ABSTRACT

Title of Document: NUTRIENT AND ENERGY ACQUISITION BY HARLEQUIN DUCKS FORAGING FOR AN EXOTIC CRAB, *CARCINUS MAENAS*, AND A NATIVE CRAB, *HEMIGRAPSUS OREGONENSIS*

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Changes in prey species availability can present energetic challenges to wintering western North American harlequin ducks (*Histrionicus histrionicus*). The goal of this study was to examine the feeding behavior of captive harlequins and compare energy and nutrient contents of native crab, *Hemigrapsus oregonensis* to invasive exotic crab, *Carcinus maenas*. Intake rate, gut retention time, and assimilation efficiency did not differ between crab species. Green crabs had significantly larger (P=0.0034) meat-to-carapace ratio, 79% greater (P=0.0168) fat, and 15% greater (P=0.0058) energy than yellow shore crabs. Yellow shore crabs required 130% more (P=0.0301) force for carapace failure. Gross energy intake rate and assimilable energy intake rate did not differ between crab species. Therefore, energetically and nutritionally, green crabs provide a viable food option to harlequins, if yellow shore crabs are not available. However, the potential impacts of green crabs as an invasive species must be considered within an overall ecological context.

NUTRIENT AND ENERGY ACQUISITION BY HARLEQUIN DUCKS FORAGING FOR AN EXOTIC CRAB, *CARCINUS MAENAS*, AND A NATIVE CRAB, *HEMIGRAPSUS OREGONENSIS*

By

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Advisory Committee:
Professor Mary Ann Ottinger, Chair
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Dedication

To Mam, Dad, and Benjamin
for all of your help and enthusiasm, even with poop collections

To Ilana
my best friend and inspiration

To Phil
my "twin," for our lunch dates, car conversations, and bumping into me all over campus and College Park

To Arik
for your encouragement, creative consultations, and stats and writing expertise

and especially to Ruthie
who would have loved meeting the ducks

And to all of you for your love, patience, and support.
I couldn't have done this without you.

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Introduction

The Harlequin Duck (Histrionicus histrionicus)

Until recently, little was known about the ecology of harlequin ducks (*Histrionicus histrionicus*), and research efforts related to life history, population status, movements, and conservation of this species continue to provide new information (Robertson and Goudie 1999). Harlequin ducks are small diving ducks in the family Anatidae (tribe Mergini) and in North America are found in both the Pacific and Atlantic flyways. In 1990, due to declining populations, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) listed the Eastern North American population of harlequin ducks as an endangered species. Subsequently, as a result of a COSEWIC reevaluation of that population, the designation was down listed to species of special concern in 2001 (COSEWIC 2006).

The molting and winter range of harlequins includes rocky marine intertidal and subtidal regions on both the east and west coasts of North America and is largely determined by prey availability (Robertson and Goudie 1999; Figure 1). Western North American molting grounds are found primarily in coastal British Columbia, Alaska, the Aleutian Islands, the Strait of Georgia, Hecate Strait, Puget Sound, and Juan de Fuca Strait (Robertson and Goudie 1999). In the Pacific flyway, harlequins are found wintering in these same regions, primarily on the coasts of British Columbia, southern Alaska, the Aleutian Islands, Oregon, Washington, and California, and also in Puget Sound and Juan de Fuca Strait (Robertson and Goudie 1999). In the Atlantic flyway, harlequins winter from southwest New Brunswick, southeast Newfoundland, south and east Nova Scotia, to coastal Maine, Rhode Island,

and Massachusetts, with small populations consistently wintering down to Maryland (Norton 1896; Tufts 1986; Vickery 1988; Goudie 1991; Mittelhauser 1991, 1993; Montevecchi et al. 1995; Robertson and Goudie 1999). Harlequins move into inland freshwater habitats to breed, typically along fast-moving rivers (Robertson and Goudie 1999).

Goudie and Ankney (1986) found that harlequins wintering at Cape St. Mary's, southeastern Newfoundland typically fed within approximately 11 m from shore. In Washington, wintering harlequins typically remained an average of approximately 59 m from shore (Hirsch 1980; Robertson and Goudie 1999). Wintering harlequins typically feed in intertidal and subtidal areas usually less than 10 m and no more than 20 m deep (Robertson and Goudie 1999).

Goudie and Ankney (1986) showed that, when compared to the food habits of larger diving ducks, smaller diving ducks such as *H. histrionicus* consume prey that provide relatively high energy per gram of live mass. Crustaceans make up an important part of the harlequin diet (Cottam 1939; Goudie and Ankney 1986; Fischer and Griffin 2000), with *H. oregonensis* and the purple shore crab *H. nudus* (a close relative) representing a significant portion, particularly during winter and molt (Cottam 1939; Vermeer 1983; Gaines and Fitzner 1987; Robertson and Goudie 1999; Rodway and Cooke 2002). Cottam (1939) found that between January and September, 57% of the west coast harlequin's diet was comprised of crustaceans, of which *H. oregonensis* and *H. nudus* represented the largest portion (14% of total diet). *Hemigrapsus* spp. represented the major proportion of prey taken by harlequins collected from Comox, Vancouver Island, British Columbia (in the Strait of Georgia;

Vermeer 1983; Cottam 1939), and *H. oregonensis* was the most common crab consumed by harlequins collected from Sequim Bay, Puget Sound, Washington in November through January (Gaines and Fitzner 1987) as well as from the Strait of Georgia, British Columbia (Vermeer 1983) in March, October and November. Additional primary winter diet items of the harlequin include other species of crabs, as well as amphipods and gastropods (Robertson and Goudie 1999).

One specimen of *Hemigrapsus* spp. collected from a harlequin duck gizzard was 26 mm x 20 mm x 10 mm, and one relatively full gullet and gizzard contained the remains of 60 such crabs (Cottam 1939). Rodway and Cooke (2002) attribute the relatively high occurrence of *Hemigrapsus* spp. in the harlequin diet during molt to the larger proportion of organic content in crabs as compared to other hard-shelled organisms (as determined by Guillemette et al. 1992). It is important that harlequins have access to habitats with high crab productivity not only because of their reliance on crabs as a prey item during molt and winter (Rodway and Cooke 2002), but also because they are sensitive to variations in food availability (Rodway 1998); harlequins' winter range is highly influenced by prey availability (Robertson and Goudie 1999).

Due to their preference for rocky, near-shore habitats during molting and winter, harlequins are especially susceptible to human impacts, including illegal hunting, oil spills, and habitat disturbance (Montevecchi et al. 1995). These impacts are significant particularly because the growth of harlequin populations is limited in part by a relatively late age of first reproduction and low annual fecundity (Robertson and Goudie 1999; Esler et al. 2002).

Harlequins presented a favorable test case for this study because of the known competitive interactions between the green crab and yellow shore crab on the west coast of North America (Grosholz and Ruiz 1995; Grozholz and Ruiz 1996; McDonald et al. 1998; Grosholz et al. 2000; Jensen et al. 2002). Determining the relative energy value of each crab species could provide insights into the energetics of similar prey items consumed by seaducks in east coast wintering grounds.

Invasion by the Exotic Green Crab (Carcinus maenas)

The European green crab, *C. maenas* (Portunidae) has been well-established in western Atlantic coastal waters since about 1817. Recently, this species established a presence in eastern Pacific coastal waters. The green crab was first found in the San Francisco Bay in 1989 (Grosholz and Ruiz 1996; Cohen et al. 1995). It is likely that the green crab had been transported in larval stages from the east coast of North America via seaweeds used in commercial marine packing or in the ballast water of ships (Behrens Yamada et al. 2005).

Northeastern Pacific *C. maenas* adults average 30-70 mm carapace width (Cohen et al. 1995), though males can grow to be over 90 mm (Behrens Yamada et al. 2005). This species prefers shallow, low-energy habitats with minimal wave exposure, such as protected bays and estuaries (Jensen et al. 2002). *C. maenas* can tolerate a large range in salinity from 4 to 34 ppt and in intertidal zones with 1.4 ppt salinity (Cohen et al. 1995) and a large range in temperature from 22° C (average summer surface-temperature) to between -1 and 0° C (average winter ocean-temperature; Cohen et al. 1995; Sverdrup et al. 1947; Carlton and Cohen 2003).

Recruitment of young *C. maenas* is higher following warm winters than cold winters (Behrens Yamada et al. 2006). Range expansion of *C. maenas* can occur quickly and is highly dependent on coastal water currents; for example, the presence of *C. maenas* in the Pacific Northwest has been attributed to warm seawater temperatures and strong currents resulting from an El Niño event in 1997/1998 (Behrens Yamada et al. 2005). C. *maenas* also consumes greater amounts of invertebrates in warmer water (Cohen et al. 1995). In the early 1990s, the eastern Pacific green crab population was described as providing "hundreds per trap" overnight (Cohen et al. 1995).

In new habitats, exotic species may spread rapidly in part due to a lack of competitive, predatory, or parasitic relationships with native species (Simberloff et al. 2000; Torchin et al. 2001; Behrens Yamada et al. 2005). From its initial invasion of San Francisco Bay in 1989, *C. maenas* has expanded to cover a range of at least 1600 km of eastern Pacific coastline (Grosholz et al. 2000) from Morro Bay, California to Vancouver Island, British Columbia (Jensen et al. 2002; Figure 1). Its generalized diet and its ability to survive in a wide range of salinities and temperatures may propel it to fill a potential range from Baja California, Mexico to southern Alaska (Cohen et al. 1995; Figure 1). There are concerns that *C. maenas* could permanently change West coast ecosystems (Behrens Yamada et al. 2005) as it is a strong predator that preys upon a wide variety of species representing 104 families and 158 genera in five plant, protist and 14 animal phyla (Cohen et al. 1995).

As an invasive species becomes established, it may have negative ecological impacts, including predation on native species, introduction of parasites, and

competition with native species (Jensen et al. 2002). On the east coast of North America *C. maenas* has been implicated in the 1950s decline of commercial stocks of *Mya arenaria*, the soft-shelled clam (Glude 1955; Ropes 1968; Welch 1968) and continues to prey heavily on these clams, particularly smaller size classes (Floyd and Williams 2004). It is thought that *C. maenas* has also been responsible for declines in commercially significant populations of hard clams (*Mercenaria mercenaria*) and bay scallops (*Argopecten irriadians*; Walton 1997; Rogers 2001; Holmes 2001). Grosholz and Ruiz (1996) began long-term monitoring of bivalve populations in Bodega Harbor a decade prior to the introduction of the green crab and found a significant decline in bivalve populations (*Transennella* spp.) after green crab colonization. Significant declines in the populations of native clams, *Nutricola* spp., the yellow shore crab, *H. oregonensis* (Grosholz et al. 2000), and the commercially important Manila clam (Japanese littleneck clam), *Venerupis philippinarum* (Grosholz and Ruiz 2002) in California have also been attributed to the presence of *C. maenas*. Other populations, such as those of the Dungeness crab, *Cancer magister*, may be at risk due to competition with *C. maenas* (McDonald et al. 2001).

The use of a parasitic barnacle to control populations of green crabs has been suggested (Kareiva 1996) as an alternative to the use of pesticides, and trapping and removal of the green crab have been utilized on both coasts of the U.S. In 2006, more than 10,000 green crabs were removed from across five sites in Bodega Harbor, California, and as a result that population has now been mostly depleted (E. Grosholz and C. deRivera personal communication 2007).

Effects of the Exotic Green Crab on the Native Yellow Shore Crab (Hemigrapsus oregonensis)

The native western North American yellow crab, *H. oregonensis*, is presently found in the low to high intertidal zones of bays and estuaries from Resurrection Bay, Alaska to Bahia de Todos Santos in Baja California, Mexico (Figure 1), specifically in rocky habitats, gravel shores, and the upper centimeters of sandy mudflats (Oliver and Schmelter unpublished data; Grosholz et al. 2000) where harlequins commonly feed. Adult individuals have been found to measure up to 35 mm carapace width for males and 29 mm for females (Oliver and Schmelter unpublished data). Oliver and Schmelter (unpublished data) found specimens of *H. oregonensis* in Yaquina Bay, Oregon in salinities ranging from 24 to 29 ppt, under rocks ranging in size from 30 to 50 cm resting on cobble and set shallow in the sediment; *H. oregonensis* can tolerate salinities down to 4 ppt.

Like the yellow shore crab, *C. maenas* prefers mudflats, sand and rock substrates, fine substrates, as well as mats of *Enteromorpha* (green alga) and *Zostera* (eelgrass) beds (Cohen et al. 1995; Oliver and Schmelter unpublished data). In Bodega Bay Harbor, California, both *C. maenas* and *H. oregonensis* are found on sand with approximately 20-40% rock cover; rocks are approximately 20-30 cm along the longest axis (Jensen et al. 2002). In sheltered areas such as Bodega Bay, California, the green crab has colonized intertidal habitats between 0.7 and 1.4 m above mean lower low water (MLLW; Jamieson et al. 1998).

C. *maenas* outcompetes *H. oregonensis* for food, although *H. oregonsensis* may be a superior competitor for shelter (Jensen et al. 2002; McDonald et al. 1998).

Grosholz and Ruiz (1995) found that *C. maenas* will prey on *H. oregonensis* of equal or lesser size in a laboratory setting, although Jensen et al. (2002) did not find this in their manipulations. In gut content analyses and field experiments, Grozholz and Ruiz (1996) and Grosholz et al. (2000) found evidence that *C. maenas* preyed upon *H. oregonensis* in natural settings. Because the green crab can live in the same habitats as *H. oregonensis* and is very tolerant to changes in salinity and temperature, *C. maenas* has the potential to displace the native crabs from their habitats (Oliver and Schmelter unpublished data). The ability of *C. maenas* to live on mudflats and fine substrates may have dramatic effects on the populations of *H. oregonensis*. These habitats often act as refuges for *H. oregonensis* from the more dominant purple shore crab, *H. nudus* (Low 1970; Daly 1981).

Grosholz et al. (2000) found that the mean number of *H. oregonensis* along the central California coast declined by nearly ten-fold during the initial period of *C. maenas* colonization and population increase in the early 1990's, possibly due to predation by *C. maenas*. The population of *H. oregonensis* remained low for four years following the initial green crab invasion (Grosholz et al. 2000). Because *C. maenas* preys on the smaller *H. oregonensis*, Oliver and Schmelter (unpublished data) predicted that *H. oregonensis* may have difficulties maintaining its position in the ecosystem. Furthermore, concerns that the 2005 year-class of *C. maenas* will act as a larval source until 2011 (Behrens Yamada et al. 2006) suggest that further monitoring and investigation of the impacts of the green crabs' presence in Pacific waters is warranted.

Potential Impacts of the Green Crab on Community Structure

Both *C. maenas* and *Hemigrapsus* spp. are preyed upon by organisms in higher trophic levels, including other crabs, shrimp, fish, otters, birds and seals (Cohen et al. 1995). A change in abundance of bivalves and other prey species due to the green crab's presence could affect the ecology of such predators, including migrating shorebirds (Jamieson et al. 1998). The presence of invasive animal species has been shown to effect changes in diving duck and other aquatic bird populations (Phelps 1994). Richman and Lovvorn (2003, 2004) found that shifts in the dominant invertebrate prey species, including the competitive displacement of a native clam by an invasive clam, can impact the feeding behavior of diving ducks and seaducks. However, there is still little known about the impacts of invasive invertebrate species on seaducks. Furthermore, competition for prey between *C. maenas* and birds remains unknown (Grosholz 2002; Jamieson et al. 1998), as does the potential control of *C. maenas* populations by bird predation.

In summary, the evaluation of trophic-level interactions between ducks and prey species has implications for the relationship of harlequins to western and eastern U.S. and Canadian ecosystems. Changes in the availability of food resources have been shown to alter the abundance and presence of waterfowl feeding in certain areas, for example the redhead (*Aythya americana*) wintering on the Chesapeake Bay (Perry et al. 1981). As a voracious predator, strong competitor, and parasite host (Behrens Yamada et al. 2005; Cohen et al. 1995), *C. maenas* has caused declines of native invertebrate populations (Jensen et al. 2002; Grosholz and Ruiz 1996; Grosholz et al. 2000; Grosholz and Ruiz 2002) and has the potential to stimulate shifts in community

structure, such as through interactions with birds and other predators (Grosholz 2002; Jamieson et al. 1998; Cohen et al. 1995). However, few studies have quantified competitive and trophic-level impacts of the invasive green crab.

The continuing spread of the green crab and subsequent competition with the native crab could affect harlequins that rely on the native crab as a food resource during molt and winter. If the green crab is not as energetically beneficial as the native crab, then the harlequins may not be able to obtain enough energy for maintenance during winter, molting, or to build up adequate reserves to migrate to breeding grounds. This could result in a decline in the harlequin population or movement into different wintering areas, which could be energetically costly.

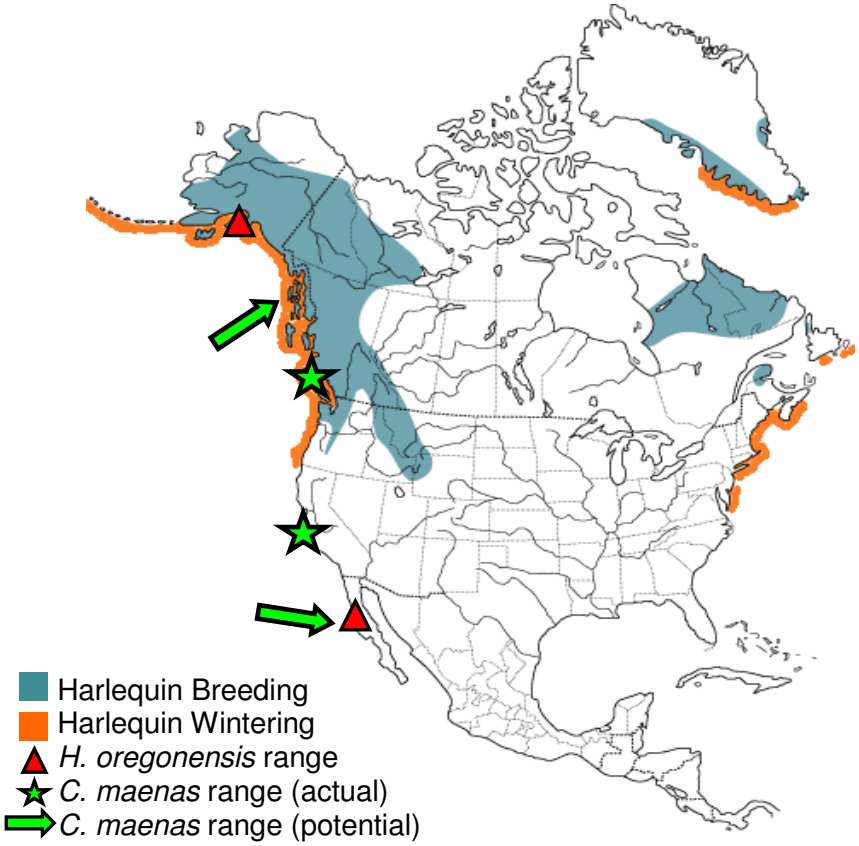

Figure 1. North American distribution of the harlequin duck, *Histrionicus histrionicus* (modified from Robertson and Goudie 1999), documented range of the native yellow shore crab, *Hemigrapsus oregonensis*, and actual and potential ranges of the exotic green crab, *Carcinus maenas*.

Summary, Goal, and Objectives

Crabs (primarily *H. oregonensis*) have been identified as important food items to molting and wintering harlequins, necessitating access for harlequins to habitats with high crab productivity (Vermeer 1983; Rodway and Cooke 2002). Potential harlequin population changes due to a change in prey availability may indicate a need for further evaluation of human impacts on the western harlequin population (such as hunting and habitat degradation) and potential establishment of refuge areas to minimize human impacts and offset potential impacts of the invasive green crab.

If the presence of green crabs in western coastal waters is found to be detrimental to harlequins in light of 1) displacement of important prey items, such as the yellow shore crab and 2) inadequate nutritive benefit, then more emphasis should be placed on conservation and management of western harlequin populations. Alternatively, it is possible that green crabs pose no energetic challenge or are perhaps even energetically beneficial to harlequins. In this case, the primary issue would be the habitat availability for and survival of the yellow shore crab population.

The overall goal of this study was to examine feeding behavior of harlequin ducks and determine the relative energy and nutrient values of the native North American yellow shore crab, *H. oregonensis* and the competing invasive exotic green crab, *C. maenas*.

The specific objectives were as follows:

1. Compare intake rates of yellow shore crabs and green crabs by captive harlequin ducks foraging in a controlled laboratory setting; and
2. Determine the nutrient and energy composition, crushing resistance, harlequin gut retention time, and digestibility of yellow shore crabs and green crabs.

Results from this study provide important baseline information about the western harlequin population and provide a basis for future population-level comparisons.

Methods

Experimental Design and Procedures

The U.S. Geological Survey Patuxent Wildlife Research Center (Patuxent) in Laurel, Maryland has a colony of captive diving ducks and seaducks that includes lesser scaup (*Aythya affinis*), canvasback (*Aythya valisineria*), surf scoter (*Melanitta perspicillata*), white-winged scoter (*Melanitta fusca*), and long-tailed duck. In January 2007, Patuxent acquired 20 harlequin ducks (14M:6F; hereafter referred to as harlequins) raised in Washington State by aviculturist Arnold Schouten. The lineage of these harlequins originated with captive parent harlequins that were collected as eggs from the Morse Creek and Dosewallips River areas of Washington. Patuxent provided the facilities for this study, including dive tanks for foraging energetics analysis, crab aquaculture equipment, duck assimilation trial cages, drying oven, and all equipment and materials necessary for the care of captive ducks. All procedures involving the ducks in this study were approved by the Patuxent Wildlife Research Center and the University of Maryland Institutional Animal Care and Use Committees.

All harlequin ducks were maintained in open-air enclosures with six to seven ducks per pen. Each pen contained a pool of water (circumference 5 m and depth 0.75 m) with continuously flowing fresh water and surface pipe drains in the center of each pool. The pools also had aerators to create bubbles in the winter to reduce ice formation. Ducks were fed Mazuri® Sea Duck Diet (21.5% crude protein, 5.0% crude fat, and 4.5% crude fiber) *ad libitum*. Grit was provided *ad libitum* next to the feed trays. Two large dive tanks (2.4m x 1.8m x 2.4m) installed in a temperature-

controlled building were equipped with underwater cameras and other equipment for diving duck energetic studies. Live green crabs were obtained from Massachusetts and California, and live yellow shore crabs were obtained from Washington. Live purple shore crabs (*H. nudus*) incidentally obtained with the yellow shore crabs were used for harlequin dive training.

Collection and Maintenance of Crabs

Green crabs were obtained with assistance from Salem State College, Massachusetts (collected from Smith Pool and just outside the dam separating Smith Pool from Salem Sound); Cape Cod Cooperative Extension and Woods Hole Sea Grant, Massachusetts (collected from Cape Cod); Portland State University, Washington (collected from Cheney Gulch, Bodega Harbor, California). Live yellow shore crabs and purple shore crabs were obtained from Friday Harbor Laboratories, Washington (collected in Friday Harbor, at 48° 32' 45" N, 123° 01' 05" W). Field conditions for *H. oregonensis* and *H. nudus* specimens were 8.5° C and 31 ppt salinity at the time of collection. The crabs were maintained (separated by species) in a closed-system, temperature and salinity-regulated aquaculture facility at Patuxent (Figure 2).

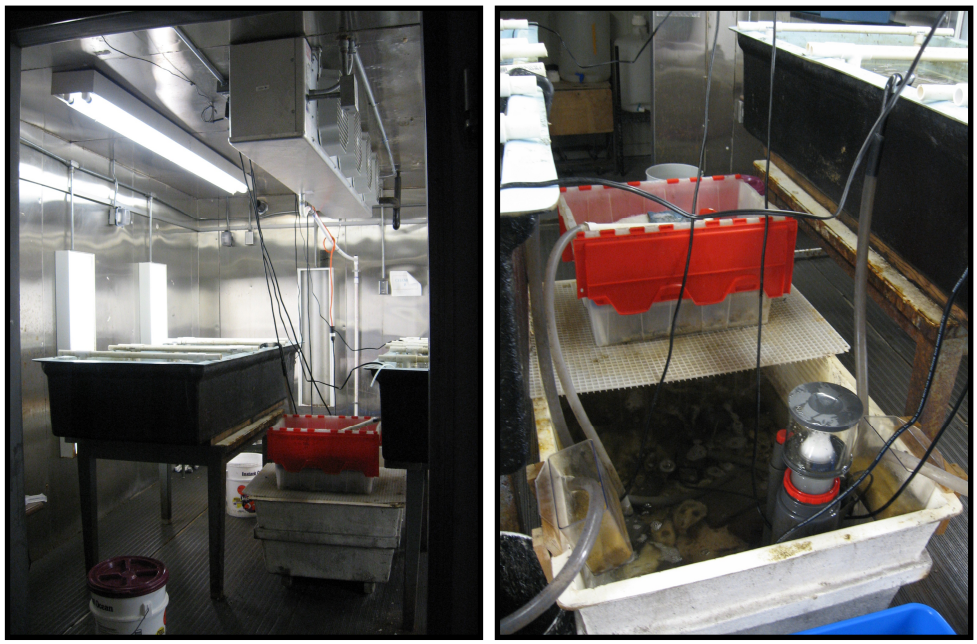

Figure 2. One of two temperature-controlled environmental chambers at Patuxent Wildlife Research Center containing closed-system invertebrate aquaculture systems.

Each aquaculture system included two large fiberglass tanks equipped with hanging baskets made of PVC and plastic mesh, in which refugia (oyster shells) were provided for the crabs. Two outflow pumps attached to plastic tubing in a smaller, central tub provided water flow to each tank. Outflow from the tanks was conducted through PVC pipes or plastic tubing and was pumped through filters to remove debris and through bioballs supporting bacteria beneficial to water quality. Water circulation within each tank was driven by two powerheads, one of which also injected oxygen into the water. Each central tub was also equipped with a protein skimmer.

Excess live or frozen individuals of hooked mussels (*Ischadium recurvum*) from a concurrent seaduck study were fed to the crabs. Because the crabs used can

tolerate a wide range of salinities, the salinity of the aquaculture systems was maintained at 18 ppt in deference to the salinity tolerance of the hooked mussels, and the temperature was maintained at approximately 17° C.

Nutrient Composition, Crab Carapace Strength, and Digestibility

The objectives of these experiments were to 1) compare nutrient values for the yellow shore crabs and green crabs by quantifying ash free dry mass (AFDM), lipid, and nitrogen (protein) content; 2) determine whether a difference exists in assimilation efficiency for harlequin ducks feeding on yellow shore crabs as compared to green crabs; and 3) determine whether a difference in carapace strength (in terms of compression strength) exists between yellow shore crabs and green crabs.

Nutrient Composition

The net energy value of a food item was determined by the gross energy provided by the food item and the amount of energy that was assimilated from that food item by the consumer. To determine prey composition, specifically energy content using bomb calorimetry, as well as ash, nitrogen, and lipid content, 10 groups of crabs of each species (each *C. maenas* sample contained two crabs, and each *H. oregonensis* sample contained 4-6 crabs) were weighed to the nearest 0.001g and then oven dried at 50°C for approximately 24 hours to constant mass. Dry weights were determined for each individual, and then the crabs were sent to The Center of Excellence for Poultry Science (CEPS) Central Analytical Laboratory at the University of Arkansas for analysis (Association of Analytical Communities (AOAC) Method 990.03; AOAC 920.39c; American National Standards Institute (ANSI) and American Society for Testing and Materials (ASTM) Standard D2015-77; AOAC

923.03, and AOAC 934.01). Groups of crabs, rather than individual crabs, were necessary in order to generate enough dry mass for analyses.

Crab Carapace Strength

Because crabs are consumed whole, an Imada tensile load frame and force meter with a computer interface in the University of Maryland mechanical engineering laboratory of Dr. Hugh A. Bruck was used to determine the compression strength of the carapace of each species, to approximate resistance of the crabs to duck gizzard crushing action. For consistency, compression required for carapace failure (the point of first major carapace breakage) was measured across middle of the dorsal side of each crab carapace and claws were removed from all crabs (as harlequins sometimes do when feeding on crabs).

Assimilation Efficiency (Digestibility)

Feeding trials were conducted to determine the amount of energy that the ducks assimilated from each crab species (Table 1 and Figure 3). Using a random number method, nine male harlequin ducks were selected to participate in the trials. There were two separate trials per duck, during which each of the two crab species was presented, with a total of nine replicates per trial in the cross-over design. Trials were conducted between December 17 and 27 during the time that wild harlequins in western North America naturally would be at wintering grounds (Robertson and Goudie 1999).

Using a random number method, the harlequins were placed in individual metal cages with removable trays lined in plastic. Feeding trials began with a 24 h acclimation period (Acclimation Period 1) during which the harlequins were fasted

and excreta were collected every 4 h. Excreta included both feces and nitrogen waste (uric acid), which were collected and analyzed together. Water was offered *ad libitum* throughout the trials. After Acclimation Period 1, a single feeding of a measured quantity of fresh whole crab was administered. Harlequins were initially permitted to feed at will, but their intake was limited and variable. Therefore, ducks were fed a constant amount by hand. During feeding, an individual duck's bill was gently held open in order to place a crab at the back of the bill, beyond the airway. The duck was provided with time to swallow the crab and also some water. If multiple crabs accumulated in the proventriculus, sufficient time was provided for the duck to process the crabs towards the gizzard. Lesser scaup have been shown to reach satiation at approximately 25 g under hand-feeding conditions (Richman and Lovvorn 2004), and this mass of invertebrate prey has been used for feeding trials conducted in other seaduck studies (Richman and Lovvorn 2004, Berlin 2008). However, due to their smaller size, harlequins were fed approximately 10 g of crab during feeding. Several ducks regurgitated whole or partial crabs after feeding (see Results, *Assimilation Efficiency (Digestibility)*).

During Phase 1 of the assimilation trials, the crab species fed to each duck was randomly selected, such that green crabs were fed to four ducks (ducks B, F, H, and I) and yellow shore crabs to five ducks (ducks A, C, D, E, and G; Table 1 and Figure 3). Excreta were collected every 4 h for 72 h. After Phase 1 was completed, all ducks were weighed, released to the outdoor pens, and fed Mazuri® Sea Duck Diet *ad libitum* for a 48 h rest period. Then the ducks were returned to the cages for a second 24 h acclimation period (Acclimation Period 2) during which the harlequins

were again fasted, and excreta were collected every 4 h. For Phase 2 of the assimilation trials, the two prey options were switched such that green crabs were fed to ducks A, C, D, E and G, and yellow shore crabs were fed to ducks B, H, and I. Duck F was removed from the trial during Phase 2 due to complete regurgitation of prey items and significant signs of stress. Again, approximately 10 g of fresh mass of whole crab was administered to each duck during this second feeding and excreta were collected every 4 h for 72 h.

Table 1. The number of captive male harlequin ducks (*Histrionicus histrionicus*) and associated food items, green crabs (*Carcinus maenas*) and yellow shore crabs (*Hemigrapsus oregonensis*), that were used in prey assimilation trials, and the duration of each trial segment. Ducks were assigned letters (A-I) for identification.

Number of Ducks	Food Item	Duration (h)	Trial Segment
9 (A-I)	Mazuri® Sea Duck Diet	24	Acclimation Period 1
4 (B, F, H, I)	Green crab	72	**Assimilation Phase 1**
5 (A, C, D, E, G)	Yellow shore crab	72	**Assimilation Phase 1**
9 (A-I)	Mazuri® Sea Duck Diet	48	Rest Period
9 (A-I)	Mazuri® Sea Duck Diet	24	Acclimation Period 2
5 (A, C, D, E, G)	Green crab	72	**Assimilation Phase 2**
3 (B, H, I)	Yellow shore crab	72	**Assimilation Phase 2**

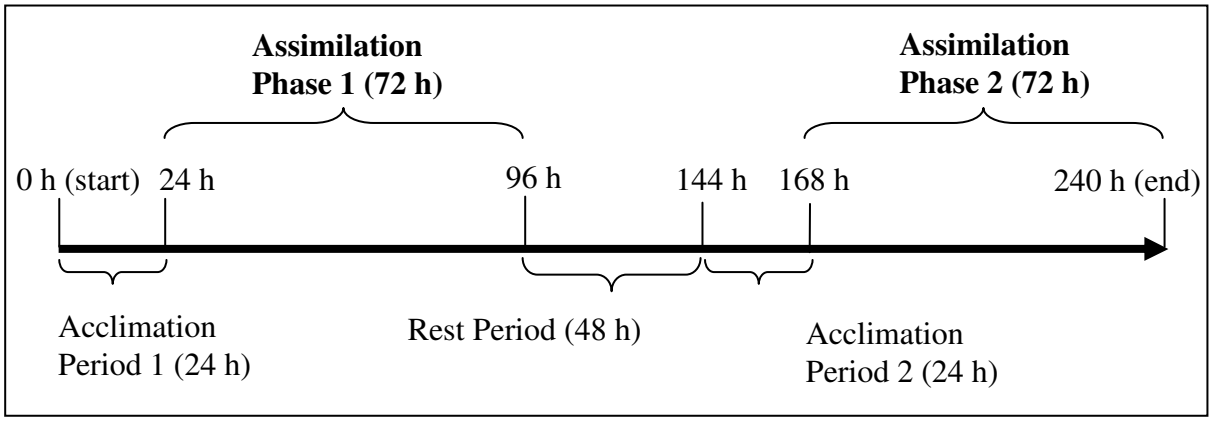

Figure 3. The timeline for Phases 1 and 2 of trials assessing captive harlequin duck (*Histrionicus histrionicus*) assimilation of green crabs (*Carcinus maenas*) and yellow shore crabs (*Hemigrapsus oregonensis*), including acclimation, assimilation, and rest periods.

Excreta were collected in plastic specimen cups with a spatula, 10 mL sulfuric acid was added to each specimen cup to prevent losses of nitrogen present in the excreta, and each sample was frozen until analyzed. In preparation for analysis at the CEPS lab in Arkansas, samples were oven dried at 50° C to constant mass. Subsamples were ground and homogenized at the CEPS lab and analyzed in February and March 2008 for energy, lipid, nitrogen, and ash content.

Based on these data the following values were calculated:

- Assimilation Efficiency (AE) = (Gross energy intake – gross energy excreted)/Gross energy intake
- Nitrogen Balance (NB) = (Nitrogen intake – Nitrogen excreted) x 36.5

The value 36.5 is the mean energy content (kJ) per gram urine-nitrogen in birds (Titus et al. 1959; Sibbald 1982; Richman and Lovvorn 2003).

- Assimilated Energy Corrected for Nitrogen Balance (AE_N) = [Gross energy intake – (gross energy excreted + nitrogen balance)]/ Gross energy intake

Correction for nitrogen balance is needed to account for 1) fractions of excreta attributable to nutrients absorbed and re-excreted into the gut, as well as endogenous losses, and 2) difficulty in separating uric acid from fecal matter in avian excreta (Klasing 1998). If left uncorrected, assimilation efficiency may be underestimated (Richman and Lovvorn 2003).

Measures were taken to reduce ducks' distress from being caged or from a change in diet, including the following: ducks were gradually familiarized with the presence of and handling by researchers prior to assimilation trials; water for caged birds were monitored regularly during the day; ducks in assimilation cages were maintained in a cool, quiet, well-ventilated indoor facility; indoor lights were turned off during the night (the building received natural sunlight); and breathable shades (towels) were placed on each cage to minimize stress due to any exterior activity. Ducks were monitored regularly for signs of distress.

Gut Retention Time

Another integral aspect of foraging energetics is the time required to process food in the gut. The objective of this experiment was to determine whether a difference exists in gut retention time of harlequin ducks feeding on green crabs as compared to yellow shore crabs. The time required to find, handle, and ingest food may exceed gut processing time (Jeschke et al. 2002; Richman and Lovvorn 2003); therefore it is important to determine the sum of foraging time and digestive processing time. If this sum exceeds the time available for foraging, differences in gut retention time between prey can affect the acquisition of nutrients and energy (Guillemette 1994, 1998; Richman and Lovvorn 2003).

Mean gut retention time (MRT) represents the time it takes for 50% of digesta to clear the digestive tract (Klasing 1998) and is equal to $\sum E_i t_i / \sum E_i$, where E_i is the mass of excreta produced during collection period *I*, and t_i is the time since the trial feeding (Richman and Lovvorn 2003). The amount of time required for 98% of digesta to clear the digestive tract is about four times MRT, but for the purposes of comparison, it is more useful to compare MRT rather than total retention time (Klasing 1998). Absolute values of MRT can vary according to how long sampling is continued beyond the time when most of a meal has been excreted (Hilton et al. 1998; Richman and Lovvorn 2003).

Crab Feeding and Dive Training

Training of the harlequin ducks to dive in the outdoor pools and the dive tanks at Patuxent was necessary because the harlequins were hatched and raised in captivity. Because the ducks relied on a pellet diet at Patuxent, training them to feed on live crabs both in their pens and at the bottom of the dive tanks was also necessary. Training of harlequins to acclimate to feeding on live crabs began in April and training of harlequin ducks to dive in the dive tanks began in May.

When the harlequins were first acquired in January, they rarely dived in the outdoor pools. Dried corn was placed in the pools to encourage diving. However, if left unconsumed, corn led to water quality problems in the pools. Furthermore, duck consumption of the high-energy corn declined in the summer. Therefore, at the beginning of July, mealworms (*Tenebrio molitor*) approximately 2.54 cm (1 inch) in length were purchased from Rainbow Mealworms in Comton, California and placed, typically in groups of 50 per day, in small plastic trays containing small cobble

substrate at the bottom of each pond. The mealworms did not foul the water and were readily consumed by the ducks.

Concurrent with outdoor pond dive training, other ducks from the captive colony that were known to dive consistently, including lesser scaup, a canvasback, and long-tailed ducks, were used in dive tank training sessions with the harlequins, initially with dried corn as a diving incentive at the bottom of the dive tank. Dive tank water levels were initially dropped to approximately 1.4 m to encourage harlequin diving. Dive sessions typically lasted approximately 2-4 h and were taped using underwater video equipment, then later downloaded and reviewed to evaluate success of training sessions. Again, dried corn was not a sufficient incentive for the harlequins to dive, so in July, sinking food pellets were used in the dive tanks. However, the pellets disintegrated and created serious water quality problems in the tanks. Therefore, mealworms were used as a dive incentive in the dive tanks. Once harlequins began to dive during training sessions, prey trays (Figure 4) were added to the tank bottom to familiarize harlequins with the trays' presence. On a given day, if a group of harlequins was not being trained to dive in the dive tanks, the group was provided with mealworms in its pen to reinforce diving behaviors.

In order to acclimate the ducks to feeding on crabs, purple shore crabs (*H. nudus*; physiologically and ecologically similar to yellow shore crabs and obtained incidentally with the collection of yellow shore crabs) and black-fingered mud crabs (*Panopeus herbstii*; obtained incidentally with the hooked mussels collected from the Chesapeake Bay) were provided to the harlequins in their feeding tubs. In this study, *H. nudus* and *P. herbstii* were used only for harlequin training purposes. *H. nudus*

was distinguished from *H. oregonensis* primarily by a lack of hair covering the legs and deep purple or red spots covering the pinchers of the former (Meinkoth 1981).

In order to encourage harlequins to feed during a dive trial, the following actions were taken: 1) two days prior to a dive trial, a reduced amount of Mazuri® Sea Duck Diet was provided to the pen containing the duck scheduled to participate in the trial; and 2) the day before the dive trail, all food was withheld from that pen except 15-20 yellow shore crabs or purple shore crabs.

Intake Rates

The objective of this experiment was to determine whether a difference in intake rate (functional response) exists for harlequin ducks foraging for yellow shore crabs as compared to green crabs. Intake rates (number of prey consumed per second foraging) as a function of prey density have been determined in previous studies on sessile prey by Berlin (2008) for surf scoters, Richman and Lovvorn (2004) for lesser scaup, and Richman and Lovvorn (2003) for white-winged scoters.

This study utilized nine male harlequin ducks and two food items, green crabs and yellow shore crabs (both approximately 15-30 mm carapace width). During a dive trial, as described below, an individual duck was offered only one species of crab. There were four separate dive trials for four ducks, during which each of the two crab species were presented in two separate densities (20 m^{-2} and 80 m^{-2}). These two densities reflected those in which both *H. oregonensis* and *C. maenas* naturally would be found and also accounted for the relatively low number of sufficiently small *C. maenas* individuals available. Trials were conducted between October and December, after the male harlequins in the study had completed molting and during

the time that wild harlequins in western North America naturally would be at wintering grounds (Robertson and Goudie 1999).

There is a range in observations of naturally-occurring *H. oregonensis* and *C. maenas* densities. While high concentrations of molting harlequin ducks have been observed in British Columbia in areas with *Hemigrapsus* spp. densities over 400 m^{-2} (Robertson & Goudie 1999), Grosholz et al. (2000) observed a mean (± 1 SE) of 18.7 ± 3.4 *H. oregonensis* individuals per pitfall trap (traps were set at 50 m intervals along a Bodega Bay Harbor, CA shoreline transect) prior to the introduction of *C. maenas* and 2.04 ± 0.46 *H. oregonensis* individuals after the introduction of *C. maenas*. *H. oregonensis* densities in Grays Harbor, WA have been observed to range from a high of 180 m^{-2} to a low of 10 m^{-2} (Visser et al. 2004, Jensen et al. 2007). Grozholz and Ruiz (1995) caught fewer than 100 *C. maenas* in more than 100 pitfall traps set 100 to 500 m apart in Bodega Harbor. Behrens Yamada et al. (2006) found that the catch per unit effort (CPUE) per 100 trap-days ranged from 65 to 192 *C. maenas* individuals in 1998 and dropped to 0-15 individuals by 2002, though CPUE has increased slightly in recent years due to the appearance of strong year classes of crabs in 2003 and 2005. As of 2007, an estimated maximum of 20 m^{-2} of *H. oregonensis* were being found in the highest density areas of Bodega Harbor (C. deRivera personal communication 2007).

Due to limited availability of green crabs small enough for harlequin consumption, five ducks were included in just two dive trials, during which only yellow shore crabs were presented in the two densities (Table 2). Of the 14 male harlequin ducks, five were eliminated from the trials using a random number method.

Additionally, a random number method was used to determine the dive order, dive tank, and species and density of crab used in each trial.

Table 2. The number of captive male harlequin ducks (*Histrionicus histrionicus*) and associated prey items – either green crabs (*Carcinus maenas*) or yellow shore crabs (*Hemigrapsus oregonensis*) – and densities used in dive trials.

Number of Ducks	Prey Item	Density of Prey (m^{-2})
4	Green crab	20
4	Green crab	80
9	Yellow shore crab	20
9	Yellow shore crab	80

Two large aquaria (dive tanks) were constructed and installed at Patuxent several years prior to the start of this study (Figure 5) and were used to examine prey preference and the cost of diving. Each tank was covered by a removable PVC-framed netted cage to prevent ducks from leaving the aquaria during trials, as all ducks are fully-feathered.

To test prey preference, yellow shore crabs or green crabs were distributed throughout a grid of four trays (representing a total of 1.0 m^2) loosely filled with sand at 2.54 cm depth. Large shells covered approximately 20% of each tray to simulate natural conditions and provide refuge for the crabs. The trays were lowered to the bottom of each dive tank prior to the start of a dive trial. To contain the crabs, semi-flexible plastic sheeting 33 cm in height (window weather-proofing slightly more flexible than Plexiglas) was attached to the perimeter of each grid, and flexible plastic sheeting (disposable cutting boards) was attached to each tray to cover space remaining between the trays when placed in a grid (Figure 4).

Figure 4. Grid of trays representing 1 m^2 and fitted with plastic sheeting along the perimeter to contain crabs used in dive trails with foraging captive harlequin ducks (*Histrionicus histrionicus*). The trays are shown at the bottom of a dive tank, with sand-and-shell substrate and crabs.

On the day of a dive trial, individual ducks were caught by hand-net in their open-air enclosure (pen) at the Patuxent Wildlife Research Center seaduck complex and transported directly (carried in an animal crate) to the dive tank building, which is immediately adjacent to the duck pens.

Trials were recorded using an underwater video camera, and footage was later analyzed to determine the amount of time each duck spent searching for prey in the tray area. The time spent foraging was measured from the video as the time the bill entered and left the top of the trays. Each duck was allowed to forage for crabs until no more than approximately 10% of the prey was consumed (typically about 4 h). During the course of the dive trial, external activity in the dive tank building was minimized, though ducks in the tanks were checked on regularly. At the end of a trial, ducks were caught by net and immediately returned to their appropriate pen in the seaduck complex. At the end of each trial the trays were raised and the number of

remaining crabs was determined and recorded. Crabs not consumed in an individual trial were used, if possible, in subsequent trials.

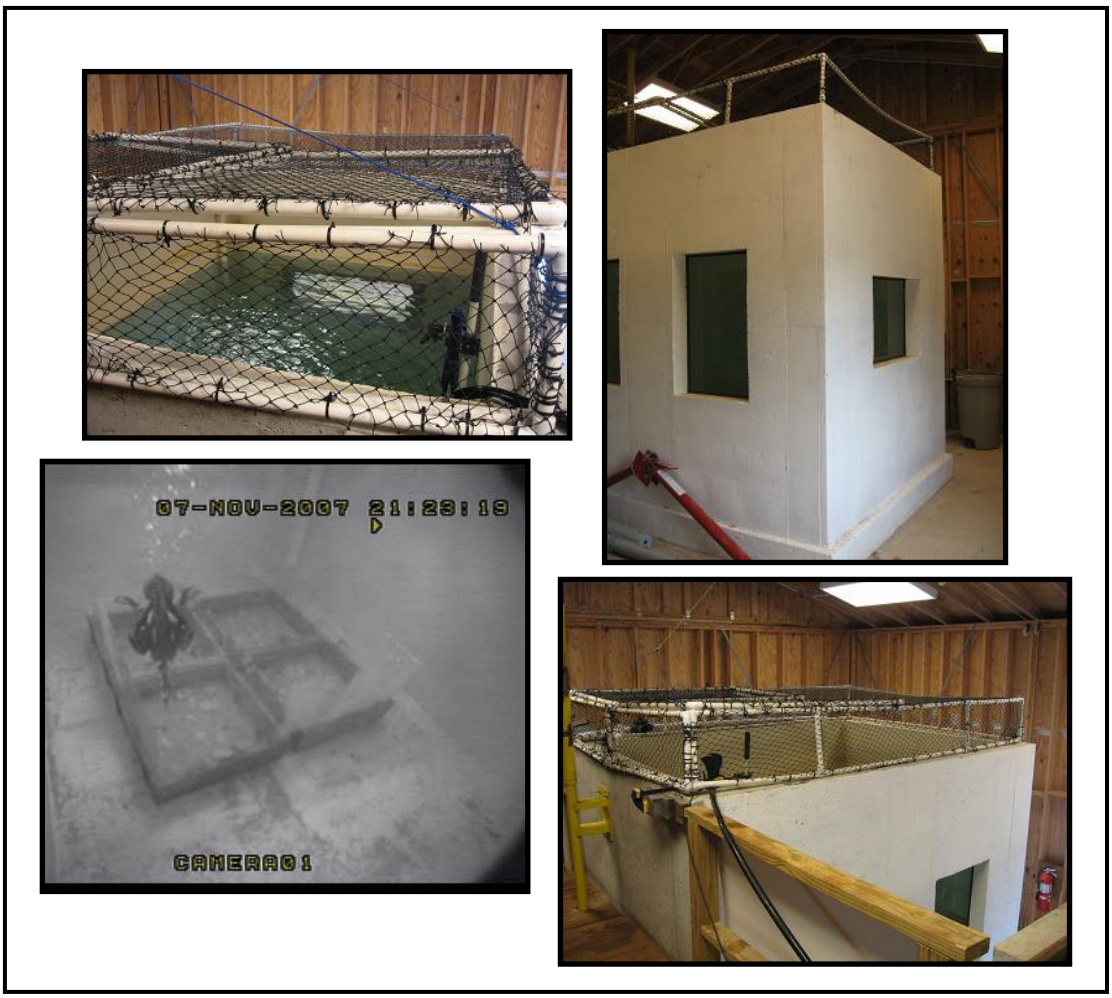

Figure 5. One of two dive tanks (2.44m x 1.83m x 2.44m) constructed at the USGS Patuxent Wildlife Research Center for seaduck diving studies, and a harlequin duck (*Histrionicus histrionicus*) foraging for crabs.

For experimental trials, running (circulating) water in the dive tanks was shut off because harlequins were observed playing in water falling down to the water's surface during training sessions rather than diving. The total water depth for dive trials was maintained at 1.8 m.

Harlequin Weight Trends

The body mass of the 14 male and 6 female harlequins at Patuxent was obtained monthly between January 2007 and February 2008 using a hanging balance and a small mesh laundry bag. For analytical purposes, seasons were defined as follows: winter (December-February); spring (March-May); summer (June-August); and autumn (September-November).

Data Analysis

Data distributions were assessed for normality using the Shapiro-Wilk test and plotting of histograms. Intake rates (# crabs $\cdot$ s^{-1}) of ducks as a function of crab density were determined for each species of crab and analyzed for differences in slope and intercept (analysis of covariance, PROC MIXED, SAS Institute 2003). Mean retention time and energy content of duck excreta and prey items were analyzed using a two-way ANOVA (PROC GLM, SAS Institute 2003). Duck body mass and percent composition of crabs used in feeding trials were analyzed using unpaired *t*-tests, as was crab compression force, and harlequin gross energy intake rate and assimilable energy intake rate (PROC TTEST, SAS Institute 2003). Harlequin body mass trends were analyzed using repeated measures ANOVA (PROC MIXED, SAS Institute 2003). All tests were considered significant at the 5% level and all analyses were completed using SAS (SAS Institute 2003).

For statistical testing, the following null hypotheses were established:

1. There is no difference between *H. histrionicus* intake rates (number of prey consumed per second of search time) of *C. maenas* and *H. oregonensis*.
2. There is no difference in the nutrient and energy composition, crushing resistance, harlequin gut retention time, and assimilation efficiency (digestibility) between *C. maenas* and *H. oregonensis*.

Results

Nutrient Composition, Crab Carapace Strength, and Digestibility

Nutrient Composition

Significant differences in nutrient composition were found between the two crab species (Table 3). In order to produce sufficient dry mass required for laboratory analyses, samples consisted of multiple crabs. Therefore, ash (carapace) and AFDM (organic content) are reported as percentages of crab dry mass; water content and dry mass content are reported as percentages of crab fresh mass. Crabs were substantially (>64%) comprised of water, and green crabs contained 14% more water (P=0.0115) than yellow crabs. Approximately half of crab dry matter was comprised of organic content (AFDM) and half of inorganic ash. Green crabs contained significantly more AFDM than yellow shore crabs (P=0.0014), and this is reflected in the significantly larger meat-to-carapace (AFDM-to-ash) ratio of green crabs as compared to yellow shore crabs (P=0.0034).

While mean percent nitrogen (N) did not differ significantly between crab species, fat content of green crabs was 79% greater (P=0.0168) and energy content was 15% greater (P=0.0058) than that of yellow shore crabs. Nitrogen was calculated from prey protein content, such that percent N is equal to percent protein divided by the constant 6.25 (Block and Bolling 1946).

Table 3. Mean (±1 SE) mass or percent composition of captive male harlequin ducks (*Histrionicus histrionicus*) and prey (*Carcinus maenas* or *Hemigrapsus oregonensis*) used in feeding trials (December 17 to 24), and *P* values for unpaired *t*-tests between crab species.

Measurement†	*C. maenas*	*H. oregonensis*	*P**
Duck mass			
Initial (g)[a]	643 ± 22	663 ± 22	0.5291
Final (g)	531 ± 20	544 ± 21	0.6716
Loss (%)	17.51 ± 0.98	17.96 ± 1.72	0.8574
*P**[ab] (Initial vs. Final)	<0.0001*	<0.0001*	--
Ingesta			
Dry mass (g)[c]	2.91 ± 0.29	4.72 ± 0.26	0.0003*
Ash (%)	50.2 ± 1.63	57.45 ± 0.54	0.0014*
AFDM (%)	49.8 ± 1.63	42.55 ± 0.54	0.0014*
Water Content (%)	70.13 ± 1.88	64.24 ± 0.67	0.0115*
Dry Mass (%)	29.87 ± 1.88	35.76 ± 0.67	0.0115*
Meat (AFDM)/Carapace (Ash)	1.01 ± 0.07	0.74 ± 0.02	0.0034*
Nitrogen (%)[d]	4.95 ± 0.13	4.74 ± 0.10	0.2141
Protein (%)[d]	30.95 ± 0.80	29.63 ± 0.62	0.2089
Fat (%)	1.84 ± 0.29	1.03 ± 0.09	0.0168*
Energy (kJ/g)	8.88 ± 0.32	7.74 ± 0.17	0.0058*
Excreta			
Dry mass (g)	5.52 ± 0.77	7.88 ± 0.92	0.0656
Ash (%)	25.33 ± 2.73	30.30 ± 5.60	0.4274
Nitrogen (%)	16.28 ± 0.75	15.54 ± 1.28	0.4959
Fat (%)	2.66 ± 0.72	1.71 ± 0.39	0.2538
Energy (kJ/g)	10.76 ± 0.20	10.62 ± 0.46	0.7833

*Statistically significant difference at α=0.05.

†Percentages were arcsine-square root transformed prior to statistical testing.

[a]Data were log transformed ($X'=\log_{10}(X+1)$) to ensure normal distribution prior to statistical testing.

[b]*P* values represent a comparison of initial and final harlequin body mass in a repeated measures ANOVA (PROC MIXED, SAS Institute 2003).

[c]Data were transformed ($X'=X^2$) to ensure normal distribution prior to statistical testing because the data for *H. oregonensis* were skewed to the left (see Zar 1999).

[d]Prey protein is the source of reported nitrogen content, with %N x 6.25 = % protein.

Crab Carapace Strength

Yellow shore crabs required 130% more (P=0.0165) force (N) for carapace failure than green crabs (Table 4). As with crab samples used for nutrient composition, the carapace width of available green crabs was significantly (P<0.0001) larger than that of the yellow shore crabs used in compression strength tests. Therefore, compression force is reported as force (N) per unit (mm) carapace width in order to provide a relative basis for comparison between species.

Table 4. Mean (± 1 SE) compression force (N) required for carapace failure in green crabs (*Carcinus maenas*; n=10) and yellow shore crabs (*Hemigrapsus oregonensis*; n=6)[a] and *P*-values for unpaired *t*-tests between crab species. The ratio of force to carapace was calculated to account for differences in carapace width between the two crab species.

Measurement	*C. maenas*	*H. oregonensis*[a]	*P**
Force (N)[b]	52.3 ± 3.73	71.44 ± 9.13	0.0164*
Carapace width (mm)	27.26 ± 0.71	16.43 ± 0.89	<0.0001*
Force/carapace width ($N \cdot mm^{-1}$ CW)	1.91 ± 0.11	4.40 ± 0.64	0.0165*

*Statistically significant difference at α=0.05.
[a]Two biologically-unrealistic outliers were eliminated.
[b]Data were transformed ($X'=X^2$) to ensure normal distribution prior to statistical testing because the data for *H. oregonensis* were skewed to the left (see Zar 1999).

Assimilation Efficiency (Digestibility)

There were no significant differences in mean body mass between individual ducks involved in the assimilation trials (Table 3). However, the mean body mass loss of ducks involved in the assimilation trials was greater than 17% of initial body mass, and there were significant differences between the initial and final mean body mass for both groups of ducks (P<0.0001; Table 3). Due to variation in the initial wet mass of crab fed to each duck, as well as the greater percent water content of green crabs (see Results, *Nutrient Composition*), mean ingesta and excreta values are

reported as percentages of dry ingesta and excreta mass, respectively (Table 3). Mean values for excreta dry mass are larger than those reported for ingesta dry mass because the former represents the cumulative excreta collected over the course of the assimilation trials.

Although the majority of prey consumed was found to pass through the guts of harlequins used in this study by approximately 48 hours post feeding (Table 5), several ducks regurgitated whole or partial crabs up to 72 hours post feeding (possibly due to an accumulation of crabs in the esophagus or proventriculus due to feeding). Therefore, reported values for excreta content and assimilation efficiency represent excreta collected during the full 72 hours of the assimilation trials (excreta were pooled by CEPS in 24-hour increments in order to ensure sufficient dry mass for the required analyses).

Dry mass of duck excreta produced did not differ significantly between crab species. There were no differences in ash, nitrogen, fat, or energy content of excreta produced by harlequins feeding on green crabs as compared to yellow shore crabs (Table 3).

It is noteworthy that for both prey species, the mean ingesta N and energy content was less than the mean excreta N and energy content. The negative nitrogen-corrected assimilation efficiency for harlequins feeding on green crabs and the low nitrogen-corrected assimilation efficiency for harlequins feeding on yellow shore crabs is certainly related to this net loss of N and energy. After adjustment for nitrogen balance, the apparent assimilation efficiency of harlequins feeding on yellow

shore crabs did not differ significantly from that of harlequins feeding on green crabs (Table 5)

For comparative purposes, AE, NB, and AE_N were also calculated for 24 h and 48 h post feeding. By 24 h post feeding, 42% of total excreta had been produced by harlequins feeding on green crabs and 56% by harlequins feeding on yellow shore crabs. By 48 h post feeding, 72% of total excreta had been produced by harlequins feeding on green crabs and 80% by harlequins feeding on yellow shore crabs. Given that 72 h was set as the trial completion point, 100% of excreta had been produced by that time for harlequins feeding on both crab species. AE_N for harlequins feeding on green crabs was not significantly different from that of harlequins feeding on yellow shore crabs at 24 h or 48 h post feeding (Table 5).

Table 5. Mean (±1 SE) assimilation efficiency (AE), nitrogen balance (NB) and nitrogen-adjusted assimilation efficiency (AE_N) of captive male harlequin ducks (*Histrionicus histrionicus*) feeding on *Carcinus maenas* or *Hemigrapsus oregonensis* during feeding trials (December 17 to 24) for 24 h, 48 h, and 72 h post feeding. Percent excreta produced for harlequins feeding on green crabs or yellow shore crabs by the end of each time frame and *P* values for unpaired *t*-tests between crab species.

Measurement	Green Crab	Yellow Shore Crab	*P**	% Excreta Produced (G/Y)
Assimilation after 24 h				
AE (%)	56.76 ± 4.89	80.56 ± 5.79	0.0065*	
NB (kJ)	-8.82 ± 1.93	-9.35 ± 2.08	0.8538	
AE_N (%)	94.43 ± 10.37	105.81 ± 7.97	0.4070	42/56
Assimilation after 48 h				
AE (%)	-61.66 ± 24.18	-32.35 ± 10.81	0.2921	
NB (kJ)	-16.94 ± 3.09	-19.37 ± 4.33	0.6493	
AE_N (%)[a]	6.67 ± 14.37	17.62 ± 6.22	0.5903	72/80
Assimilation after 72 h				
AE (%)	-132.40 ± 35.60	-78.90 ± 13.32	0.1892	
NB (kJ)	-28.45 ± 5.37	-31.42 ± 6.22	0.7216	
AE_N (%)[a]	-19.77 ± 19.91	2.37 ± 8.98	0.3632	100/100

[a]Data were reflected (see Quinn and Keough 2002) and log transformed ($X' = \log_{10} X$) to ensure normal distribution prior to statistical testing.

Gut Retention Time

An examination of mean dry mass of excreta produced over 72 h by harlequins after the initial feeding of either green crabs or yellow shore crabs (at time 0) suggested 50% complete gut passage by 16-20 hours for yellow shore crabs and by 28-32 hours for green crabs (Figure 6). Therefore, mean retention times representative of these timeframes were compared between prey species for total collection durations of 16, 20, 24, 28, and 32 h after feeding. In a two-way ANOVA (PROC GLM, SAS Institute 2003), the mean gut retention time (MRT) did not differ significantly (P=0.4423) between harlequins feeding on green crabs and harlequins

feeding on yellow shore crabs at any of the time points post feeding that were analyzed (Table 6). There were no significant interactions between time and species (P=0.9450).

Table 6. Mean (±1 SE) gut retention time (MRT) for captive male harlequin ducks (*Histrionicus histrionicus*) fed a known quantity of green crabs (*Carcinus maenas*) and yellow shore crabs (*Hemigrapsus oregonensis*), for 16, 20, 24, 28, and 32 hours after feeding.

	Time Post Feeding (h)				
Crab Species	16	20	24	28	32
C. maenas	8.34 ± 0.39	9.20 ± 0.45	11.27 ± 0.71	13.11 ± 0.71	14.44 ± 0.96
H. oregonensis	8.46 ± 0.52	9.09 ± 0.58	10.34 ± 0.95	12.48 ± 1.24	13.65 ± 1.23

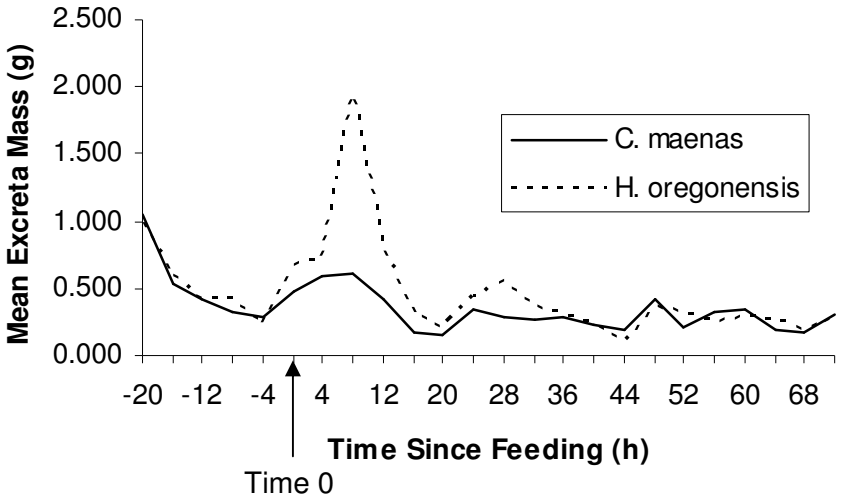

Figure 6. Dry mass of excreta (g) produced by captive male harlequin ducks (*Histrionicus histrionicus*) fed a known quantity of green crab (*Carcinus maenas*) and yellow shore crab (*Hemigrapsus oregonensis*) at time 0.

Crab Feeding and Dive Training

Yellow shore crabs were first fed to the harlequins in their pens in April. Ducks were observed sometimes shaking the crabs – presumably to disable pinchers (Robertson and Goudie 1999) – prior to swallowing them whole. Over three

consecutive days in July, 20-25 black-fingered mud crabs were provided to harlequins in their pens; by the last feeding, the ducks were consuming the majority of crabs provided. When mealworms were first provided to harlequins at the bottom of the pen ponds in mid-July, it took over 10 minutes for the ducks to start diving. However, the ducks quickly acclimated to this feeding technique and by the end of July they dived for the mealworms almost immediately. Regular feeding of mealworms in ponds was continued through the end of September.

Initial training attempts in the dive tanks proved relatively unsuccessful. For example, three harlequins placed in a training session with two lesser scaup and a canvasback at the end of May did not dive except to escape from the net upon removal from the dive tank. Between May and September, 58 training sessions were conducted. By mid-July, the harlequins were diving consistently for mealworms, including in the presence of human observers. By the end of August, individual ducks were diving successfully alone. At this point, a mealworm/crab mix was used during training sessions, along with a sand/rock substrate mix in the 1 m^2 tray sets. The first instance of harlequins, as a group, consuming only crabs in the dive tank was August 24 .

Intake Rates

Between October and December, 26 dive trials were conducted: 18 with harlequins foraging for yellow shore crabs, and eight with harlequins foraging for green crabs (the latter lower number was due to a lack of availability of sufficiently small green crabs). There was neither a significant difference in crab intake rate between harlequins feeding on green crabs as compared to yellow shore crabs (the

main effect), nor a significant difference in the intercept of regressions of intake rates on crab density, by prey species (Table 7). Due to variations in the total time each duck spent in the dive tank during a foraging trial, the search duration, number of dives, and number of crabs consumed were not statistically compared directly. Instead, intake rate (crabs consumed per second of search time) of harlequins consuming green crabs was compared to that of harlequins consuming yellow shore crabs. There were no significant interactions between species and density (P=0.9333). Therefore, the interaction term was eliminated from the ANOVA and the statistical analysis was performed again. There was a statistically significant difference (P=0.0444) between the low (20 crabs) and high (80 crabs) densities of green crabs presented to ducks, with more crabs of both species consumed per unit time at the high density. However, there was no significant difference in intake between yellow shore crab densities (Table 7).

Gross Energy Intake Rate and Assimilable Energy Intake Rate

There was no significant difference between crab species for harlequin gross energy intake rate or assimilable energy intake rate (Table 8), as determined according to the following equations:

- Gross Energy Intake Rate ($kJ \cdot s^{-1}$) = Gross Energy Intake (kJ) x Intake Rate (# crabs $\cdot s^{-1}$)
- Assimilable Energy Intake Rate ($kJ \cdot s^{-1}$) = Gross Energy Intake Rate ($kJ \cdot s^{-1}$) x Assimilation Efficiency (%)

Table 7. Mean (±1 SE) initial and final body mass for captive male harlequin ducks (*Histrionicus histrionicus*), search duration, intake rate, and intercept for harlequins foraging on green crabs (*Carcinus maenas*) and yellow shore crabs (*Hemigrapsus oregonensis*) between October and December. Analysis of covariance was used to compare intake rates as a function of density, by crab species (PROC MIXED, SAS Institute 2003).

Measurement	*C. maenas*	*H. oregonensis*	*C. maenas*	*H. oregonensis*	*P**
Density[a]	20 m^{-2}		80 m^{-2}		0.0444* (*C.m.*) 0.1624 (*H.o.*)
Duck mass					
Initial (g)	600 ± 17.80	601 ± 17.36	635 ± 39.67	618 ± 17.86	
Final (g)	593 ± 16.52	598 ± 14.51	640 ± 34.88	608 ± 16.23	
Search duration (s)	351.75 ± 33.85	333.53 ± 155.42	607.43 ± 152.10	186.37 ± 72.02	
No. dives	57.5 ± 35.84	34 ± 13.01	67 ± 11.95	29 ± 9.78	
No. crabs consumed	2.50 ± 1.50	3.78 ± 2.08	14.00 ± 6.65	8.33 ± 4.02	
Intake rate (crabs · s^{-1})[b]	0.003 ± 0.002	0.008 ± 0.002	0.020 ± 0.007	0.024 ± 0.011	0.9333
Intercept					0.7203

*Statistically significant difference at α=0.05.

[a]Statistical analysis was conducted without the species*density interaction, which was not significant in a previous test (*P*=0.9333).

[b]Data were log transformed ($X'=\log_{10}(X+1)$) to ensure normal distribution prior to statistical testing.

Table 8. Mean (±1 SE) gross energy intake rate ($kJ \cdot s^{-1}$) and assimilable energy intake rate ($kJ \cdot s^{-1}$) for captive male harlequin ducks (*Histrionicus histrionicus*) foraging on green crabs (*Carcinus maenas*) and yellow shore crabs (*Hemigrapsus oregonensis*) between October and December, and *P* values for unpaired *t*-tests between crab species.

Measurement	*C. maenas*	*H. oregonensis*	*P**	*C. maenas*	*H. oregonensis*	*P**
Density	20 m^{-2}			80 m^{-2}		
Gross Energy Intake Rate ($kJ \cdot s^{-1}$)[a]	0.022 ± 0.013	0.064 ± 0.019	0.1987	0.173 ± 0.589	0.188 ± 0.082	0.7369
Assimilable Energy Intake Rate ($kJ \cdot s^{-1}$)[b]	-0.006 ± 0.007	-0.003 ± 0.005	0.7153[b]	-0.026 ± 0.038	0.010 ± 0.021	0.3730

*Statistically significant difference at α=0.05.

[a]Data were arcsine-square root transformed prior to statistical testing.

[b]Data were log transformed ($X'=\log_{10}(X+1)$) to ensure normal distribution prior to statistical testing.

Harlequin Weight Trends

From the time of their arrival at Patuxent in January, harlequins were provided with *ad libitum* Mazuri® Sea Duck Diet. However, seasonal trends in mean body mass for both female and male ducks were apparent (Figure 7). In a repeated measures ANOVA (PROC MIXED, SAS Institute 2003), there was a significant difference in weight between males and females for all seasons (winter P=0.0270, spring P=0.0003, summer P=0.0001, and autumn P=0.0072). For females, summer weights were significantly lower when compared to winter weights (P=0.0116). For males, summer weights were significantly lower when compared to spring weights (P=0.0125; Table 9). October, November, and December weights for male harlequins used in dive trials during these months were excluded from analyses.

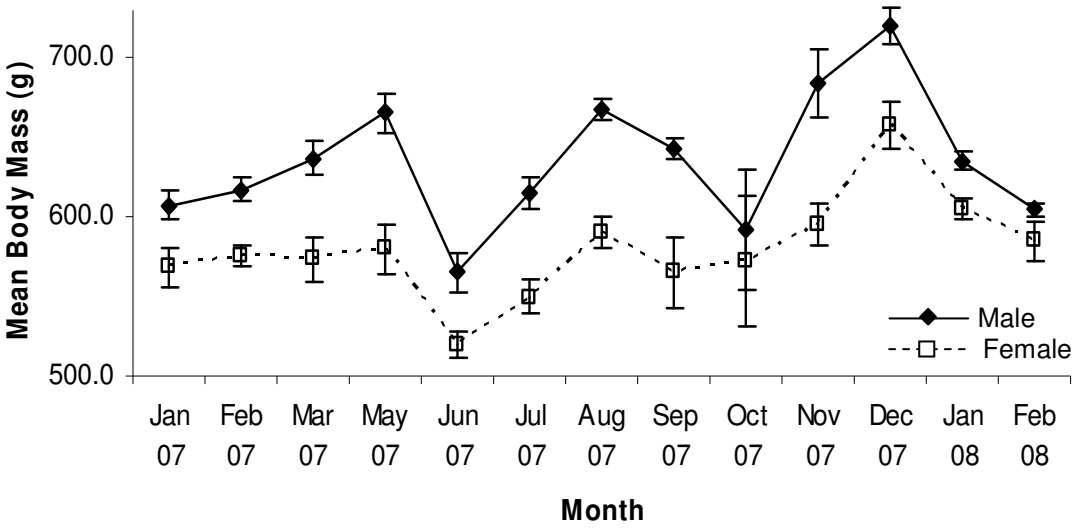

Figure 7. Mean body mass (g) ± 1 SE for captive male and female harlequin ducks (*Histrionicus histrionicus*) at the USGS Patuxent Wildlife Research Center, January through December 2007 (14M:6F except 5M:6F October-December) and January-February 2008 (13M:6F). Body mass measurements were not recorded for April.

Table 9. Means (± 1 SE) for seasonal body mass (g) of captive male (n=5-14) and female (n=6) harlequin ducks (*Histrionicus histrionicus*). Seasons were defined as follows: winter (December-February); spring (March-May); summer (June-August); and autumn (September-November); within-column values followed by the same letter were not significantly different ($P>0.05$).

Season	Male Body Mass (g)	Female Body Mass (g)
Winter	624.75 ± 5.21ab	598.33 ± 7.55a
Spring	651.43 ± 8.21a	576.67 ± 9.80ab
Summer	615.71 ± 8.64b	553.33 ± 8.59b
Autumn	640.83 ± 11.23ab	577.22 ± 15.53ab

Discussion

This study compared the composition of green crabs to yellow shore crabs and the feeding behavior of harlequins in response to each crab species. Foraging behavior and energy gain (as determined by a comparison of crab intake rates, gut retention time, and assimilation efficiency) did not differ between harlequins consuming exotic green crabs as compared to native yellow shore crabs. Green crabs provided a significantly greater balance of organic matter (AFDM)-to-inorganic matter (carapace or ash), fat, and energy to harlequins. Furthermore, the significantly lower compression strength of green crabs indicates that they are potentially easier to digest than yellow shore crabs, although the two species did not differ in terms of gross energy intake rate or assimilable energy intake rate. Based on these results, it appears that the invasive exotic green crab poses no energetic or nutrient challenge to harlequin ducks wintering in western North America but rather presents potential energetic and nutritive benefits to the ducks. Therefore, the first null hypothesis (there is no difference between *H. histrionicus* intake rates of *C. maenas* and *H. oregonensis*) is not rejected, the second null hypothesis (there is no difference in the nutrient and energy composition, crushing resistance, harlequin gut retention time, and assimilation efficiency (digestibility) between *C. maenas* and *H. oregonensis*) is rejected.

The net energy and nutrient values of both crab species to harlequins is discussed below, taking into consideration prey characteristics and composition, the physiology and efficiency of duck digestion, and duck foraging behavior. These

findings are considered in the context of invasive species concerns and implications for waterfowl conservation and management.

The Net Value of Crab Energy and Nutrients to Harlequins

Intake Rate and Functional Response to Prey

This study revealed no differential in harlequin intake rate by crab type. The basis of a functional response to prey is that predators consume more prey as prey numbers increase (Valiela 1995). A Type II functional response is typical of diving ducks foraging for benthic prey (Richman and Lovvorn 2004); intake rate approaches an asymptote as prey density increases. The rate of consumption decelerates as prey density increases due to decreases in motivation or prey capture efficiency (Valeila 1995). Holling (1966) defined the components of functional response to include the following: 1) The rate of successful search for prey; 2) The time the predator spends searching; 3) The time required for the predator to handle prey; 4) The predator degree of hunger; and 5) The manner in which prey inhibits the predator. Functional response can be constrained by a multitude of predator and prey factors. In this study, level of hunger (as determined by digestion and assimilation rate (Valiela 1995)) did not affect prey intake rate between crab species. Gut capacity was not assessed but presumed constant in this study. Relevant prey factors for this study include the ability to find cover, mobility, and aggressiveness. Although yellow shore crabs utilize cover more effectively than green crabs (Jensen et al. 2002; McDonald et al. 1998; *personal observation*) and may differ in their aggressiveness towards a predator (*personal observation*), a significant difference in intake rate between the two prey items was not observed. However, an additional factor in this

study is the nature of the laboratory setting. Specifically, dive trials were conducted in freshwater dive tanks, which may have contributed to behavioral effects in the marine crabs used.

The primary goal of this study was to compare harlequin feeding behavior on the invasive green crab and the native yellow shore crab. Therefore, the focus was on analysis of duck intake rates at a low and high density of each crab species, rather than on quantifying functional response and energy expenditure during diving. In order to obtain true functional response curves reflecting the ducks' response to varying densities of prey, the response to additional densities (≥ 3 total) of each prey item would need to be measured. Utilizing additional densities would also enable the comparison of the functional response of harlequins foraging for mobile prey to previously published functional response models for seaducks foraging for sessile prey (Richman and Lovvorn 2003, 2004; Berlin 2008). Other seaducks similar to harlequins that also eat mobile prey in wintering habitats include long-tailed ducks (*Clangula hyemalis*), which consume amphipods, mysids, isopods, and fish (Robertson and Savard 2002; Cottam 1939; Johnson 1984; Sanger and Jones 1984; Goudie and Ankney 1986), as well as red-breasted mergansers (*Mergus serrator*), which prey on fish, crustaceans, worms, insects, and amphibians (Titman 1999).

Dive trials in this study consisted of a single isolated duck diving in a contained area, so social factors inherent in seaduck populations (such as competition with other foraging ducks or, conversely, cooperation with conspecifics) were not represented. In a study that compared dive time budgets between tufted ducks (*Aythya fuligula*) diving in a laboratory setting to those in the wild, Halsey et al.

(2006) noted that laboratory diving experiments often produce underestimates of dive effort. Therefore, future work on seaduck foraging energetics should incorporate cooperative or agonistic diving behaviors and examine the effects of these behaviors on intake rate. In addition, it is possible that each duck acclimated to the general location of prey in the dive tank, so future work should integrate the effects of unpredictable prey location.

Digestion and Assimilation of Prey

Despite the significantly higher energy and fat content of green crabs, there was no significant difference in mean gut retention time between prey species in this study. Intuitively, the retention time for food that has a high energy density or is harder to physically or chemically break down should be longer than for food that is low in energy density or more easily digested (Hilton et al. 1998). The significantly higher ash content of yellow shore crabs and the significantly higher energy and fat content of the green crabs may both have prolonged digestion time in the harlequins. In calculating MRT for eight North Atlantic seabird species feeding on energy-dense fish, Hilton et al. (2000) found that by 19 hours post feeding the excreta of most of the seabirds in the study resembled bile, and the researchers assumed all prey to have passed through the gut by this point. In calculating mean retention time for the current study, it was assumed that the fasting period prior to feeding led to complete passage of the Mazuri® Sea Duck Diet and also that 100% of unassimilated ingesta had passed completely through the gut by 72 h post-feeding. Furthermore, endogenous losses and any individual physiological digestive differences between ducks were assumed to have negligible impacts on retention.

Nitrogen-adjusted assimilation efficiency (AE_N) of yellow shore crabs and green crabs did not differ significantly. However, the mean assimilation efficiency (± 1 SE) of both yellow shore crabs (-19.77% ± 19.91) and green crabs (2.37% ± 8.98) was low relative to similar studies. Captive lesser scaup consuming two species of clam had mean (± 1 SD) nitrogen-adjusted assimilation efficiencies of 78.9% ± 9.0 (*Potamocorbula amurensis*) and 63.4% ± 9.3 (*Macoma balthica*; Richman and Lovvorn 2004). Captive common eiders (*Somateria mollissima*) consuming two species of clam (meat plus shell) had mean (± 1 SD) nitrogen-adjusted assimilation efficiencies of 67.3% ± 6.9 (*Nuculana radiate*) and 75.9% ± 10.1 (*Macoma calcarea*; Richman and Lovvorn 2003). Captive surf scoters (*Melanitta perspicillata*) consuming two bivalves (meat plus shell) had mean metabolizable energy efficiencies (± 1 SD) of 48.17% ± 31.64 (the mussel, *Ischadium recurvum*) and 15.29% ± 35.30 (the clam, *Mulinia lateralis*; Berlin 2008).

Given that harlequins expend energy to digest, transport, and metabolize different substances such as lipids and N (Valiela 1995), there are a few possible explanations for the negative assimilation efficiency of yellow shore crabs and the low AE_N of green crabs, ranging from digestion efficiency to measurement constraints to study design parameters. For example, in a study of eight species of piscivorous seabirds, Hilton et al. (2000) found that species consuming high energy diets had inefficient digestion. However, it is unlikely that the relatively high energy content of crabs would explain such low assimilation efficiencies in the harlequins, particularly given the findings of similar studies with captive seaducks (Richman and Lovvorn 2003, 2004; Berlin 2008), as previously stated. Levey and Karasov (1989)

found that there can be a lag in digestive efficiency when a bird first switches to a new diet, which may be a factor to consider in this type of trial.

Alternatively, bomb calorimetry has been shown to yield underestimated energy values for materials comprised of a high percentage of ash (Paine 1966). However, again, the previously mentioned diving duck studies showed a high percentage of ash in prey with relatively high assimilation efficiencies (Richman and Lovvorn 2003, 2004; Berlin 2008). Also, the percent duck body mass loss in these studies as well as energy content of food items were comparable to the current study (Richman and Lovvorn 2003, 2004; Berlin 2008). However, unlike previous studies, the excreta from the ducks in the current study contained *more* energy $\cdot$ g^{-1} than did the food administered, due perhaps to insufficient food intake to meet maintenance needs during the trial period.

Although radioactive and other markers have been used in digestion studies in order to track precisely ingesta as it passes through an organism's digestive system (Warner 1981; Valiela 1995), the preferred method to assess assimilation efficiency would be to feed ducks a precise quantity of prey over an extended period of time until a "steady state" of excretion is attained and then to analyze excreta mass collected over a known time interval (Blaxter et al. 1956). However, in order to provide a more suitable environment to complete a longer trial using such a "steady state" approach, larger caging would need to be situated in the duck pens (a more familiar setting for the ducks; A. Berlin, *personal communication*).

Regarding assimilation study design, because of limitations in prey availability, harlequins were fed a portion of either yellow shore crab or green crab at

the start of each assimilation trial and excreta produced from that initial feeding were collected over a period of 72 hours. However, the use of this approach incorporates a few assumptions and also has potential drawbacks. First, as noted previously, it was assumed that there was no carryover from the Mazuri® Sea Duck Diet after the 24 h fast period prior to the trial. Also, feedings potentially represented a larger portion of food delivered over a shorter period of time than harlequins would naturally consume, but this resulted in the initial amount of prey being overall relatively small. Next, although the harlequins in this study were raised from eggs in captivity and thus acclimated to a captive setting and accustomed to human handling, moving harlequins from their regular pen environment into indoor cages elicited a stress response in some of the ducks (most notably demonstrated by pacing or other agitation), which may have affected the digestive process and was not quantified. Finally, although assimilation efficiency was corrected for nitrogen balance, it was not possible to specifically isolate excreta representative of crab intake from excreta due to above-baseline endogenous losses (such as those due to starvation), which may have lead to an underestimate of assimilation efficiency.

Assimilation efficiency (AE) and nitrogen balance (NB) were determined at 72 h post feeding in order to ensure that a maximum amount of crab ingesta had been digested in determining AE_N. However, it was difficult to assess at what time point post feeding the ingesta had been fully digested. It is possible that, on average, harlequins in the assimilation trials had completed digestion of crabs prior to the end of the trials, at 72 h post feeding. Therefore, for comparative purposes, AE_N was also calculated for 24 h and 48 h post feeding, and there were no significant differences at

either time point in AE_N of harlequins feeding on green crabs as compared to yellow shore crabs. It is possible that, on average, by 48 h post feeding the majority of crab ingesta had been digested by the harlequins. In summary, given that there were no significant differences between crab species in terms of the harlequins' response, the relative value of each crab species to harlequins can be attributed to the inherent nutrient and value, and carapace strength of each prey item.

Prey Composition

This study showed that green crabs offer significantly more organic (AFDM) content relative to inorganic (ash) content to harlequins than yellow shore crabs. For these analyses, each crab species was examined for AFDM, protein (nitrogen) and lipid (fat), as well as energy content. The analyses indicated that the mean (± 1 SE) energy content of green crabs was 8.88 ± 0.32 kJ/g, whereas for yellow crabs it was 7.74 ± 0.17 kJ/g. The significantly higher energy value of green crabs suggests that it would be feasible for harlequins to switch to consuming green crabs should the population of yellow shore crabs continue to decline. However, a holistic examination revealed there may be no ultimate difference in nutritional benefit between crab species to harlequins in terms of energy, because gross energy intake rate and assimilable energy intake rate did not differ significantly between the two crab species.

Whole green crabs were found to contain a mean (± 1 SE) percentage of 30.95 ± 0.80 protein, 1.84 ± 0.29 fat, and 70.13 ± 1.88 water, whereas yellow shore crabs were found to contain a mean (± 1 SE) percentage of 64.24 ± 0.67 protein, 1.03 ± 0.09 fat, and 29.63 ± 0.62 water. These findings are slightly higher than those of

Skonberg and Perkins (2002), who determined that claw meat of large green crabs (mean CW 79.7 ± 3.9 mm) from the Gulf of Maine contained a mean (± 1 SD) percentage of 16.8 ± 0.3 of protein, 0.5 ± 0.1 of fat, and 79.0 ± 0.7 of moisture, and leg meat contents were similar, except that fat content was 1.2 ± 0.2%. The difference between the findings of the current study and that of Skonberg and Perkins (2002) may be due to the fact that they studied just mean claw and leg content. Given that harlequins typically swallowed crabs whole, overall content consumed may have been less because sometimes pinchers were removed intentionally or during handling (*personal observation*; Robertson and Goudie 1999).

Although no significant differences were observed in this study relative to dietary protein content between green crabs and yellow shore crabs, these two crustaceans represent sources of a substantial amount of protein for harlequins. Protein intake is most important from hatching until adulthood, reproduction, and molting (Klasing 1998). In an analysis by Klasing (1998), white pekin ducks required 22% protein in their diet during growth and 15% during egg-laying; chickens required 18% protein for growth, 15% for egg-laying, and 5.3% for maintenance. Bos (2002) used N as a measure of protein intake and determined that brant geese (*Branta bernicula bernicula*) have been shown to select foods with higher N content over those with lower N content.

This study determined that green crabs had 79% greater lipid content than yellow shore crabs. Lipid intake in ducks is an essential source of energy, fatty acids, and pigments (such as those of eyes, feathers, and skin; Klasing 1998). The storage of lipids is also important to duck maintenance between meals and during migration,

and it is critical to both male and female ducks for reproductive success (Klasing 1998). For example, male ring-necked ducks (*Aythya collaris*) have been shown to expend fat reserves while caring for mates and female ring-necked ducks used fat stores for egg production (Hohman et al. 1988). Similarly, Bond (2005) found that pre-migration nutrient and energy acquisition at wintering grounds by female harlequin ducks is critical to egg production.

Crabs tested in this study required a mean (± 1 SE) force (N) of 52.3 ± 3.73 N (green crabs) and 71.44 ± 9.13 N (yellow shore crabs) for carapace failure. In compression loading tests on small areas of the carapace of adult snow crabs (*Chionoecetes opilio*), Dutil et al. (2000) found that failure of the carapace cuticle occurred in the range of 34 to 52 N, depending on carapace width (60 mm<CW<140 mm). The significantly higher force required to compress yellow shore crabs indicates that harlequins would likely need to expend more effort to initially break down this species in the gizzard. In this study, tests of crab carapace compression strengths were used to approximate the relative grinding effort required of a duck gizzard provided some insight into the energy needed for the duck to digest each crab species. Previous tests for carapace strength have utilized point force penetration tests (Barshaw et al. 2003, on lobsters) and compression of small sections of carapace (Dutil et al. 2000, on snow crabs). In the current study, tests using point force carapace penetration and compression of a small section of crab carapace were tried, but because the muscular duck gizzard contracts to grind prey from all directions, a uniform compression strength test was determined to best approximate gizzard effort. It was assumed that measurements of carapace compression strength from alternative

directions would be comparable to compression on the dorsal side of the carapace. All crabs used in this study appeared to be at a similar molt stage. For future carapace compression strength studies, it is recommended that molt stage be quantified and consistent between individuals. Despite the difference in compression strength between green crabs and yellow shore crabs, overall assimilation efficiency between these two crab species did not differ significantly, perhaps due to physiological adaptations by harlequins to digestion of the native yellow shore crab.

In summary, energetically and nutritionally, green crabs present a viable food option to harlequins, should yellow crabs become unavailable and a switch to green crabs occurs. Recent food habits analyses have shown that green crabs are consumed by bufflehead (*Bucephala albeola*), an Atlantic seaduck species (Perry et al. *in prep*). However, the potential impacts of green crabs as an exotic invasive species must be considered.

Invasive Species Considerations

Although green crabs do not present any apparent challenges to harlequin ducks in terms of energy or nutrients, it is important to consider potential threats that green crabs may pose at an ecosystem level. Green crabs are an intermediate host of parasites including the acanthocephalan *Profilicollis botulus*, and the trematodes *Maritrema subdolum* and *Microphallus claviformis*, helminths which are thought to have caused mortality in common eiders by restricting digestive functions (Thompson 1985; Thieltges et al. 2008). Acanthocephalans carried by green crabs are being investigated in recent eider deaths on Cape Cod (Madin 2008). Thompson (1985) found that the rate of infection in eiders was related to the number of green crabs

consumed, and alternative prey such as blue mussels (*Mytilus edulis*) was important to reducing green crab consumption. Should harlequin ducks feed on green crabs, transmission of such parasites may be a possibility and represent a new population threat. Alternative prey such as yellow shore crabs would take on higher importance. However, Thompson (1985) determined that in Scotland, smaller green crabs (under 20 mm) – which would be more likely consumed by harlequins than larger green crabs – were rarely infected with *P. botulus*.

The Nature Conservancy Global Marine Invasive Species database assigns threat scores to introduced species based on ecological impact, geographic extent, invasive potential, and management difficulty on a global level (Molnar et al. 2008). Out of a total possible score of 4 for each category, the green crab has been rated as follows (Molnar et al. 2008):

- Ecological impact: **3** – "Disrupts multiple species, some wider ecosystem function, and/or keystone species or species of high conservation value (e.g., threatened species)"
- Geographic extent: **4** – "Multi-ecoregion"
- Invasive potential: **4** – "Currently/recently spreading rapidly (doubling in <10 years) and/or high potential for future rapid spread"
- Management difficulty: **3** – "Reversible with difficulty and/or can be controlled with significant ongoing management"

These scores demonstrate a potential problem with the green crab in regard to other species.

Grosholz (2005) pointed out that there may be indirect effects of invasive marine species (positive interactions distinct from any direct competitive or predation effects), which typically have been overlooked. His work showed that green crabs introduced to the eastern Pacific consumed sufficient numbers of the native clam *Nutricola* spp. to remove competitive effects on and enable a population explosion of a historic (but previously benign) clam invader, *Gemma gemma*. Although it does not appear that harlequins consume *Nutricola* spp. or *G. gemma*, the latter has been found to comprise a notable portion of the diet of scoters (*Melanitta* spp.) feeding in the Chesapeake Bay (Perry et al. 2007), an area which has also been invaded by the green crab (Fofonoff et al. 2003). Grosholz (1997) estimated that, without management intervention, it would take only 500 days (1.36 years) for green crabs to consume all individuals of *Nutricola* spp. in Bodega Harbor, CA. More pertinent to the current study, the rate of green crab predation on yellow shore crabs (89%) in Bodega Harbor was found to be significantly higher than rates of cannibalism (22%) by adult green crabs on juvenile green crabs (Grosholz 1997).

On the other hand, strong evidence exists to support the resilience of native communities faced with an exotic competitor. For example, Porter and Savignano (1990) found that the introduction of the generalist fire ant, *Solenopsis invicta* in Texas resulted in a decline in the abundance and species richness of native arthropods. Although species richness of native ant communities declined by 70%, primarily due to competition with *S. invicta*, the authors suggested that this change would not persist due to possible counteradaptation by native species. Indeed, 12 years later, Morrison and Porter (2003) found a positive correlation between

population densities of *S. invicta* and arthropod diversity, which could indicate that the long-term presence of this introduced species enhanced, rather than suppressed, species diversity.

Green crab populations in the western Atlantic have recently declined, in part due to competition with the newly established invasive exotic Asian shore crab, *H. sanguineus* (Jensen et al. 2002; Griffen et al. 2007; E. Enos personal communication 2007). A recent evaluation of the distribution of green crabs in Bodega Bay Harbor revealed that predation by large native crabs, such as *Cancer* spp., may limit the spread of green crabs in the eastern Pacific region, a phenomenon which green crabs invading the western Atlantic two centuries ago did not face (Jensen et al. 2007).

Jensen et al. (2007) noted that yellow shore crab population declines attributed by Grosholz et al. (2000) to the arrival of green crabs may simply have been a result of life history traits (meroplanktonic larvae, short life spans) of yellow shore crabs, and that a significant reduction of yellow shore crabs by green crabs in Bodega Bay Harbor is unlikely. In fact, Torchin et al. (1996) noted that the symbiotic egg predator nemertean, *Carcinonemertes epialti* hosted by yellow shore crabs has been shown to feed and reproduce on *C. maenas* eggs, which could potentially control green crab populations.

Additionally, adaptive changes in organisms have been observed in response to the presence of the green crab. For example, thickened shells have been observed in the blue mussel, *Mytilus edulis* (Stokstad 2006), and phenotypic adaptation has been found in the dog whelk, *Nucella lapillus* (Vermeij 1982) in response to the

presence of the green crab on the east coast of North America. These responses could indicate adaptive resilience of native populations to the presence of this predator.

There were initial indications that the introduction of the green crab, *C. maenas* had the potential to alter the biodiversity of native invertebrates, including the possible competitive exclusion of populations of the native yellow shore crab, *H. oregonensis*. However, as they expand their new range on the North American west coast, it is unclear what the impact of green crabs will be on other intertidal crab species, such as *H. oregonensis*, which are also ecologically important to the marine community as contributors to biodiversity and as prey for birds and other predators. It is also uncertain whether declines of *H. oregonensis* that were identified as concurrent with the introduction of *C. maenas* on the west cost of North America are continuing, or if yellow shore crab populations have stabilized. In a 1998 testimony before a state committee, a California oyster aquaculturist attributed personal annual economic losses up to $30,000 because of green crab predation (Rudnick et al. 2000). Despite such initially observed reductions in commercially important shellfish populations, it is unclear if there have been continued modifications to biodiversity in intertidal communities in which *C. maenas* is present. Jensen et al. (2007) assert that claims of cumulative annual fishery and aquaculture losses over $40 million due to green crab predation did not account for mitigation of green crab impacts by predation of green crabs by large native crabs.

Now, nearly 20 years after the introduction of the green crab to the west coast of North America, it is worth investigating whether intertidal communities have stabilized in the presence of this invader or if declines in native invertebrate

populations continue, and what effects, if any, *C. maenas* has had on intertidal community structure. Although many studies have examined the initial impact of an introduced species on native species abundance and diversity, few have attempted to document long-term effects and possible ecosystem resilience. A reevaluation of the hypothesis that the green crab is a potentially responsible agent of change in yellow shore crab populations, as well as intertidal ecosystems, would represent a step towards filling this gap in ecological documentation.

Harlequin Conservation and Management Implications

A shifting prey base, which may result from the invasion of the green crab, has the potential to impact the survival and range of wintering harlequins (Rodway 1998; Robertson and Goudie 1999), and the ducks' ability to store essential nutrients for maintenance, molting, migration and reproduction. Success in nutrient and energy storage can be assessed by analyzing duck weight trends, if consideration is given to seasonal changes in muscle mass related to migration.

An analysis of captive harlequin weight in this study revealed important weight trends that are reflected in studies of other captive and wild duck populations. Analyses between January 2007 and February 2008 showed a significant difference in weight between males and females, as well as significantly lower summer weights in comparison to winter for females and to spring for males. Although the harlequins in the current study did not breed during the study period, the study findings support theories regarding endogenous rhythms apparent in both captive and wild ducks (Reinecke et al. 1982; Perry et al. 1986). During summer breeding in wild birds, fat

stores are utilized while attending to mates (for males) and during egg production (for females; Klasing 1998).

Perry et al. (1986) reported supporting evidence for endogenous rhythms of weight gain and loss in canvasbacks, redheads, mallards, and black ducks (*Anas rubripes*), specifically because all of these species lost body mass during the winter despite having sufficient food. The male harlequins in this study had lower body mass during the winter despite sufficient food supply, though a comparison to other seasons shows that losses were not significant. Avian species subjected to an unpredictable winter food supply tend to store more fat than species that have a reliable food source (Klasing 1998).

Harlequins are likely more energetically restricted than their varied and adaptable diet would suggest. Fischer and Griffin (2000) found that harlequins in the Aleutian Islands of Alaska spent 80% (males) and 87% (females) of the evening foraging and emphasized the need for an examination of harlequin starvation risk in the event of food scarcities or cold temperatures. Changes to the consistency in food availability at harlequin wintering grounds therefore may be an important consideration. Because the green crab invasion has the potential to affect food availability for wintering harlequins, data such as those provided in the current study are important to evaluations of the effects of a shifting prey base on harlequin acquisition and storage of energy.

Therefore, concerning the development of harlequin management and conservation plans, it is important to consider and predict new species invasions or range expansions, related trophic interactions, and rapid response and control. A

more thorough understanding of the long-term impacts of *C. maenas* is critical in light of the economic resources invested in management plans proposed and enacted since the introduction of this species. Financial resources diverted towards control intervention based on precautionary approaches could be better evaluated based on scientifically-derived data to determine the actual impact of green crabs on habitat and other species. Control efforts have been targeted at green crabs in the eastern Pacific and on the Atlantic coast of North America. Specifically based on the findings of this study, these efforts appear possibly premature in terms of harlequin duck population management. However, the findings of this study must be considered within a larger ecological context.

The western North American coastal marine ecosystem can be represented by a conceptual framework, which is comprised of several factors, specifically the predator, prey, invasive species impacts, and human impacts (Figure 8). Each factor is characterized by multiple attributes and processes, and complex interactions exist among the factors. The focal elements of this study were the characteristics of and interactions between just one predator (the harlequin duck) one native prey item (the yellow shore crab), and one invasive species (the green crab). It is essential that the relationship of these elements to the larger ecosystem be considered in developing harlequin conservation and management plans.

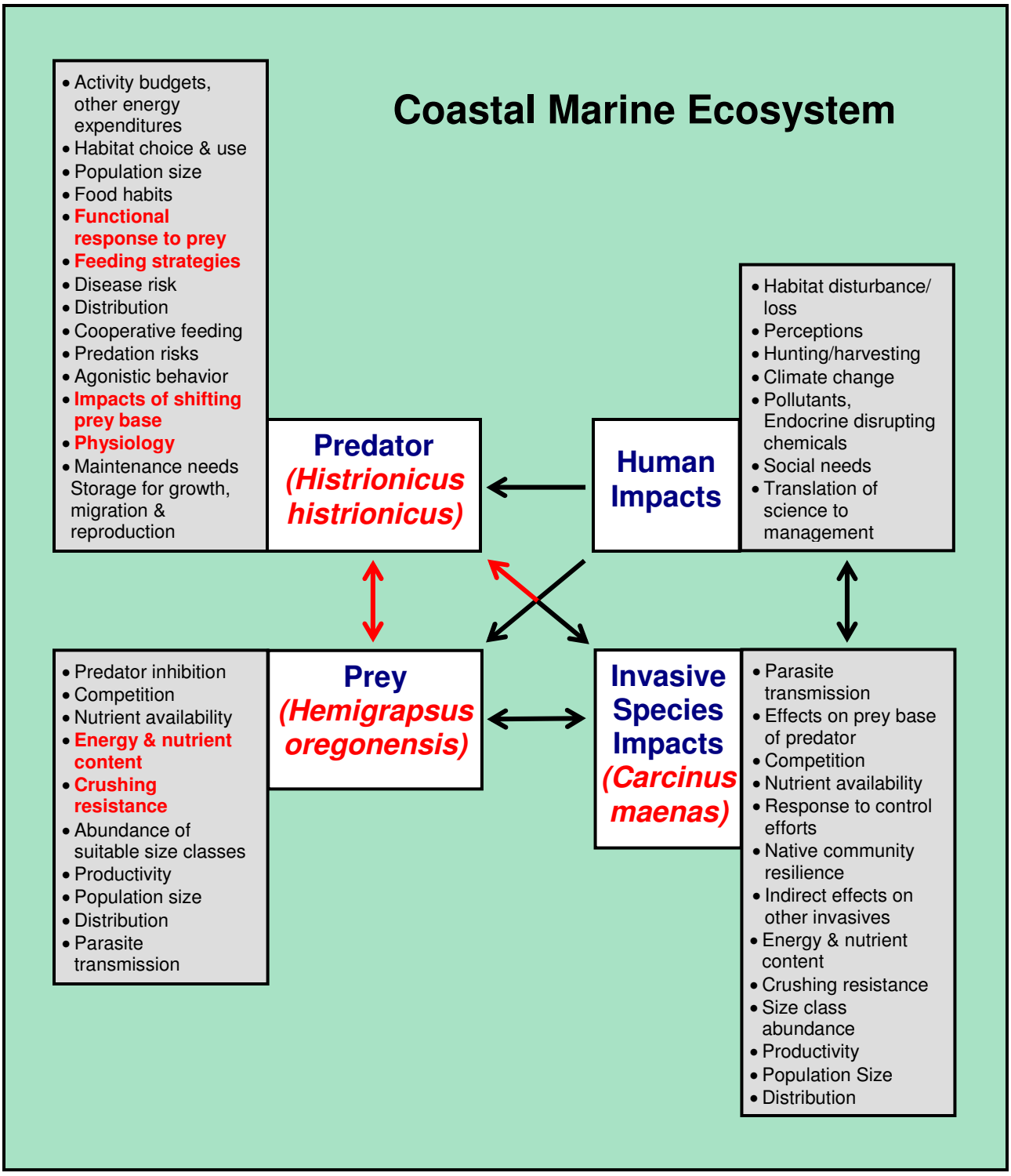

Figure 8. Theoretical western North American coastal marine ecosystem framework, comprised of four main factors: the predator, prey, human impacts, and invasive species impacts. Factors, characteristics and interactions considered in this study are in red.

Conclusions

In this study, captive male harlequin ducks were successfully trained to forage in a laboratory setting for native yellow shore crabs and the competing invasive exotic green crabs. The findings of this study indicate that there would be no net nutritional or energetic deficit to harlequins, if the population of yellow shore crabs were depleted and the ducks switched to feeding on green crabs. In order to place the findings of this study in a broader context, further data collection and analysis are needed. The collection of data on the most current dispersion of the green crab would enable a projection of long-term green crab population characteristics and potential impacts on native species. Such data would also facilitate the quantification of energetic effects of any dispersion differences between crab species (Lovvorn and Gillingham 1996) on the foraging behavior, habitat use, and ecosystem role of harlequins. Recent, detailed food habits data for harlequins is needed, especially now that the green crab has broadened its range since its introduction. Furthermore, the creation of a model to incorporate energetic relationships between trophic levels (Grosholz et al. 2000; Berlin 2008) would facilitate seaduck management decisions, particularly regarding exotic species introductions and native species declines.

Appendix

Protocol for Excreta Collections

At the scheduled collection time:

1. Pull out bottom tray of cage as smoothly as possible.
2. During collection, check water levels of dish attached to the side of each duck's cage. If water is low, refill.
3. Use spatula to scrape all excreta off of plastic liner and put excreta into green-topped container. If needed, rinse spatula with distilled water so the water (& excreta) flow into container. If excreta are very watery, remove tray fully and pour contents into container. Try to get as much excreta as possible off of the tray and into the container.
4. Using a permanent marker, label each container with appropriate date, time, and cage letter (A through I) – write directly on the plastic of the container, *not* the paper label.
5. Measure out 10 mL sulfuric acid from squeeze bottle into graduated cylinder (fill to top line on cylinder), and add acid to green-topped container with excreta.
6. Screw green cap firmly onto container. Make sure it is labeled with details noted in #4 above.
7. After collecting from each duck, rinse spatula with distilled water and wipe dry with paper towel before collecting from the next duck.
8. Repeat for all nine ducks, using a clean container for each duck. Slide trays back under cages as smoothly as possible so as not to disturb ducks.
9. After collection, clean spatula one last time using distilled water & paper towels.

10. Immediately place containers in chest freezer.

11. Leave room lights off in dive tank building and close door firmly.

12. Observe each duck for signs of stress. If duck is very lethargic/not alert or very unsettled (pacing, flapping wings, etc.), make a note of the time and duck and call me as needed.

Literature Cited

Barshaw, D.E., K.L. Lavalli, and E. Spanier. 2003. Offense versus defense: responses of three morphological types of lobsters to predation. Marine Ecology Progress Series 256:171-182.

Behrens Yamada, S., B.R. Dumbauld, A. Kalin, C.E. Hunt, R. Figlar-Barnes, and A. Randall. 2005. Growth and persistence of a recent invader *Carcinus maenas* in estuaries of the northeastern Pacific. Biological Invasions 7:309-321.

Behrens Yamada, S., A. Randall, J. Leischner, and L. Gibbs. (2006, June). Status of the European green crab in Oregon and Washington estuaries: progress report. [Online]. Available: http://www.aquaticnuisance.org/OSU%20GREEN%20%20Monitoring%20June%202006.pdf [January 24, 2007].

Berlin, A. 2008. Foraging values of *Mulinia lateralis* and *Ischadium recurvum*: energetics effects of surf scoters wintering in the Chesapeake Bay. Ph.D. Dissertation. University of Maryland, College Park. 137 pp.

Blaxter, K.L., N. McC. Graham, and F.W. Wainman. 1956. Some observations on the digestibility of sheep, and on related problems. British Journal of Nutrition 10(2):69-91.

Block, R.J. and D. Bolling. 1946. The amino acid composition of proteins and foods. Science 103(2675):431-432.

Bond, J.C. 2005. Nutrient acquisition and allocation strategies for reproduction by harlequin ducks. Master's thesis, Simon Fraser University, Burnaby, Canada. 86 pp.

Bos, D. 2002. Grazing in coastal grasslands: brent geese and facilitation by herbivory. Ph.D. Dissertation. University of Groningen, Groningen, The Netherlands.

Carlton, J.T. and A.N. Cohen. 2003. Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *Carcinus aestuarii*. Journal of Biogeography 30:1809-1820.

Cohen, A.N., J.T. Carlton, and M.C. Fountain. 1995. Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Marine Biology 122(2):225-237.

Committee on the Status of Endangered Wildlife in Canada (COSEWIC). (2006, August) Canadian Species at Risk. [Online]. Available: http://www.cosewic.gc.ca/eng/sct0/rpt/rpt_csar_e.pdf [September 11, 2006].

Cottam, C. Food habits of North American diving ducks. 1939. U.S. Department of Agriculture Technical Bulletin 643, Washington, D.C.

Daly, G.P. 1981. Competitive interactions among three species of shore crabs in the intertidal zone. Ph.D. Dissertation. University of Oregon, Eugene, Oregon.

Dutil, J.-D., C. Rollet, R. Bouchard, and W.T. Claxton. 2000. Shell strength and carapace size in non-adult and adult male snow crab (*Chionecetes opilio*). Journal of Crustacean Biology 20(2):399-406.

Esler, D., T.D. Bowman, K.A. Trust, B.E. Ballachey, T.A. Dean, S.C. Jewett, and C.E. O'Clair. 2002. Harlequin duck population recovery following the 'Exxon Valdez' oil spill: progress, process and constraints. Marine Ecological Progress Series 241:271-286.

Fischer, J.B. and C.R. Griffin. 2000. Feeding behavior and food habits of wintering harlequin ducks at Shemya Island, Alaska. Wilson Bulletin 112(3):318-325.

Floyd, T. and Williams, J. 2004. Impact of green crab (*Carcinus maenas* L.) predation on a population of soft-shell clams (*Mya arenaria* L.) in the southern Gulf of St. Lawrence. Journal of Shellfish Research 23:457-462.

Fofonoff P.W., G.M. Ruiz, G. Steves, A.H. Hines, and J.T. Carlton. 2003. National Exotic Marine and Estuarine Species Information System. [Online]. Available: http://invasions.si.edu/nemesis/. [March 29, 2008].

Gaines, W.L. and R.E. Fitzner. 1987. Winter diet of the harlequin duck at Sequin Bay, Puget Sound, Washington. Northwest Science 61(4):213-215.

Glude, J.B. 1955. The effects of temperature and predators on the abundance of the soft-shelled clam, *Mya arenaria*, in New England. Transactions of the American Fisheries Society 84:13-26.

Goudie, R.I. and C.D. Ankney. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology 67(6):1475-1482.

Goudie, R.I. 1991. The status of the harlequin duck (*Histrionicus histrionicus*) in eastern North America. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, Ontario.

Griffen, B.D., T. Guy, and J.C. Buck. 2007. Inhibition between invasives: a newly introduced predator moderates the impacts of a previously established invasive predator. Journal of Animal Ecology 77:32-40.

Grosholz, E.D. and G.M. Ruiz. 1995. Spread and potential impact of the recently introduced European green crab, *Carcinus maenas* in central California. Marine Biology 122:239-247.

Grosholz, E.D. and G.M. Ruiz. 1996. Predicting the impact of introduced marine species: Lessons from the multiple invasions of the European green crab *Carcinus maenas*. Biological Conservation 78:59-66.

Grosholz, E.D. 1997. The impact of the introduced European green crab on benthic invertebrates in Bodega Harbor, CA. *In* Centre for Research on Introduced Marine Pests, Technical Report Number 11: Proceedings of the First International Workshop on the Demography, Impacts and Management of Introduced Populations of the European crab, *Carcinus maenas* (R.E. Thresher, Ed.).

Grosholz, E.D., G.M. Ruiz, C.A. Dean, K.A. Shirley, J.L. Maron, and P.G. Connors. 2000. The impacts of a nonindigenous marine predator in a California bay. Ecology 81(5)1206-1224.

Grosholz, E.D. and G.M. Ruiz. 2002. Management plan for the European green crab: submitted to the Aquatic Nuisance Species Task Force. [Online]. Available: http://www.anstaskforce.gov/GreenCrabManagementPlan.pdf.

Grosholz, E.D. 2005. Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. Proceedings of the National Academy of Sciences 102(4):1088-1091.

Guillemette, M., R.C. Ydenberg, and J.H. Himmelman. 1992. The role of energy intake rate in prey and habitat selection of common eiders *Somateria*

mollissima in winter: a risk-sensitive interpretation. Journal of Animal Ecology 61:599-610.

Guillimette, M. 1994. Digestive-rate constraint in wintering common eiders (*Somateria mollissima*): Implications for flying capabilities. The Auk 111(4):900-909.

Guillimette, M. 1998. The effect of time and digestion constraints in common eiders while feeding and diving over blue mussel beds. Functional Ecology 12:123-131.

Halsey, L.G., O.J. Brand, A.J. Woakes, and P.J. Butler. 2006. Experiments on single diving birds in the laboratory often measure dives of decreased effort. Ibis 148:164-166.

Hilton, G., D. Houston, and R. Furness. 1998. Which components of diet quality affect retention time of digesta in seabirds? Functional Ecology 12:929-939.

Hilton, G.M., R.W. Furness, and D.C. Houston. 2000. A comparative study of digestion in North Atlantic seabirds. Journal of Avian Biology 31:36-46.

Hirsch, K.V. 1980. Winter ecology of sea ducks in the inland marine waters of Washington. Master's thesis, University of Washington, Seattle, Washington.

Holling, C.S. 1966. The functional response of invertebrate predators to prey density. Memoirs of the Entomological Society of Canada 48:1-85.

Holmes, D. 2001. The green crab invasion: a global perspective, with lessons from Washington State. Master's Thesis, The Evergreen State College, Olympia, Washington.

Hohman, W.L., T.S. Taylor, and M.W. Weller. 1988. Annual body weight change in ring-necked ducks (*Aythya collaris*). Pp. 257-269 *In* Waterfowl in Winter (M.W. Weller, ed.). University of Minnesota Press, Minneapolis.

Jamieson, G.S., E.D. Grosholz, D.A. Armstrong, and R.W. Elner. 1998. Potential ecological implications from the introduction of the European green crab, *Carcinus maenas* (Linneaus), to British Columbia, Canada, and Washington, USA. Journal of Natural History 32:1587-1598.

Jensen, G.C., P.S. McDonald, and D.A. Armstrong. 2002. East meets west: competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus* spp. Marine Ecology Progress Series 225:251-262.

Jensen, G.C., P.S. McDonald, and D.A. Armstrong. 2007. Biotic resistance to green crab, *Carcinus maenas*, in California bays. Marine Biology 151:2231-2243.

Jeschke, J., M. Kopp, and R. Tollrian. 2002. Predator functional responses: discriminating between handling and digestibility prey. Ecological Monographs 72:95-112.

Johnson, S.R. 1984. Prey selection by Oldsquaws in a Beaufort Sea lagoon, Alaska. Pp. 12–19 *In* Marine birds: their feeding ecology and commercial fisheries relationships (G. A. Sanger and P. F. Springer, eds.). Canadian Wildlife Service Special Publication, Ottawa, ON.

Kareiva P. 1996. Contributions of ecology to biological control. Ecology 77(7): 1963-1964.

Klasing, K.C. 1998. Comparative Avian Nutrition. CAB International, Oxon, UK. 350 pp.

Levey, D.J. and W.H. Karasov. 1989. Digestive responses of temperate birds switched to fruit or insect diets. The Auk 106:675-686.

Lovvorn, J.R. and M.P. Gillingham. 1996. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. Ecology 77(2):435-451.

Low, C. 1970. Factors affecting the distribution and abundance of two species of beach crabs *Hemigrapsus oregonensis* and *H. nudus*. Master of Science Thesis. Zoology, University of British Columbia, Vancouver, British Columbia.

McDonald, P.S., G.C. Jensen, and D.A. Armstrong. 1998. Green crabs and native predators: Possible limitations on the west coast invasion. Journal of Shellfish Research 17(4):1283.

McDonald, P.S., G.C. Jensen, and D.A. Armstrong. 2001. The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. Journal of Experimental Marine Biology and Ecology 258:39-54.

Madin, K. 2008. Scientists investigate mysterious duck die-offs. Oceanus, Woods Hole Oceanographic Institute. [Online]. Available: http://www.whoi.edu/oceanus/viewArticle.do?id=36646. [March 29, 2008].

Meinkoth, N.A. 1981. National Audubon Society: Field Guide to Seashore Creatures. Knopf Publishing Group. 816pp.

Mittelhauser, G. 1991. Harlequin ducks at Acadia National Park and coastal Maine, 1988–91. Island Res. Cntr., College of the Atlantic, Bar Harbor, ME.

Mittelhauser, G. 1993. Status of harlequin ducks, 1993. Report to the endangered and nongame wildlife grants program, Maine Dept. Inland Fisheries and Wildlife, Bangor.

Molnar, J.L., R.L. Gamboa, C. Revenga, and M.D. Spalding. 2008. Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment. Early release.

Montevecchi, W.A., A. Bourget, J. Brazil, R.I. Goudie, A.E. Hutchison, B.C. Johnson, P. Kehoe, P. Laporte, M.A. McCollough, R. Milton, and N. Seymour. 1995. National Recovery Plan for the harlequin duck in eastern North America. Report No. 12. Recovery of Nationally Endangered Wildlife Committee, 30 pp.

Morrison, L.W. and S.D. Porter. 2003. Positive association between densities of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), and generalized ant and arthropod diversity. Environmental Entomology 32(3)548-554.

Norton, A.H. 1896. Recent observations on *Histrionicus histrionicus* in Maine. The Auk 13:229-34.

Oliver, J. and A. Schmelter. Unpublished data. Life history of the native shore crabs *Hemigrapsus oregonensis* and *Hemigrapsus nudus* and their distribution, relative abundance and size frequency distribution at four sites in Yaquina Bay, Oregon.

Paine, R.T. 1966. Endothermy in bomb calorimetry. Limnology and Oceanography 11:126-129.

Perry, M.C., R.E. Munro and G.M. Haramis. 1981. Twenty-five year trends in diving duck populations in Chesapeake Bay. Trans. N. Amer. Wildl. Natur. Resour. Conf. 46:299-310.

Perry, M.C., W.J. Kuenzel, B.K. Williams, and J.A. Serafin. 1986. Influence of nutrients on feed intake and condition of captive canvasbacks in winter. Journal of Wildlife Management 50(3):427-434.

Perry, M.C., A.M. Wells-Berlin, D.M. Kidwell, and P.C. Osenton. 2007. Temporal changes of populations and trophic relationships of wintering diving ducks in Chesapeake Bay. Pages 4-16 *In* Erwin, R.M., B.D. Watts, G.M. Haramis, M.C. Perry, and K. A. Hobson (eds.). Waterbirds of the Chesapeake Bay and vicinity: harbingers of change? Waterbirds 30 (special publication 1).

Phelps, H.L. 1994. The Asiatic clam (*Corbicula fluminea*) invasion and system-level ecological change in the Potomac River Estuary near Washington, D.C. Estuaries 17(3):614-621.

Porter, S.D. and D.A. Savignano. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 71: 2095-2106.

Quinn, G.P. and M.J. Keough. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, United Kindgom. 537 pp.

Reinecke, K.J., T.L. Stone, and R.B. Owen, Jr. 1982. Seasonal carcass composition and energy balance of female black ducks in Maine. Condor 84: 420-426.

Richman, S.E. and J.R. Lovvorn. 2003. Effects of clam species dominance on nutrient and energy acquisition by spectacled eiders in the Bering Sea. Marine Ecology Progress Series 261:283-297.

Richman, S.E. and J.R. Lovvorn. 2004. Relative foraging value to Lesser Scaup ducks of native and exotic clams from San Francisco Bay. Ecological Applications 14(4):1217-1231.

Robertson, G.J. and R.I. Goudie. 1999. Harlequin duck (*Histrionicus histrionicus*). *In* The Birds of North America, No. 466 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Robertson, G.J. and J-P.L. Savard. 2002. Long-tailed duck (*Clangula hyemalis*). *In* The Birds of North America, No. 651 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Rodway, M.S. 1998. Activity patterns, diet, and feeding efficiency of harlequin ducks breeding in northern Labrador. Canadian Journal of Zoology 76(5): 902–909.

Rodway, M.S. and F. Cooke. 2002. Use of fecal analysis to determine seasonal changes in the diet of wintering harlequin ducks at a herring spawning site. Journal of Field Ornithology 73(4):363–371.

Rogers, R. 2001. The green menace: the European green crab. Environmental Practice 3:93-95.

Ropes, J.W. 1968. The feeding habits of the green crab, *Carcinus maenas*. Fisheries Bulletin 67:183-203.

Rudnick, D.A., K.M. Halat, and V.H. Resh. 2000. Distribution, ecology, and potential impacts of the Chinese mitten crab (*Eriocheir sinensis*) in San Francisco Bay.

Technical Completion Report, Project Number UCAL-WRC-W-881. University of California Water Resources Center. [Online]. Available: http://repositories.cdlib.org/wrc/tcr/rudnick. [March 29, 2008].

Sanger, G.A. and R.D. Jones, Jr. 1984. Winter feeding ecology and trophic relationships of oldsquaws and white-winged scoters on Kachemak Bay, Alaska. Pp. 20–28 *in* Marine birds: their feeding ecology and commercial fisheries relationships (G. A. Sanger and P. F. Springer, eds.). Canadian Wildlife Service Special Publication, Ottawa, ON.

SAS Institute, Inc. 2003. SAS/STAT Software. Version 9.1. SAS Institute, Inc. Cary, NC.

Sibbald, I.R. 1982. Measurement of bioavailable energy in poultry feeding stuffs: a review. Canadian Journal of Animal Science 62:983-1048.

Simberloff D., T. Dayan, C. Jones, and G. Ogura. 2000. Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. Ecology 81:2086-2099.

Skonberg, D.I. and B.L. Perkins. 2002. Nutrient composition of green crab (*Carcinus maenas*) leg meat and claw meat. Food Chemistry 77:401-404.

Stokstad, E. 2006. Native mussel quickly evolves fear of invasive crab. Science 313: 745.

Sverdrup, H.U., M.W. Johnson, and R.H. Flemming. 1947. The oceans, their physics, chemistry and general biology. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 1087 pp.

Thieltges, D.W. B. Hussel, J. Hermann, K.T. Jensen, M. Krakau, H. Taraschewski, and K. Reise. 2008. Parasites in the northern Wadden Sea: a conservative ecosystem component over 4 decades. Helgoland Marine Research 62(1):37-47.

Thompson, A.B. 1985. Transmission dynamics of *Profilicollis botulus* (Acanthocephala) from crabs (*Carcinus maenas*) to eider ducks (*Somateria mollissima*) on the Ythan Estuary, N.E. Scotland. Journal of Animal Ecology 54:605-616.

Titman, R.D. 1999. Red-breasted Merganser (*Mergus serrator*). *In* The Birds of North America Online (A. Poole, Ed.). The Birds of North America, Inc., Philadelphia, Pennsylvania.

Titus, H.W., A.L. Mehring, D. Johnson, L.L. Nesbit, Jr., and T. Tomas. 1959. An evaluation of MCF (Micro-Cel-Fat), a new type of fat product. Poultry Science 38:1114-1119.

Torchin, M.E., K.D. Lafferty, and A.M. Kuris. 1996. Infestation of an introduced host, the European green crab, *Carcinus maenas*, by a symbiotic Nemertean egg predator, *Carcinonemertes epialti*. The Journal of Parasitology 82(3):449-453.

Torchin, M.E., K.D. Lafferty, and A.M. Kuris. 2001. Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biological Invasions 3:333-345.

Tufts, R.W. 1986. Birds of Nova Scotia. 3rd ed. Nimbus Pubications. Ltd. and Nova Scotia Museum, Halifax.

Valiela, I. 1995. Marine Ecological Processes. 2nd ed. Springer-Verlag, New York. 686 pp.

Vermeer, K. 1983. Diet of the harlequin duck in the Strait of Georgia, British Columbia. The Murrelet 64(2):54-57.

Vermeij, G.J. 1982. Phenotypic evolution in a poorly dispersing snail after arrival of a predator. Nature 299:349-350.

Vickery, P.D. 1988. Distribution and population status of harlequin ducks (*Histrionicus histrionicus*) wintering in eastern North America. Wilson Bulletin 100:119-126.

Visser, E.P., P.S. McDonald, and D.A. Armstrong. 2004. The impact of yellow shore crabs, *Hemigrapsus oregonensis*, on early benthic phase Dungeness crabs, *Cancer magister*, in intertidal oyster shell mitigation habitat. Estuaries 27:699-715.

Walton, W.C. 1997. Attempts at physical control of Carcinus maenas within coastal ponds of Martha's Vineyard, MA (northeastern coast of North America). Proceedings of the first international workshop on the demography, impacts and management of introduced populations of the European crab, Carcinus maenas: 20-21 March 1997. Centre for Research on Introduced Marine Pests, Hobart, Tasmania, Australia. Technical Report 11.

Warner, A.C.I. 1981. Rate of passage of digesta through the gut of mammals and birds. Nutrition Abstracts and Reviews Series B 51(12):789-820.

Welch, W.R. 1968. Changes in abundance of the green crab, *Carcinus maenas* (L.) in relation to the recent temperature changes. Fisheries Bulletin. 67:337-345.

Zar, J.H. 1999. Biostatistical Analysis. 4th ed. Prentice-Hall, Inc., Upper Saddle River, New Jersey. 929 pp.