis* cost more for a surf scoter to obtain despite these advantages. It is possible that *M. lateralis* provides only the bare minimum energy level to meet the scoter's daily energy requirement, therefore, when the minimum values were used in the model a negative energy balance occurs.

There was no effect of attachment strength on expenditure, however, this could be an artifact of the intake rate and density being based upon single mussels attached to the substrate not in mussel clumps. There is a need for research on the foraging energetics of surf scoter preying on large clumps of mussels. Savard et al. (1998) reported scoters

bringing mussel clumps to the surface while foraging. In addition, a determination of the relative abundance of the preferred size class (18-24 mm) within the existing oyster beds. If this size class is depleted within one season then the scoters may be forced to prey on *M. lateralis*, which is only valuable to wintering scoters in higher densities.

Based on the results of this model it is clear how important the energy intake was to the scoter's foraging energetics. Even though *I. recurvum* consisted of a harder shell and higher ash content, with its high protein content, decreased search time due to increased visibility, and its occurrence in dense concentrations within a patch lends itself to be a very profitable food item for the scoter. If the proposed restoration efforts of the oyster bars come to fruition then the Bay could definitely sustain more scoters over winter. If this restoration occurs and we do not observe an increase in scoter numbers over time, the population declines presumably are influenced by some factor other than foraging energetics, such as a decline in recruitment or increased harvest rates.

However, energy intake was based on the functional responses of single ducks diving in an experimental dive tank, which does not take into account that surf scoters are synchronous divers (Savard et al. 1998). They have been observed diving one right after the other, which reduced the drag on each individual much like a bicyclist in a race. This would reduce the amount of energy expended while diving. In addition, Halsey et al. (2006) noted a decrease in surface duration and an increase in dive-to-pause ratio as the number of ducks increased. This indicated a decrease in rest and an increase in diving effort as the number of conspecifics increased and was explained by a resultant increase in competition for food. The lower work rate of individual diving ducks was probably the behavioral response of the ducks once they had learned that there was no competition

for the food source. To better understand the effects of synchronous diving and competition for food resources on this energetics model, more research is needed.

Kidwell (2007) noted that the substrates in the Bay are very patchy, therefore, it would be of interest to estimate the distance between prey patches to apply to the model. The areas that have the densest concentrations of *M. lateralis* shift from year to year (pers. comm. V. Kennedy). Basically, one might find a dense concentration in a location one year and in the next year in the same location only find a few individuals. Finding these new “hot beds” of clams on a yearly basis could be an extra cost associated with obtaining this prey item. The model shows that the most costly activity is flying, so the greater distance between prey patches would increase the overall cost associated with obtaining *M. lateralis*. Most likely, the scoters immediately forage on the dense mussel beds in November when they arrive in the Bay. After they have refueled and possibly depleted the optimal size of mussels, they might go in search of the high density clam beds. It would be interesting to learn more about the ecology and population biology of *M. lateralis*. Does this species have an infinite number of possible locations within its salinity and substrate range or are they limited in distribution and only a few areas are able to sustain them? If this were the case, then once a scoter learned where these areas were every year it could search them to find the “hot bed” and reduce the chance of wasted effort.

The scoters may switch during the end of winter before migration to prey more on the clam and soft bodied organisms rather than the mussel, owing to the physiological constraints of flying. Dekinga et al. (2001) found that red knots (*Calidris canutus*) increased their gizzard mass 147% when they switched from soft food to hard shelled

food. In addition, reversible changes in gut length in response to changes in the diet have been reported to occur in ducks within five days (Drobney 1984, Kehoe et al. 1988). Internal organ mass may directly affect flying performance of birds. Because the costs of flight increase with body mass (Kvist et al. 2001) and maneuverability may be impaired at heavier masses (Kullberg et al. 1996, Metcalfe and Ure 1995), minimizing digestive organ mass may be an important consideration. Sedinger (1997) suggested that the small ceca in waterfowl reflect a balance between costs of flight for waterfowl and the benefits of the ceca for nutrient balance. In addition, reducing the size of the digestive organs would also increase the space available for fat deposition just before departure on migratory flights. Therefore, there may be a physiological advantage for the surf scoters foraging on a lower ash and thinner-shelled bivalve.

The model in this study determined the energy balance for surf scoters preying upon *M. lateralis* and *I. recurvum*, but more information was necessary to increase the accuracy of the model. *I. recurvum* was a very valuable prey item for wintering surf scoters. However, scoters could preferentially prey on both organisms (along with other species) based on their physiological requirements during the winter months by obtaining the high profit mussel when they first arrive after migrating south and switching to the clam when their digestive constraints for migration require them to consume a soft-shelled prey item. It would be beneficial to examine the food habits data of surf scoters in the Bay more carefully to see if there is a seasonal effect involved in their prey selection.

In summary, this model provided a platform to determine the relative foraging values of *I. recurvum* and *M. lateralis* to estimate the effects of changes in the benthos on

the flow of energy provided for wintering surf scoters. This study enhanced the realization that more information is needed to accurately determine these effects. In addition, this model created an integral framework that can be applied to a larger management population model for wintering surf scoters. This population model can incorporate all the factors that would influence the numbers and distribution of wintering surf scoters in the Chesapeake Bay.

Table 12. The parameters used to estimate foraging energetics of *Ischadium recurvum* and *Mulinia lateralis* for surf scoters wintering in the Chesapeake Bay based on mean and variation of like variable observed in the field.

<i>Ischadium recurvum</i>			
	minimum	mean	maximum
Water Temp (°C)	1	4.3	20
Density (# / m ²)	30	1500	3000
Handling Time Coefficient	5.02	6.40	7.78
Search Time Coefficient	2.80	101	200
Body Weight (g)	900	975	1050
Descent Duration (s)	0	6.1	18.3
Bottom Duration (s)	0	7.87	19.58
Ascent Duration (s)	0	4.2	16.4
Total Dive Duration (s)	0	18.17	54.27
Work of Stroking (W)(ml O ₂)	0	11.99	34.59
Diving Metabolic Rate (MR)(ml O ₂ /s)	3.52	4.26	5.00
Resting Metabolic Rate (RMR)(ml O ₂ /s)	0.276	0.320	0.36
Cost of Descent (kJ/s)	0.00	1.02	0.98
Cost at Bottom (kJ/s)	0.00	0.73	0.85
Resting Time (s)	31320	30600	29880
Foraging Duration (s)	20880	19800	19080
Flying Time (s)	34920	31860	28800
Swimming Time (s)	27000	25560	24120
<i>Mulinia lateralis</i>			
	minimum	mean	maximum
Water Temp (°C)	1	4.3	20
density (# / m ²)	15	200	1000
handling time coefficient	0.218	0.667	1.12
search time coefficient	-901.6	-640.8	-380
body weight (g)	900	975	1050
Descent Duration (s)	0	6.1	18.3
Bottom Duration (s)	0	6.52	10.02
Ascent Duration (s)	0	4.2	16.4
Total Dive Duration (s)	0	16.82	44.72
Work of Stroking (W)(ml O ₂)	0	11.00	27.58
Diving Metabolic Rate (MR)(ml O ₂ /s)	3.52	4.26	5.00
Resting Metabolic Rate (RMR)(ml O ₂ /s)	0.276	0.320	0.36
Cost of Descent (kJ/s)	0.00	0.94	0.78
Cost at Bottom (kJ/s)	0.00	0.81	1.32
resting time (s)	31320	30600	29880
Foraging duration (s)	20880	19800	19080
Flying Time (s)	34920	31860	28800
Swimming Time (s)	27000	25560	24120

Table 13. The driving variables used to determine the net energy balance (kJ) per day of foraging of a surf scoter wintering in the Chesapeake Bay. The minimum and maximum values corresponded to the variation of each parameter reported in Table 12.

<i>Ischadium recurvum</i>			
Intake	minimum	mean	maximum
Metabolized Energy Intake Total (kJ)	95,804	118,655	139,143
Expenditure			
Dive Work (kJ)	0	698	702
Flying cost (kJ)	8,032	7,328	6,624
Swimming Cost (kJ)	191	196	199
Resting Cost (kJ)	348	339	205
Detachment Work (kJ)	2.E-05	4.E-05	6.E-05
Gizzard Work (kJ)	9.E-02	1.E-01	1.E-01
Total Energy Expenditure (kJ)	8,571	8,560	7,730
Energy Balance (kJ)	87,233	110,095	131,413
<i>Mulinia lateralis</i>			
Intake	minimum	mean	maximum
Metabolized Energy Intake Total (kJ)	-77	-5,988	34,313
Expenditure			
Dive Work (kJ)	0	696	807
Flying cost (kJ)	8,032	7,328	6,624
Swimming Cost (kJ)	191	196	199
Resting Cost (kJ)	348	339	205
Gizzard Work (kJ)	8.E-02	1.E-01	1.E-01
Total Energy Expenditure (kJ)	8,571	8,558	7,835
Energy Balance (kJ)	-8,648	-14,546	26,478

Table 14. Results of sensitivity analyses; each driving variable was increased/decreased based on the maximum/minimum values reported in Table 12 and the percent difference from the mean energy balance examined.

<i>Ischadium recurvum</i>	Observed Means	Increase Intake	Increase Dive Work	Increase Nutrient Work	Increase Flying Cost	Increase Swimming Cost	Increase Resting Cost	Increase Detachment Work	Increase Gizzard Work	All High
Energy Balance (kJ)	1.101E+05	1.306E+05	1.101E+05	1.101E+05	1.108E+05	1.101E+05	1.102E+05	1.101E+05	1.101E+05	1.314E+05
% Mean Balance		118.6%	100.0%	100.0%	100.6%	100.0%	100.1%	100.0%	100.0%	119.4%
<i>Mulinia lateralis</i>										
Energy Balance (kJ)	-2.31E+04	1.72E+04	-2.32E+04	-2.31E+04	-2.24E+04	-2.31E+04	-2.30E+04	NA	-1.45E+04	1.86E+04
% Mean Balance		-74.44%	100.48%	100.00%	96.95%	100.01%	99.42%	NA	62.96%	-80.69%
<i>Ischadium recurvum</i>	Observed Means	Decrease Intake	Decrease Dive Work	Decrease Nutrient Work	Decrease Flying Cost	Decrease Swimming Cost	Decrease Resting Cost	Decrease Detachment Work	Decrease Gizzard Work	All Low
Energy Balance (kJ)	8.344E+08	8.724E+04	1.108E+05	1.101E+05	1.094E+05	1.101E+05	1.101E+05	1.101E+05	1.101E+05	8.723E+04
% Mean Balance		79.2%	100.6%	100.0%	99.4%	100.0%	100.0%	100.0%	100.0%	79.2%
<i>Mulinia lateralis</i>										
Energy Balance (kJ)	6.70E+08	-1.72E+04	-2.24E+04	-2.31E+04	-2.38E+04	-2.31E+04	-2.31E+04	NA	-1.45E+04	-8.65E+03
% Mean Balance		74.42%	96.99%	100.00%	103.05%	99.98%	100.04%	NA	62.96%	37.43%

Overall Discussion:

This research plays an integral role in determining the effects of changes in the benthos on the status of seaducks in the Chesapeake Bay. This project is part of a larger project, which entails creating a simulation model that can be used by managers for seaducks wintering on the Chesapeake Bay. There are restoration plans in effect over the next ten years for large scale restoration of oyster beds in the Chesapeake Bay. If these efforts take place this would provide a huge increase in the available habitat for mussels, which could result in a population expansion in surf scoters. This model would allow for these possible changes in the benthos to be monitored and the effects on scoter populations could then be determined. Presently the models that exist on the Chesapeake Bay exclude waterfowl on the basis that they have little effect on the ecosystem; therefore there is a need for ecosystem models that include the effect of waterfowl. This study created a model that represents the flow of energy between the benthos and the scoter populations, which will aid in creating an accurate population model for wintering scoters on the Chesapeake Bay. Without a basic understanding in how these prey resources are utilized by scoters the quantification of the changes in the benthos is not possible. In order to better manage the wintering population of surf scoters the connection between the habitat changes, prey resources, and scoter utilization need to be calculated.

Ultimately, a management model that incorporates all the factors that influence surf scoter populations wintering on the Bay would be needed (Figure 19). It is possible that the surf scoter could be considered a keystone predator in the Bay during winter and could be used to monitor the health of the Bay from a waterfowl standpoint. The hooked

mussel could also be considered a keystone prey that could be used to monitor the status of predators, other prey species, and water quality.

Not only does this study show the effects of changes in food resources on surf scoters, but numerous other waterfowl species have been affected by the changes in the Bay ecosystem. With a dramatic decline in a food source an organism has to shift food resources in order to obtain its daily energy requirement. Wintering Canada geese (*Branta canadensis*) switched from aquatic plants to agricultural crops in 1940s and 1950s, which coincided with a decrease in submerged aquatic vegetation (SAV) and an increase in pollutant-tolerant invertebrates (*Rangia* and *Corbicula* spp.). The demise of SAV beds in early 1970s contributed to high mortality in soft-shelled clams. However, the increase in agriculture provided an alternative food for field feeding species during the winter. The greater snow goose (*Chen caerulescens*) switched from marsh-plant shoots and rhizomes to feeding on agriculture crops in the late 1970s in the mid-Atlantic (Hindman 1989). Tundra swans (*Cygnus columbianus*) had also been dependent on SAV during winter, but they were forced to abandon these food items because of the large-scale SAV decline in 1972 and 1973 resulting in a switch to agricultural food sources. Perhaps as a result of the decline in SAV, tundra swan numbers have declined in Maryland and increased in North Carolina where SAV is thriving. Most diving ducks have also been affected by the decline in SAV and are preying upon more invertebrate prey (Perry and Uhler 1988). Lesser scaup (*Aythya affinis*) consumed *Mulinia lateralis* and *Rangia cuneata* and greater scaup (*Aythya marila*), buffleheads (*Bucephala albeola*), and ruddy ducks (*Oxyura jamaicensis*) consumed surf clams. Redhead (*Aythya americana*) and American wigeon (*Anas americana*) decreased in numbers and

distribution because of the deteriorated conditions of estuarine plant and animal foods.

This overwhelming evidence shows that ecosystem changes in the food resources in the Bay directly affect the numbers and distribution of waterfowl that winter in the Bay.

Not only do changes in availability directly affect the presence of waterfowl, but there are also indirect or secondary effects of ecosystem changes that could influence the presence of waterfowl, especially diving ducks and seaducks. For example, climate change of unknown proportions is probably occurring and there is evidence of changes in the abundance and distribution of vertebrates that may be due to this change. Sea level in the last 100 years has risen 10.5 cm, 4 cm from thermal expansion, 4 cm from melting mountain glaciers, and 2.5 cm from the partial melting of the Greenland ice sheet (Hindman 1989). A number of secondary effects from this rise have been noted, such as changes in ocean circulation, coastal upwellings, and modifications of oceanic productivity. For example, the zooplankton volume in California has decreased by 80% since 1970 while the sea surface temperature increased by 1.5°C and a 40% decrease in pelagic seabird abundance occurred (Veit et al. 1996). If sea levels continue to rise then this could indirectly alter the energy balance for surf scoters preying on invertebrates in the Bay. Changes in the distribution and abundance of invertebrates due to sea level rise and other climate change factors could cause ducks to expend more energy during the search and capture of food organisms. In addition, with the increase in water temperature the frequency of anoxic events in the Bay could increase and become more widespread causing direct mortality of prey and further reducing the food availability to wintering waterfowl, especially the diving ducks.

Further, if breeding grounds do not freeze due to increasing atmospheric temperatures there could be less incentive to migrate to the Bay. If there are fewer ducks, then increased competition for space by invertebrates could influence overall health and quality of bivalve populations resulting in a reduction in species diversity as dominant bivalves outcompete lesser species. Numerous studies have shown the important effects of seaduck predation on intertidal populations and communities (Guillemette et al. 1996, Hamilton 2000, Larsen and Guillemette 2000). The large body size, high metabolic rates, and gregarious nature of seaducks leads to high rates of predation and potentially important effects on prey abundance. To date, studies documenting the effects of seaduck predation have mainly focused only on mussel prey used as a primary part of their diet. Moreover, these studies have documented the effect of seaducks on mussel populations that can significantly reduce the abundance of mussels in rocky intertidal communities. These significant effects of seaducks on mussel populations exacerbate other environmental pressures on mussel populations and lead to subsequent changes in community structure.

Because mussels are dominant competitors for space, their depredation creates open habitat for competing species (Paine 1966, 1974). Lacroix (2001) documented complete local extirpation of some mussel beds by surf scoters in coastal British Columbia. The presence of seaducks as top predators may also affect community dynamics by limiting the abundance of competing predators. Hamilton (2000) found that exclusion of common eiders (*Somateria mollissima*) led to an increase in the abundance of dogwhelks, *Nucella lapillus*, as whelks were benefited from the lack of interspecific competition for available mussel prey. The effects of seaduck predation on infaunal

bivalve abundance in soft-bottom habitats were documented by Lewis et al. (2007). By selectively preying on the most abundant infaunal animals, scoters assumed a particularly important role in structuring these communities. Selective predation by scoters resulted in reduced variation in the relative abundance of prey by decreasing the abundance of the most common species. Lewis et al. (2007) and Kidwell (2007) both showed the ability of scoters to deplete their winter food sources and assume a significant predation role in the ecosystem. Therefore, the strong predation potential of scoters requires the presence of wintering areas with robust bivalve populations. Previous studies in the Dutch Wadden Sea have linked significant over-winter mortality of common eiders to shortages of bivalve food supplies (Camphuysen et al. 2002). In areas used by wintering scoters, availability of bivalve stocks should be considered when reviewing potentially negative activities, such as foreshore development, commercial bivalve harvesting, and potentially positive activities, such as oyster and submerged aquatic vegetation restoration efforts, which may significantly affect bivalve numbers.

There are serious plans for large-scale oyster restoration efforts to take place in the next ten years in Chesapeake Bay. These efforts include creating usable habitat with oyster shell for oyster larvae to settle upon and develop. There also are plans for the possible introduction of the non-native *Crassostrea ariakensis* (Gottlieb and Schweighofer 1996). Both these methods should provide additional available habitat for mussel larvae settlement, but more information is needed on the interaction between this non-native oyster and the settlement of mussel larvae. If these two species compete for resources then there could be an antagonistic relationship and they may not provide any

additional habitat for mussels. This would further reduce the available prey for wintering scoters, especially if the exotic oyster outcompetes the native oyster.

Surf scoters are just one of three scoter species that winter in the Chesapeake Bay. The white-winged scoter (*Melanitta fusca*) and black scoter (*Melanitta nigra*) winter in fewer numbers than the surf scoters, which could be due to competition for food resources. When two species compete for a common resource, the dominant species is usually limited geographically by the physical environment or food resource, whereas the excluded species is found in areas beyond the geographic limits tolerated by the dominant species. That is, the survival of excluded species depends on a greater tolerance of environmental conditions than is present in the dominant species. Perry et al. (2006b) used satellite transmitters to track black and surf scoters movements and noted that black scoters traveled further south into Pamlico Sound, North Carolina and one scoter went as far south as Florida coastline. However, winter aerial surveys document that black scoters typically winter further south than the other scoter species. This could be an indication that they are being displaced due to competition for increasingly limited food resources in the Bay or that their smaller body size is energetically relevant. It was also noted that no scoters wintered in Delaware Bay, a nearby estuary that could be utilized by wintering scoters, which could be due to the lack of preferred invertebrate prey, but future benthic sampling would be needed to determine prey availability relative to the Chesapeake Bay. A similar situation could be occurring for white-winged scoters, but very little is known on the movements of this species in the Atlantic flyway.

In addition to perturbations in the food resources available to scoters in the Bay, the altering distribution of scoters could also be influenced by human disturbance. Due

to increased regulations on Canada geese hunting there has been an increase in guided hunting of seaducks on the Chesapeake Bay (Perry et al. 2006b). Both hunting disturbance and increased boat traffic during fishing season could negatively affect the energy balance of scoters wintering in the Bay. Perry and Deller (1996) noted that hunting disrupted daily movement patterns of ducks and some ducks adapted to hunting by limiting their activities. Flying cost contributes the most to the total energy a scoter expends during a day. If this cost is increased with more flying time due to increased human disturbance, then scoters would have to forage more often to counterbalance the extra energetic expenditure. However, several studies demonstrated that disturbance to waterfowl by hunters resulted in reduced energy gains, which could affect survival (Frederickson and Drobney 1979, Gaston 1991, Perry and Deller 1996). Therefore, diving for the most energetically efficient prey item would be the most beneficial selection by wintering scoters during this time of increased stress. It would be extremely beneficial to wintering scoter populations to create sanctuary areas in the Bay where they could take refuge during these stressful anthropogenic events.

In summary, this study has provided some insight into the foraging ecology of wintering surf scoter on the Chesapeake Bay. However, there are still many questions; such as an accurate determination of the cost of diving, how much energy is expended flying between prey patches, what is the size structure composition of the mussel beds, the variability in prey patch occurrence, and the effect of synchronous diving behavior on energy expenditure while diving that need to be answered before an accurate scenario of whether surf scoters can truly survive on *M. lateralis* if the sudden disappearance of *I. recurvum* occurred.

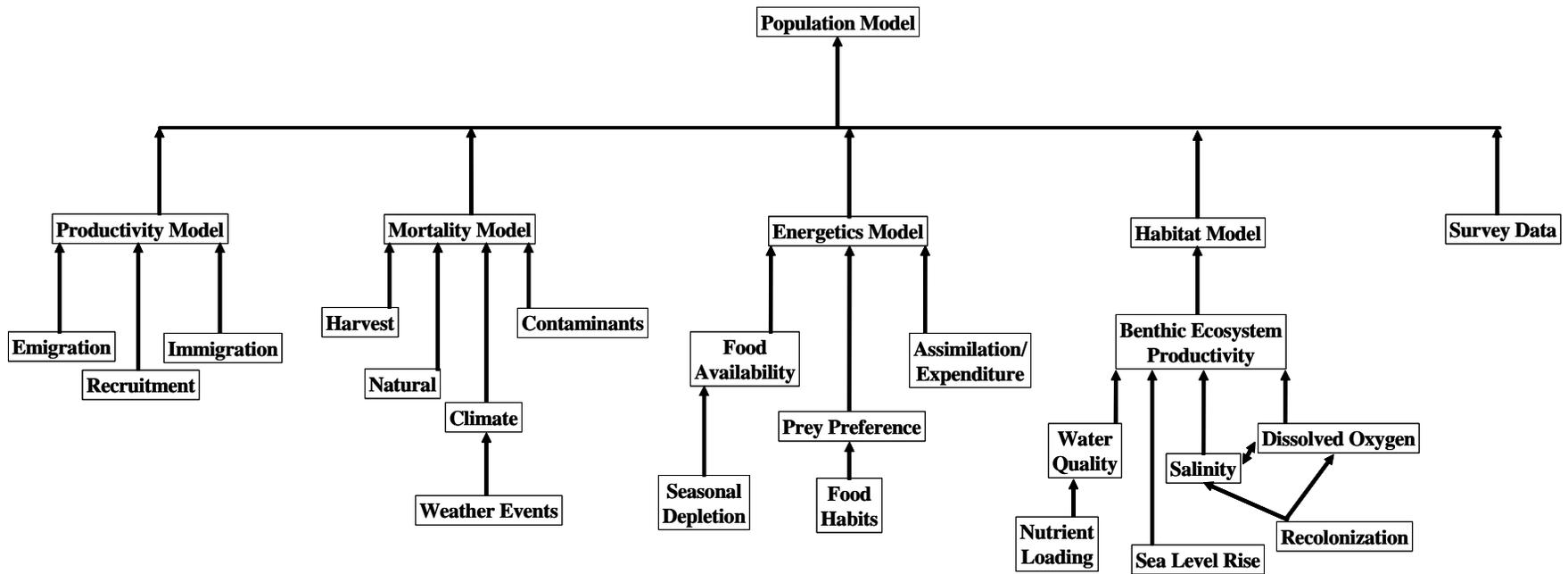


Figure 19. A visual representation of a theoretical surf scoter population model created for the management of wintering scoter populations on the Chesapeake Bay. This study provided information for the energetics model component of this overall population model. Further information is needed before this model can come to fruition.

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