DIVING AND FORAGING BEHAVIOUR OF WINTERING COMMON EIDERS (*Somateria mollissima*) AT CAPE ST. MARY'S, NEWFOUNDLAND

by

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ABSTRACT

I studied the foraging behaviour of Common Eiders in southeastern Newfoundland in the winters of 1995-1996. Eiders are marine diving ducks which forage diurnally for benthic, sessile prey. They congregate in flocks to feed and rest, even synchronizing diving and surfacing. I timed dive and pause durations and overall time spent feeding and resting to determine whether eiders incurred phsyiological debt while diving and to test the hypothesis that eiders vary dive and pause durations to maximize foraging effort in relation to ecological variables.

Some of the variability in diving patterns was related to prey type. When eiders fed on urchins and returned to the surface with one per dive, they dived and paused longer than when they fed on mussels and swallowed several underwater. Eiders did not maximize foraging time at the ocean bottom, regardless of prey type or success, nor did they appear to optimize breathing time at the surface. Eiders rarely exceeded their predicted aerobic dive limit (83 seconds) and there was no evidence of exhaustion or postponed recovery within the range of dives recorded. Sex and (male) age had no effect on diving performance, possibly because body size differences between these cohorts were not sufficient to influence diving ability, eiders were not diving near their physiological limits, or individuals were coordinating diving activity.

Common Eiders intensified foraging efforts for mussels, their preferred prey, at low and falling tides by reducing the amount of time spent on the surface between dives and by feeding for longer durations. Seasonal changes in eider foraging, including shorter pauses between mussel dives, longer resting bouts after mussel feed bouts, longer urchin dive durations and shorter urchin handling times suggested depletion of invertebrate populations. Kleptoparasitism had no effect on foraging parameters but predation risk from hunters at some sites was associated with decreased feeding times. Overall, dive duration and ecological factors explained only 35% and 43% of the observed variation in pause duration for eiders feeding on urchins and mussels, respectively. While some of the remaining variation may include responses to weather conditions, I believe coordination of individual Common Eiders with their flockmates, i.e. social factors, played a large role in determining dive and pause duration. Flocking may increase vigilance for predators and/or increase the probability of finding patchy prey; diving and surfacing together would maintain cohesion while foraging underwater. To date, foraging in diving vertebrates has been explained in terms of risk-sensitivity, breathing optimization, reduction in body heat loss, and maximization of a currency such as energy intake. However, diving in social foragers such as wintering Common Eiders may be more easily understood in terms of social interactions than currency maximization.

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Chapter I
General Introduction

Diving as a foraging method is found in a range of vertebrates as diverse as sea snakes, otters, seals and penguins. While certain diving characteristics such as method of propulsion, angle, and travel speed may vary considerably among species, all divers face a fundamental constraint of not being able to obtain oxygen while underwater. Intuitively then, diving has always been considered a physiologically costly exercise and the pause spent at the surface between dives has been regarded as necessary "recovery" time during which an animal unloaded carbon dioxide accumulated in muscles, replenished oxygen supply to tissues, processed metabolites (mainly lactic acid) and regenerated heat (MacArthur 1984; Ydenberg 1988). The relationship between dive and subsequent pause duration has therefore been considered somewhat inflexible, with a strong positive correlation predicted between dive and pause duration. Many studies have documented this general pattern (Stonehouse 1967; Cooper 1986; Nolet *et al.* 1993, Watanuki *et al.* 1996), and some studies have incorporated physiological cost and recovery into explanations of variation in diving performance (Ydenberg and Forbes 1988; Ydenberg and Guillemette 1991; Wanless *et al.* 1993). For example, Ydenberg and Forbes (1988) suggested that Western Grebes *Aechmophorus occidentalis* feeding on moving schools of fish worked intensively at exploiting a school and spent little time at the surface between dives, presumably delaying total recovery until the school had escaped or the grebe was exhausted. By working hard while the school was accessible and deferring recovery from physiological debt until later, the grebe may have been able to maximize the number of fish caught (Ydenberg and Clark 1989). Some diving birds may remain underwater long enough to exhaust their available oxygen stores and, thus, may have to resort to anaerobic metabolism. However, physiological studies have indicated that most voluntary dives by birds are aerobic and well within the predicted limit of their oxygen supplies (Butler 1989; Jones 1990; Wilson 1990). Such dives do not require any recovery beyond replenishment of oxygen stores (Kooyman and Davis 1987). The assumption that physiological debt and repayment (recovery) determines surface time may, therefore, be unnecessary and may detract from other factors influencing diving patterns.

One tool used to interpret diving patterns has been optimal foraging theory, an area of behavioural ecology which attempts to explain the foraging decisions of individuals according to costs and benefits of alternative actions (Stephens and Krebs 1986). To meet daily energy requirements and maximize fitness, an animal must make numerous foraging decisions, including habitat and prey choices and time allocation to various activities such as searching for food, while continuously evaluating the benefits and costs of all activities (Pyke *et al.* 1977; Caraco 1980). Several foraging models have been constructed to predict prey choice or time allocation during the dive cycle, and most make predictions on the basis of optimal energy gain or efficiency (Kramer 1988, Ball 1994; Beauchamp *et al.* 1992; Houston and

Carbone 1992). In the context of optimal foraging, diving birds may be considered central place foragers because they return to the surface after each foraging trip or dive (Houston and McNamara 1985) and, in this context, they fall into one of two sub-categories, depending on the amount of prey taken per dive, i.e., single- and multiple-prey loaders. Foraging models usually assume one or the other. Some of the more complex models involve aerobic and anaerobic metabolic pathways (Ydenberg and Clarke 1989; Carbone and Houston 1996). However, as noted above, physiological recovery may not be the most relevant parameter in many cases if birds dive for durations below aerobic dive limits.

If dive and pause durations do not reflect oxygen depletion and recovery, what factors determine the observed variation in diving patterns? Like any forager, a diving bird should be able to detect and respond to changing environmental conditions, including relatively predictable factors such as the amount of daylight available to forage and stochastic events such as severe weather or a change in the distribution of prey. These decisions are made in the context of the state of the animal, such as its fat reserves, and the expected energy balance over a given period. The likelihood of a negative energy balance may lead to adjustments in a range of foraging parameters such as intensity or duration of feeding activity or may lead to risk-prone behaviour. For example, Oystercatchers *Haematopus ostralegus* vary their intake rate in response to time stresses imposed by irregular tidal cycles (Swennen *et al.* 1989). In cold temperatures, some birds such as Snow Geese *Anser caerulescens* increase inactivity (Frederick and Klaas 1982) while others such as Mallards *Anas platyrhnychos* increased feeding (Jorde *et al.* 1984). Redheads *Aythya americana* not only fed more in the cold but also minimized energy expenditure by foraging during low tides and in shallow water (Michot *et al.* 1994). Underweight Common Eiders *Somateria mollissima* tended to feed on crabs which were much less abundant than urchins or mussels but which provided more energy once found (Guillemette *et al.* 1992). Although the mean net energy gain from feeding in crab habitat was similar to that of mussel habitat, the variance was much higher and, thus, lower weight birds were accepting a greater level of risk with regard to energy return from particular habitats.

A diving bird might adjust numerous foraging parameters in relation to its expected energy intake: dive duration, depth, habitat and prey choice, pause duration, and overall feeding and resting time. Any of these parameters may be changed according to environmental factors such as light availability, tide level and prey abundance (Wilson 1990; Monaghan *et al.* 1994). Ydenberg and Guillemette (1991) speculated that Common Eiders delayed full recovery from dives when they spent less time than expected at the surface between dives. Although it was not demonstrated that physiological debt was incurred nor recovery postponed (aerobic dive limit was not calculated), it is clear that eiders have the ability to adjust components of the dive/pause cycle. This may be an adaptation to increase energy intake when time available to forage is limited. Eiders are diurnal feeders inhabiting northern environments and must deal with short daylength, cold temperatures, heavy surf in foraging areas and, in some cases, restrictive ice conditions that may reduce available foraging time and/or increase energy demands. It is therefore possible that adjustment of the dive cycle is another option for maximizing foraging opportunities when storms, darkness or unfavourable tides are imminent. In addition, any forager, including diving birds, may alter behaviour in response to kleptoparasitism (Schenkveld and Ydenberg 1985), predation risk (Lima 1985) or, in the case of social animals, in order to coordinate with flockmates (Beauchamp 1992; Nygard *et al.* 1995).

I examined the foraging of Common Eiders wintering in Newfoundland to determine whether they adjust diving behaviour in response to ecological conditions. I will outline the specific objectives of my project below but, first, I will first describe relevant features of eider biology and of the study area.

GENERAL BIOLOGY OF COMMON EIDER

i) Distribution and general biology - Common Eiders have a holarctic breeding distribution and winter in northern coastal waters, often in association with leads and polynyas in sea ice (Bourget *et al.* 1986; Guillemette *et al.* 1993). Refreezing of open water and shifting of pack ice has been associated with mass mortality events involving several eider species in northern breeding areas (Barry 1968; Fournier and Hines 1994).

Newfoundland represents an important overwintering area for Common Eider (Mendall 1980; Bourget *et al.* 1986). Eider wintering populations in Newfoundland have been declining in recent years (Goudie 1988), as have eider populations in West Greenland (Frimer and Nielsen 1990; Frimer 1993), Russia and Alaska (Goudie *et al.* 1994). Cape St. Mary's Ecological Reserve in southeastern Newfoundland is a significant wintering site for eiders (Goudie 1981) but this area has also experienced a decrease in population levels (Goudie 1989). For example, Audubon Christmas Bird Counts at Cape St. Mary's recorded a fairly consistent decline in eider numbers from 7400 in 1979 to approximately 1745 in 1996 (American Birds 1980-1997). The factors contributing to declines are not well-understood but may be related to hunting pressure (Erskine 1990; Goudie *et al.* 1994) and oil pollution (Piatt *et al.* 1985, MacCharles 1986). From 1995-1997, aerial surveys conducted each March by Canadian Wildlife Service (CWS) have recorded an average of 2556 Common Eiders in the general area surrounding Cape St. Mary's (CWS records). Typically, significant numbers of eiders arrive at the reserve by mid-December and numbers remain high until early to mid-April (Goudie 1981, personal observation).

Common Eiders are large-bodied ducks, weighing approximately 2 kg, and are sexually dimorphic in plumage. The striking black and white plumage of the adult males is not fully attained until the fourth winter, although third-winter birds may resemble adults with the exception of more black on the upperparts (Palmer 1976, Madge and Burn 1988). Juveniles begin to acquire some white on the breast as early as their first winter and show tremendous individual variation in extent and patterning of white plumage. It is, therefore, possible to identify males as 1-, 2-, and 3+-year-olds. Females are drab brown as juveniles and attain a brighter, more barred appearance by their third year (Palmer 1976); aging females in the field can be difficult. Adult females are generally reddish-brown, although color is variable and can range from rust to grey (Madge and Burn 1988) to a light dun (personal observation).

Males usually start to breed at three years; females, generally at two or older (Palmer 1976, Baillie and Milne 1982, Madge and Burn 1988). Females do not feed at all during laying (Milne 1976) and incubation (Korschgen 1977), relying on endogenous reserves accumulated during the pre-laying period near breeding grounds rather than on wintering sites (Parker and Holm 1990). Low fat levels in eiders collected at Cape. St. Mary's from November to April, 1983-84 (R.I. Goudie, unpubl. data) support the idea that wintering eiders are not building up reserves for breeding.

Eiders collected at Cape. St. Mary's showed significant differences in weight between sex and age classes (Table I-1; R.I. Goudie, unpubl. data). There was no significant interaction between sex and age ($F_{[2,66]}$=1.02, P=0.37). Adult males were heavier than females ($F_{[1,66]}$=18.1, P=0.0001) and adults were heavier than immatures or sub-adults ($F_{[2,66]}$=3.9, P=0.026). Differences in size (Watanuki *et al.* 1996) and/or physiology and experience (Morrison *et al.* 1978, Kooyman *et al.* 1983, Le Boeuf *et al.* 1996) between sex and age classes may affect energy requirements and diving costs, and this could result in different diving behaviour. Eiders at this site carried few fat reserves throughout the season (R.I. Goudie, pers. comm.) and, since body fat and body mass are correlated in Common Eiders (Milne 1976; Parker and Holm 1990; Guillemette *et al.* 1992), I assumed there were no changes in body weight of eiders over the winter season.

ii) Social Behaviour

Eiders are gregarious and congregate in large numbers during the winter season, sometimes in flocks of several thousands (Goudie and Ankney 1988, Frimer and Nielsen 1990, Guillemette *et al.* 1993). Feeding and resting activities are coordinated (Guillemette *et al.* 1992) and little aggression is observed among feeding birds (Goudie and Ankney 1988, personal observation). Pair formation generally occurs in the fall and is frequent again in late winter and spring (Palmer 1976). I occasionally observed displays and copulation among resting birds at Cape. St. Mary's throughout the winter, starting as early as late February. There was no evidence of interference or mate-guarding among foraging birds.

The Common Eider population at Cape St. Mary's had a female-biased sex-ratio, possibly because adult male eiders tend to winter further north than females (Madge and Burn 1988) and males were

Table I-1. Body mass of Common Eiders collected at Cape. St. Mary's during the winters of 1983-84 (R.I. Goudie, unpublished data).

Sex and age class	n	Mean weight ± s.d. (g)	Min. weight (g)	Max. weight (g)
Males				
immature	3	1903.3 ± 128.6	1810	2050
subadult	8	1843.3 ± 134.1	1600	2050
adult	16	1926.9 + 143.0	1660	2100
Females				
immature	8	1657.9 + 74.9	1550	1778
subadult	2	1640.0 + 28.3	1620	1660
adult	35	1802.3 + 122.9	1580	2150

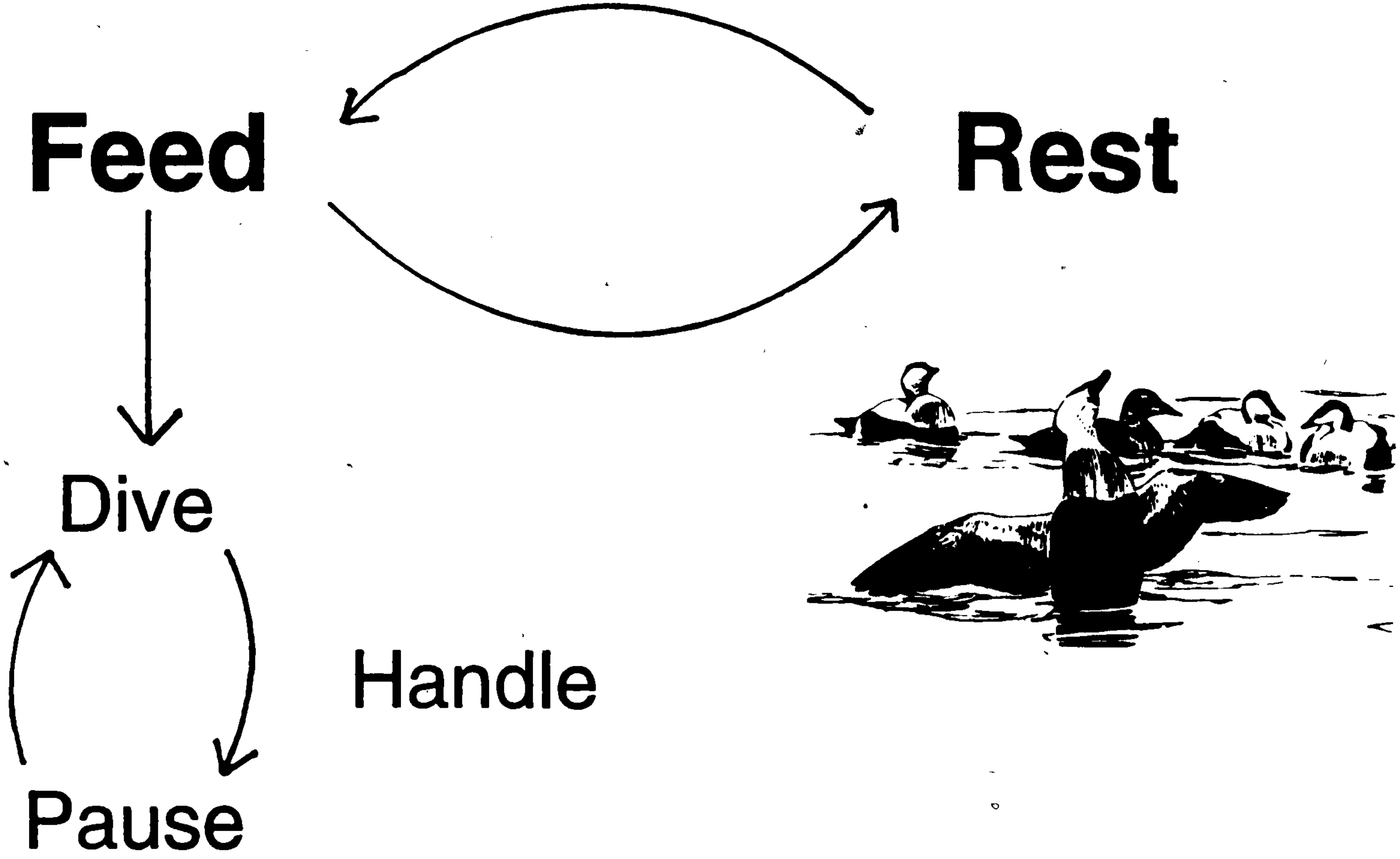
preferentially shot by hunters (R.I. Goudie, pers. comm.). I determined sex composition of 106 flocks ranging in size from 10 to 800; on average, the proportion of males (both adults and immatures) in a flock was 35 ± 14%, and ranged from 8 to 71%. Some first-year males in brown plumage may have been classified as females but I believe this margin of error to be very low since all flocks were close to shore and within good viewing distance. The percentage of males was similar in both years (1995: 36 ± 16%, 1996: 35 ± 14%; t=0.30, P=0.77). Little information is available for comparison with other wintering Common Eider populations but one study in Scotland reported in 66.7% adult males among Common Eiders (Mudge and Allen 1980). In most other wintering diving ducks, sex ratio is near unity or male-biased, e.g., 53% adult males among Steller's Eiders *Polystica stelleri* in Europe (Nygard *et al.* 1995), 66-77% adult males among Oldsquaws *Clangula hyemalis* and Velvet Scoters *Melanitta fusca* in Scotland (Mudge and Allen 1980), 50% adult males among Smew *Mergus albellus* in southern Sweden (Nilsson 1974), 67-76% males among Canvasbacks *Aythya valisineria* sexed in Maryland, Virginia and North Carolina (Haramis *et al.* 1994), and 59% males among Common Mergansers *Mergus merganser* in South Dakota and Minnesota (Anderson and Timken 1972).

iii) Foraging behaviour

Eiders feed and rest in well-defined, recognizable bouts (Guillemette *et al.* 1992, Goudie and Ankney 1988). Individuals in a flock will move inshore together to feed, diving repeatedly to the ocean bottom to obtain molluscs, echinoderms and crustaceans. Eiders swallow small prey, e.g. mussels, underwater but return to the surface with echinoderms and crabs to handle them before swallowing. Eiders roll green sea urchins *Strongylocentrotus droebachiensis* around in their bills to flatten or break off the spines and shake crabs to disarticulate them. A complete dive cycle, therefore, contains a dive, possibly a handling phase, and a pause (Fig. I-1). A series of dives comprises a feed bout (Guillemette *et al.* 1992). After feeding, the flock swims offshore again to loaf, preen and court and this period is known as a rest bout. Because eiders swallow prey with shell intact, a rest period after feeding is probably an obligatory digestive period in which the prey's exoskeleton is crushed in the muscular gizzard (Goudie and Ankney 1986, Guillemette 1994, Nehls 1995). Therefore, there are two levels of foraging to be considered: i) overall feed and rest bouts, measured on a scale of minutes, and ii) dives and pauses, measured in seconds (Fig. I-1).

Eiders are mainly foot-propelled divers while underwater but also flap the partially-opened wings during descent (Humphrey 1958, Tinbergen 1958, Lovvorn 1991). While swimming along the bottom, the wings are held in a half-extended position, apparently to counteract the effects of positive buoyancy (Humphrey 1958), and ascent is accomplished passively through buoyancy. Eiders may dive to depths of 42 m (Guillemette *et al.* 1993) but usually feed in shallower water, from 3-12 m (Nilsson 1970, Player 1971, Ryan 1985, Goudie and Ankney 1988, Guillemette et al 1993, Brager *et al.* 1995).

Figure I-1. Schematic diagram of a Common Eider foraging cycle.



Feed

Rest

Dive

Pause

Handle

Although nocturnal feeding in wintering and moulting eiders has been recorded in the Wadden Sea (Nehls 1995), eiders are mainly or exclusively day-active feeders in other areas, including southern Sweden (Nilsson 1970), Scotland (Campbell 1978, Player 1971), and the Mingan Archipelago in eastern Canada (Guillemette *et al.* 1992). Eiders at Cape St. Mary's also appear to feed only during daylight hours. Behaviour at dusk differs from daytime resting behaviour; as eiders swim offshore at sunset, they bathe intensively by slapping their wings against the water to send up spray, rather than preening calmly as they do during daytime rests. They continue swimming straight out to sea until lost to sight in increasing darkness. At dawn, an empty cove will steadily fill with groups of eiders arriving by flying or swimming in. Additional evidence for a night-long fast comes from birds collected at this site in the mid -1980's; eiders collected at first light invariably had empty stomachs (R.I. Goudie, pers. comm.).

In winter, Common Eiders may spend a considerable portion of the day feeding. Goudie and Ankney (1986) estimated that eiders at Cape St. Mary's fed on average for 56% of the day. In southern Sweden, Nilsson (1970) recorded eiders feeding for 28-58% of observations between January and March and, in the Gulf of St. Lawrence, eiders fed for 61% of the day (Guillemette *et al.* 1992). However, in the Wadden Sea, eiders fed for only 15% of the day (Nehls 1995).

Tidal influences on winter feeding have been noted in several areas, with feeding activity increased at or around low tide (Player 1971, Campbell 1978, Nehls 1995) when lower water depth would decrease travel time to the bottom. At Leith in Scotland, eiders have even been reported upending and dabbling over mussel beds at low tide (Player 1971). At Cape St. Mary's, I once observed female eiders picking through kelp on the sides of exposed rocks and climbing out onto the rocks to forage. They alternated picking and diving behaviour. In contrast to the above studies, Goudie and Ankney (1986) reported eiders feeding more during high tide.

While foraging, eiders submerge and surface with noticeable synchrony among individuals in the flock especially when feeding on mussels (Campbell 1978, Guillemette *et al.* 1993). When feeding on urchins, individual eiders tend to surface one after the other, handle urchins for varying times, but appear to pause and wait for flockmates before diving again, so that synchrony may be higher for diving than for surfacing (personal observation). Synchronous diving has been noted in other social diving ducks, including Surf Scoters *Melanitta perspicillata* (Schenkeveld and Ydenberg 1985, Beauchamp 1992) and Barrow's Goldeneye *Bucephala islandica* (Beauchamp 1992). Kleptoparasitic gulls often attended eider flocks and attempted to steal urchins as the birds surfaced (personal observation). Although other studies have recorded gulls stealing mussels from eiders and other ducks at other sites (Ingolfsson 1969, Schenkeveld and Ydenberg 1985, Beauchamp 1992), gulls rarely attended eiders that were feeding on mussels at Cape St. Mary's.

iv) Diet

Blue mussels *Mytilus edulis* are a preferred food for eiders in many areas (Player 1971, Goudie and Ankney 1986, Guillemette *et al.* 1992, Nehls 1995) but eiders also feed on green sea urchins, gastropods, and crustaceans (Goudie and Ankney 1986, Guillemette *et al.* 1992). At Cape St. Mary's, green sea urchins comprised 43-50^{+}% by mass of items found in eider gullets and blue mussels from approximately 28-33% (Ryan 1985, Goudie and Ankney 1986). At Brierly, a headland at Cape St. Mary's bordered by bedrock slabs, Ryan (1985) found that eiders preferentially selected mussels despite the predominance of urchins. Mussel habitat at this site was not usually available to eiders due to heavy surf in shallow zones. Minor dietary items included whelks, *Buccinum* and *Thais* spp., chink shells *Lacuna vincta*, top shells *Margarites helicinus* and crustaceans such as crabs and gammarid amphipods (Ryan 1985, Goudie and Ankney 1986).

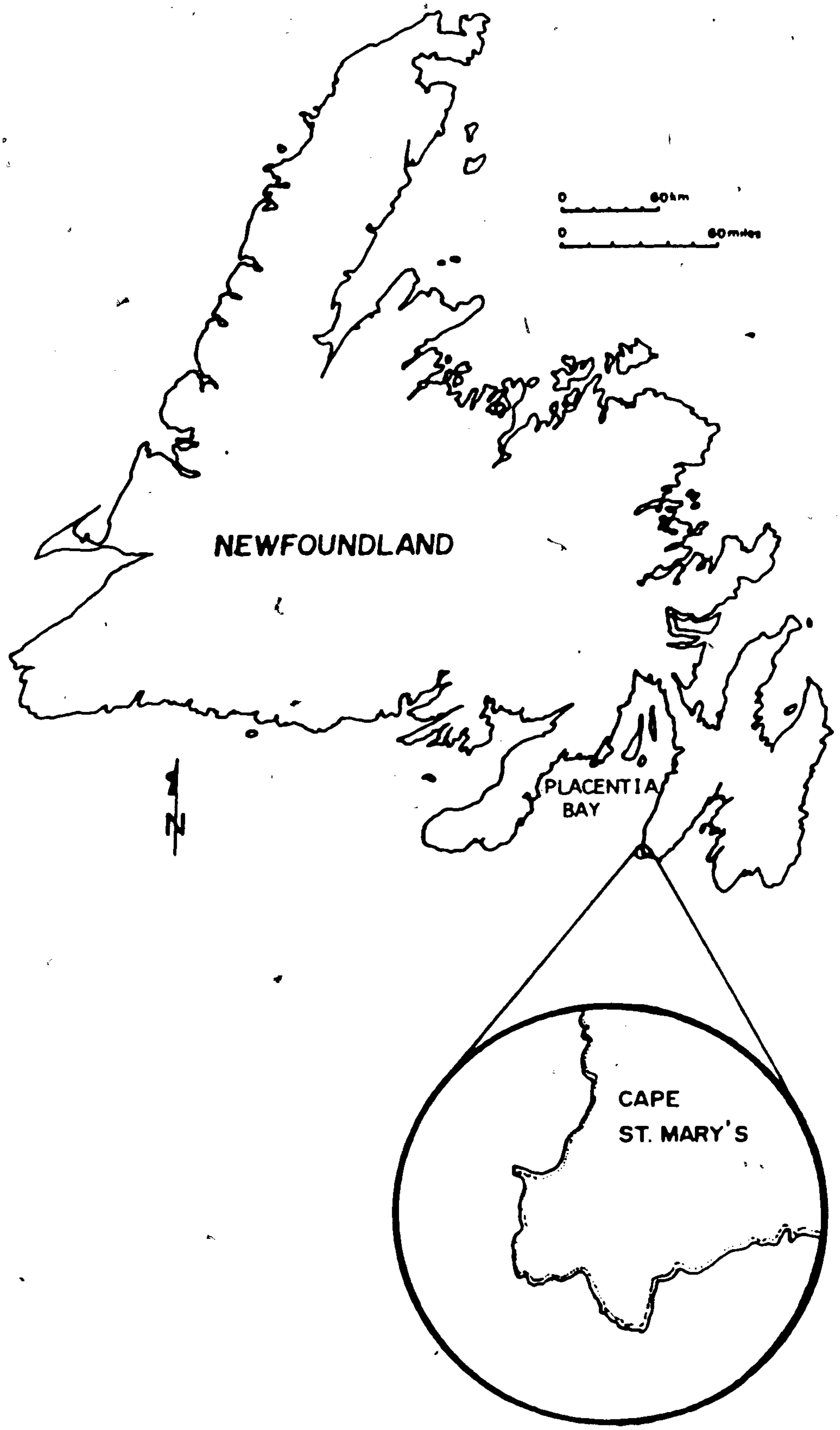
STUDY AREA

Cape St. Mary's Ecological Reserve is in southeastern Newfoundland, on the southwestern corner of the Avalon Peninsula (Fig. II-2). The reserve includes the coastline and inland subarctic barrens between Norther Head and Redland Point and extends offshore from 4.0 to 5.8 km. Its small coves and bays provide suitable wintering habitat for eiders, as well as other species of diving birds, including Black Scoter *Melanitta nigra*, Harlequin Duck *Histrionicus histrionicus*, Common Loon *Gavia immer*, Red-necked Grebe *Podiceps grisegena*, Great Cormorant *Phalacrocorax carbo* and Double-crested Cormorant *P. auritus*, Red-breasted Merganser *Mergus serrator*, and Black Guillemot *Cepphus grylle* (Goudie 1981, personal observation).

Cape St. Mary's falls into a climatic zone influenced by the offshore confluence of the cold Labrador Current and the warmer Gulf Stream. It is characterized by relatively mild winters with less than half of the precipitation falling as snow (Banfield 1983). Storms from more southerly latitudes are common and often bring freezing drizzle or freezing rain. Temperatures in January and February are usually sub-zero but wind chill can be extreme as a result of prevailing west to northwest winds at frequent high wind velocities that are amongst the highest observed anywhere in Canada (Banfield 1983). During winter, water down to depths of 100-200 metres is almost isothermal at $^{-}1$ to $^{-}1.5$ °C (Steele 1983). In April and May, sea surface temperatures reach 2-3 °C (Banfield 1983).

The terrestrial and marine topography of Cape St. Mary's contribute to the suitability of the area as a wintering ground for diving ducks. Steep cliffs rise 350 feet above sea level, preventing human disturbance and hunting except at a few sites. Hunting is prohibited within the reserve but some illegal activity occurs, especially by boat on rare days when the sea is calm. Numerous coves with various

Figure I-2. Location of Cape St. Mary's Ecological Reserve in southeastern Newfoundland.


0 60km
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N
PLACENTIA BAY
CAPE ST. MARY'S

directional exposures offer shelter from extreme winds. Heavy swells prevent the formation of landfast ice, and prevailing winds and currents rarely bring pack ice to this area (one in seven years according to local residents). Consequently, there is rarely sea ice to restrict feeding or damage intertidal fauna (Steele 1983).

There is a positive correlation between depth and distance from shore; eiders generally fed within 60 m of shore, adjacent to bedrock slabs and ledges (Ryan 1985, Goudie and Ankney 1986). The ledges provide intertidal habitat for blue mussels, chink shells and amphipods, as do numerous "sunkers", islets or rocks awash or submerged at high tides or during heavy sea swells. The gradual tapering of bedrock ledges into the water increases amplitude of onshore sea swells; the more tubulent conditions provide suitable habitat for mussels, since grinding and burial is reduced. The extreme wave exposure influences blue mussel size and distribution, partly by limiting the presence of their major predators, dog whelks (*Thais* and *Buccinum* spp.). With high wave energies, whelks tend to occur mainly in the shallow subtidal zone and in low numbers (Steele 1983) so that predation of mussels is uneven. During winter, the dog whelk (*Thais lapillus*) remains inactive in crevices or under large boulders (Steele 1983). On exposed shores, mussels occur in large numbers but are still of small to moderate size because once they grow large enough, the whole cluster becomes vulnerable to wave displacement. Bedrock ledges support extremely high densities of small mussels (< 20 mm). Water is shallow (< 3 m) up to 60 m off bedrock ledges and next to sunkers (Goudie and Ankney 1988). Water is considerably deeper off bedrock slabs (3-10 m up to 100 m from shore); mussels were generally scarce in such areas and eiders consumed predominantly sea urchins (Goudie and Ankney 1988). Tides are semi-diurnal and, thus, there are two high and two low amplitudes each lunar day (Steele 1983). The tidal range is relatively small at about 1 m. As a result, wave action is concentrated in a narrow vertical strip of coast.

OBJECTIVES

In this thesis I firstly investigate whether time required for physiological recovery from diving might influence the dive/pause relationship of foraging activity of Common Eiders at Cape. St. Mary's, Newfoundland. Secondly, I investigate whether variation in the dive/pause relationship is explained by a range of ecological factors. Finally, I present data on group foraging and suggest this may be the main determinant of dive and pause duration in this species.

The specific objectives of this thesis are:

1) To estimate the aerobic dive limit (ADL) of Common Eiders and to test the assumption that variation in pause duration involves delaying physiological recovery and incurring of a physiological debt.

2) To determine whether there are sex or age differences in diving performance.

3) To investigate adjustments in foraging effort, specifically pause duration between dives and rest bout duration between feed bouts, in response to ecological conditions:

i) time of day - Eiders may decrease pause and rest bout duration at dusk and dawn because they feed intensively before and after the overnight fast.

ii) tide level - Eiders may decrease pause and rest bout duration at low and falling tides to take advantage of decreased travel distance to bottom.

iii) time of season - Eiders may decrease pause and rest bout duration late in the season as prey depletion occurs.

iv) predation risk: Eiders may decrease pause duration at sites where predation is possible (i.e., at sites accessible by hunters) in order to shorten overall time spent inshore.

v) kleptoparasitism: Eiders may decrease pause duration in the presence of kleptoparasitic gulls. Common Eiders may choose smaller urchins which can be handled quickly and, in order to maintain energy intake, spend less time at the surface between dives. In addition, eiders may decrease rest bout duration when gulls are present as individuals choosing smaller urchins or losing urchins to gulls increase feeding time in order to maintain energy intake.

4) To consider the social aspects of eider foraging and whether they influence adjustments in dive and pause duration by individuals within a flock.

Chapter II

Aerobic Dive Limits: Do Common Eiders Incur Physiological Debt While Diving?

An understanding of the physiology of diving is essential to understanding an animal's diving and foraging performance and for predicting how dive and pause durations may be adjusted under different circumstances. Some studies have assumed physiological debt and/or delayed recovery from diving (Ydenberg and Forbes 1988; Ydenberg and Guillemette 1991). Such recovery may take two forms: i) restoration of oxygen stores and ii) metabolism of lactate, but the latter is only relevant when birds exceed their aerobic dive limit (ADL) and enter anaerobic metabolism. Before such assumptions regarding accummulated debt or delayed recovery are made, physiological flexibility or constraint must first be demonstrated by determining such parameters as oxygen stores, rate of underwater oxygen consumption, and rate at which oxygen is replenished while above water. I had four objectives in this chapter, i) to review the research on the physiology of diving in birds, ii) to describe data used to estimate oxygen stores and utilization, especially in diving ducks, iii) to use these data to estimate ADL for Common Eider, and iv) to compare the estimated ADL to empirical dive durations obtained for this species at Cape St. Mary's, Newfoundland in order to determine whether eiders incur physiological debt during foraging. Because estimation of ADL depends on several assumptions of oxygen stores and consumption rate, I discuss in detail how these estimates are derived.

DEVELOPMENT OF DIVING PHYSIOLOGY RESEARCH

Foraging by any animal usually involves some method of locomotion and an increase in energy expenditure over resting levels but diving poses particular challenges not encountered by terrestrial foragers. Air-breathing species that forage underwater (hereafter divers) must cease breathing while underwater and therefore cannot obtain oxygen during a dive. Most diving birds are positively buoyant and must counteract the upward force of buoyancy while traveling through a liquid medium much denser than air. Thermoregulation may also be a problem in cold water where heat loss is greater than in air, and at increasing depth where compression forces air out of plumage and decreases its insulating capacity. Ice cover may impose increased travel distances to food sources. Locating patchy or pelagic prey may require extensive search time. Any of these factors may result in a diving animal being underwater for longer periods than can be sustained by its oxygen stores. During a prolonged dive, an animal may have to enter anaerobic metabolism. Given these unique challenges, diving is an intriguing system for examining the decisions made by foragers to meet their energy requirements.

The difficulties involved in studying diving performance of free-living animals initially limited the discipline to species which were easily handled in the laboratory, such as the Tufted Duck *Aythya fuligula* (Butler and Woakes 1979) or domestic Mallard *Anas platyrhynchos* (Folkow *et al.* 1967) or animals whose habitat allowed semi-laboratory conditions to be constructed in the field, such as the Weddell Seal *Leptonychotes weddelli* which dives under Antarctic ice and returns to a breathing hole (Kooyman *et al.* 1973). Technological advances in both laboratory and field, such as the use of depth recorders and capillary recording devices, have increased the diversity of species studied and the level of detail involved in diving physiology studies. Nevertheless, it is still a developing field with many gaps and I rely heavily on several key studies to describe the basic physiology of diving in birds and to estimate physiological parameters for Common Eiders.

Early diving physiology studies in the 1930's and 40's, and even as late as the 80's, involved forced submersion of restrained birds and mammals (Irving 1934; Scholander 1940; Scholander *et al.* 1942, Eliassen 1960; Millard *et al.* 1973; Hudson and Jones 1986). Some of these experiments included animals such as the domestic mallard whose wild counterpart does not dive to appreciable depths but just submerges its upper half for brief periods, i.e., dabbles (Folkow *et al.* 1967). The 'classic' dive response observed under these conditions included a reduction in heart rate (bradycardia; Butler and Woakes 1979), redistribution of blood flow to most tissues except the heart and central nervous system, and a decrease in aerobic metabolism (Kooyman 1989). These general responses during diving allow the bird to conserve oxygen and remain underwater for much longer periods than would otherwise be possible if the animal maintained a normal (surface) metabolism. Any tissues receiving inadequate blood flow, and therefore oxygen supply, produce lactic acid when they enter anaerobic metabolism. When the bird surfaces, lactic acid is flushed into the blood and it may take up to six times the forced dive duration for lactic acid concentrations to return to pre-dive levels (Butler and Jones 1982). These early studies suggested that diving was a very costly activity, and historically, it was assumed that the surface pause following a dive was obligatory, allowing for restoration of oxygen stores, metabolism of lactic acid in muscles, and regeneration of body heat (Eliassen 1960; MacArthur 1984). However, these involuntary dives occurred under unnatural, stressful conditions and for durations rarely exhibited by the same species in the wild. By the 1970's, it had been recognized that most voluntary dives in birds did not involve the same extreme responses as did forced submersions (Murrish 1970; Millard *et al.* 1973; Butler and Woakes 1979).

Our knowledge of diving physiology in birds comes from studies of three main groups: penguins (Family Spheniscidae), alcids (Family Alcidae) and ducks (Family Anatidae). These groups exhibit major differences in flight ability, mode of underwater locomotion, and foraging method, and any adaptations associated with these specific characteristics affect diving performance and physiology. Penguins are flightless, heavy-bodied birds who propel themselves underwater using only their flipper-like wings. They are the most specialized of diving birds, with spindle-shaped bodies, scale-like feathers and solid bones (Kooyman and Ponganis 1990). Consequently, penguins are close to neutral buoyancy and have low drag coefficients when underwater (Baudinette and Gill 1985; Bannasch 1995). Their large bodies may aid in thermoregulation through a reduced surface-to-volume ratio and may allow higher mass-specific oxygen storage. Maximum diving depths and durations of penguins vary allometrically with body mass (Burger 1991; Schreer and Kovacs 1997). Most penguins feed on pelagic prey such as Antarctic Krill *Euphausia superba* which show diel migration through the water column. Alcids are often described as smaller, Northern Hemisphere counterparts to penguins. They use wing propulsion underwater to search for fish and crustaceans but have retained the ability to fly. They have the highest wing-loading of any bird (Greenwalt 1962) and are constrained from reducing wing size or increasing body size. Since oxygen stores scale isometrically to body mass$^{1.0}$ (Kooyman *et al.* 1983; Butler 1989) and metabolic rate scales allometrically as body mass$^{0.75}$ (Kleiber 1961; Peters 1983), alcids as a group have a decreased ability to dive aerobically for long periods compared to penguins (Croll *et al.* 1992), i.e., they have greater metabolic demands per unit mass. However, the largest alcids, the Common Murre *Uria aalge* and Thick-billed Murre *U. lomvia*, can attain depths which match or surpass those of some penguins (Piatt and Nettleship 1985; Burger 1991). In diving ducks, underwater locomotion generally involves the feet only, although some birds such as Common Eiders *Somateria mollissima* (Humphrey 1958) and Surf Scoters *Melanitta perspicillata* (Humphrey 1957) also use partially-opened wings and Oldsquaws *Clangula hyemalis* are solely wing-propelled (Snell 1985). Ducks are relatively buoyant and have high drag coefficients (Lovvorn *et al.* 1991; Stephenson 1994). They generally feed on benthic or epibenthic prey such as molluscs, crabs and amphipods, and do not dive as deeply as alcids or penguins. However, birds in all these groups routinely dive to depths far less than their maximum recorded depth.

During voluntary feeding dives in laboratories or in nature, most birds show cardiovascular responses that are intermediate between responses to forced submersion and to exercise in air (Millard *et al.* 1973; Butler 1982; Woakes and Butler 1983). The following sections consider these physiological responses - heart rate, blood flow, oxygen consumption - and other components such as respiratory frequency and oxygen storage which affect a diving animal's breath-holding ability. In the final sections, I use these parameters to calculate an aerobic dive limit for Common Eiders and compare this estimate to observed dive durations.

PHYSIOLOGICAL RESPONSES TO DIVING

Heart rate

Eliassen (1960) studied cardiovascular responses during forced dives by Common Eiders and observed a 54% drop in heart rate. Most later studies of physiology in diving ducks have focused on Tufted Ducks and Pochards (*Aythya ferina*), both bottom-feeding, foot-propelled divers. In ducks, heart rate during natural dives is usually above that seen during resting (Woakes and Butler 1983, Stephenson *et al.* 1986; Furilla and Jones 1987; Bevan and Butler 1992; de Leeuw 1997) and well above that recorded during forced submersion (Butler and Woakes 1979) but below that seen during maximum sustainable swimming (Woakes and Butler 1983; Bevan and Butler 1992). In a typical feeding dive by Pochards, heart rate increased from swimming levels of 160 beats/min to 341 beats/min just before the dive and then decreased immediately after submergence to level off at 125 beats/min after 6-8 seconds. Heart rate then remained steady at this level until it rose slightly to 212 beats/min just a second or two before emerging. During the pause, heart rate declined steadily until it suddenly rose again preceding the next dive (suggesting anticipation of the dive). Increase in heart rate just before emergence indicates anticipation of surfacing, and probably facilitates quick renewal of oxygen stores during a surface interval. In Pochards and Tufted Ducks, and presumably other diving ducks, such as the Common Eider, which ascend passively through positive buoyancy this increase in heart rate is not as great as in penguins and occurs about one second before resurfacing (Butler and Woakes 1979; Stephenson *et al.* 1986; Bevan and Butler 1992; de Leeuw 1997). Thus, in general, ducks exhibit bradycardia during dives and tachycardia between dives.

Early studies found little change in heart rate between diving and resting activities of Adelie Penguins *Pygoscelis adeliae*, Gentoo Penguins *Pygoscelis papua* and Humboldt Penguins *Spheniscus humboldti papua* (Millard *et al.* 1973; Butler and Woakes 1984). However, birds in these studies were diving under somewhat unnatural conditions and the observed dives were much shorter and less deep than those commonly recorded for these species in the wild. In contrast, heart rate in Gentoo Penguins swimming in a water channel increased from 144 beats/min at rest to 177 beats/min while underwater (Bevan *et al.* 1995). In a more realistic study, Kooyman *et al.* (1992a) recorded heart rates of Emperor penguins *Aptenodytes forsteri* free-diving from an ice hole to depths of 19-37 m and durations of 3-4 minutes. Heart rate quickly decreased during a dive from 72 beats/min (resting on ice; range 56-80) to 63 beats/min (range 60-65) during diving. Heart rate was described as increasing to over 100 beats/min "upon surfacing". The interdive tachycardia (increased heart rate) was manitained until the penguin dove again, whereupon, heart rate fell. Average heart rate during diving was 15% below the average of the lowest resting values (Kooyman *et al.* 1992a). Results from the above studies are contradictory but the most realistic experiment (emperor penguins diving from an ice hole) suggested that penguins diving in the wild experienced a decrease in heart rate, although not to the low levels recorded during involuntary submergence (Scholander et al. 1942; Kooyman 1989).

Little work has been done on cardiovascular adjustments to diving in alcids. Eliassen (1960) forcibly submerged several species of alcids and recorded average declines of 48-61% in heart rate of Common Murres, Black Guillemots *Cepphus grylle*, Atlantic Puffin *Fratercula arctica* and Razorbills *Alca torda*. Rhinoceros Auklets *Cerorhinca monocerata* also showed a dramatic decrease in heart rate when forcibly submerged (Stephenson *et al.* 1992), however, auklets diving voluntarily showed no change in heart rate from predive levels.

Blood flow

During forced submersion of birds, there is selective vasoconstriction and redistribution of blood flow with a reduction in blood flow to tissues that can withstand short-term oxygen shortage, such as visceral organs and inactive skeletal muscle, but maintenance of constant blood flow to the brain and heart (Butler 1982 and references therein). During natural dives, there is similar redistribution of blood, and blood flow may even increase to exercising skeletal muscle. For example, in the foot-propelled Tufted Duck, blood flow to the legs during diving or swimming increased by three to five times over resting levels (Bevan and Butler 1992; Butler *et al.* 1988). Rates of blood flow to legs were similar during each type of exercise, despite a lower cardiac output during diving, indicating that more extensive peripheral vasoconstriction took place when ducks were underwater. Blood flow to the brain increased while flow to the mainly inactive pectoral muscles decreased. In contrast to the Tufted Duck, in wing-propelled Adelie and Gentoo penguins, there was a decline in blood flow to leg muscles (Millard *et al.* 1973).

Decreased blood flow to the intestine during diving has implications for foraging in Common Eiders as it would presumably inhibit nutrient uptake. Eiders feeding on whole mussels and urchins crush their prey in a muscular gizzard, although it is not known whether they mechanically process prey while feeding or only while resting (Guillemette 1994). It is possible that prey are held in the esophagus for the duration of the foraging bout or are moved through the gullet to sit in the intestinal tract until digestion is resumed during a subsequent rest period. Eiders collected prior to a feed bout have empty espohagii (Guillemette 1994; R.I. Goudie, pers. comm.); this may be necessary before ingesting another meal. Guillemette (1994) used average meal size, feed and rest bout duration and transit time (time interval from ingestion to defecation of a prey item; 63.3 ± 7.2 min; Swennen 1976) of eiders feeding on mussels to estimate ingestion and digestion rates. He estimated gizzard working capacity was a minimum of 2.4 g/min if mussels were crushed during the feed bout or a maximum of 6.1 g/min if no processing occurred until the rest bout, and that the gizzard must be filled and emptied about four times to process an average-sized meal of 80g (50.7 g of shells). Guillemette (1994) concluded that digestion rate constrains energy assimilation in eiders. The extent to which energy assimilation is affected by reduced blood flow to the viscera during diving is unclear but it is probably less than the constraint of mechanical processing.

Oxygen consumption and respiratory frequency

Oxygen consumption during diving may be measured using one of three major methods: i) respirometry, which provides a direct measurement of oxygen uptake, ii) doubly labelled water and iii) heart rate. The latter two are indirect, providing a measurement of metabolic rate (which is proportional or related to oxygen consumption). In open- or closed-circuit respirometry, a bird surfaces into a chamber where gas exchange is measured by a fast-responding mass spectrometer (Woakes and Butler 1983; Bevan and Butler 1992; Castellini *et al.* 1992; Stephenson 1995; Culik *et al.* 1996). Mean oxygen consumption during mean dive durations is taken from a multiple regression analysis between dive time, succeeding surface time and oxygen uptake during surface interval. Unfortunately, respirometry is only feasible for a few species - those which can be handled in a laboratory setting (where diving depth is limited by tank size) or those such as penguins and seals which return to a specific breathing hole in ice. For all other species diving in their natural habitats, oxygen consumption must be measured indirectly. The doubly labelled water method invloves injection of an animal with water containing enriched levels of stable or radioactive isotopes of hydrogen and oxygen (Nagy 1989). Upon recapture of the animal, the concentrations of the oxygen and hydrogen isotopes (which decline over time) can be converted to oxygen consumption (Bevan *et al.* 1994; Bevan *et al.* 1995; Boyd *et al.* 1995a). This technique gives an average value for energy expenditure between initial capture (and injection) and recapture. Consequently, it is difficult to measure the metabolic costs of specific activities such as diving. However, it does provide estimates of field metabolic rate (FMR) of animals in their natural environment and validation studies have shown it to be accurate within ±7% (Nagy 1989). A relatively new method involves monitoring heart rate with implanted transmitters (Woakes and Butler 1983; Butler *et al.* 1992). The relationship between heart rate and oxygen uptake is first determined in a laboratory setting (Nolet *et al.* 1992) and the resulting regression equation is used along with heart rate data obtained in the field to determine field oxygen consumption. The accuracy of this technique is comparable to that of respirometry or doubly labelled water (Bevan *et al.* 1994; Bevan *et al.* 1995; Boyd *et al.* 1995a). Furthermore, it has the advantages of providing a detailed analysis of energetic costs of specific behaviours and, especially when a data-logging system is used, offering long-term monitoring (i.e., months) of energy expenditure.

Aerobic dive limit is dependent on the rate of oxygen consumption during diving, which is a function of metabolic rate. Since metabolic rate during diving is rarely known, many studies assume diving costs as a multiple of basal, standard or resting metabolic rate (BMR, SMR, RMR). Basal metabolic rate is the minimal rate of heat production occurring in inactive, fasting adults in their thermoneutral zone (Kleiber 1961; Peters 1983). The terms standard and resting metabolic rates are used to indicate low, but not necessarily minimal rates of respiration recorded under standardized conditions. Estimating metabolic rate is key to estimating oxygen use, and the multiplication factor used to determine diving costs can have a substantial effect on the estimate of ADL.

Diving ducks have several mechanisms to conserve oxygen while underwater (as described above), however, they are still exercising intensively while diving and this is reflected in oxygen consumption rates that are generally higher than surface resting rates. Oxygen consumption has been measured in several species of diving ducks. At mean dive duration by Tufted Ducks, mean oxygen consumption (0.566 ± 0.05 ml O_2/sec) was 3.5 times resting levels (0.163 ± 0.006 ml O_2/sec; Woakes and Butler 1983). For the same species, Bevan *et al.* (1992) estimated diving oxygen consumption (0.400 ± 0.032 ml O_2/sec) as 2.3 times resting levels (0.175 ± 0.019 ml O_2/sec). In Lesser Scaup *Aythya affinis* mean diving rate of oxygen consumption (0.862 ± 0.066 ml O_2/sec) was 3.6 times resting consumption (0.236 ± 0.008 ml O_2/sec; Stephenson 1994).

The flightlessness of penguins has evolved toward relatively heavy bodies with low buoyancy and small flipper-like wings, which make swimming at the surface relatively more costly than swimming underwater. Diving costs for large King Penguins *Aptenodytes patagonicus* have been estimated as 2.1 x RMR (Culik *et al.* 1996) and field metabolic rate (FMR; which encompasses all at-sea activity, including swimming above and below the surface) as 4.3 or 4.6 x SMR (Kooyman et al. 1992b). Estimates of diving costs for other penguins ranged from 1.3 x RMR for Humboldt Penguins (Butler and Woakes 1984), 2.9-4.3 x RMR for Adelie, Gentoo and Chinstrap Penguins (Culik *et al.* 1994), 6 x BMR for Adelie Penguins (Chappell *et al.* 1993), and 6 x RMR for Jackass Penguins *Spheniscus demersus* (Nagy *et al.* 1984). Although alcids probably have higher buoyancy than penguins (Sanford and Harris 1967, Stephenson *et al.* 1992), they may have lower diving costs than some species of penguins. In Common and Thick-billed Murres *Uria lomvia* in a laboratory setting, diving costs were 1.8 and 2.5 x RMR, respectively (Croll and McLaren 1993).

Oxygen consumption may be influenced by temperature of air and water and, hence, environmental conditions should be considered when estimating diving costs. Although Common Eiders have evolved a low thermal conductance, metabolic rate of winter-acclimatized eiders resting on water increased with decreasing air or water temperature (Jenssen *et al.* 1989). This will be an important consideration for estimates of ADL for eiders at Cape St. Mary's since water temperature in winter is approximately -1°C, much lower than in many experimental studies, and air temperature may be as low as -12°C. However, an increase in *resting metabolic rate* of winter-acclimatized birds does not imply a similar increase in *diving metabolic rate* (Bevan and Butler 1992). Diving behaviour and mean oxygen consumption for dives of mean duration were similar in Tufted Ducks diving at winter (air: 6°C; water: 7°C) and summer temperatures (air: 26°C; water: 2°C) (Bevan and Butler 1992). When simply resting on cold water, oxygen consumption was 90% higher in winter temperatures but during surface intervals between dives, oxygen consumption was only 50% greater at winter temperatures. Core body temperature at the end of a dive series was 1°C lower in winter and, therefore, Bevan and Butler (1992) concluded that Tufted Ducks allow body temperature to fall while diving in cold water rather than increase metabolic rate to maintain body heat at the expense of oxygen stores. Heat produced by active leg muscles may contribute to thermoregulation and partially compensate for heat loss in cold water (conductivity of water is 25 times greater than that of air). Similarly, De Leeuw (1996) found no significant relationship between water temperature and metabolic rate during diving by Tufted Ducks. He concluded that thermoregulatory costs of underwater activity were largely paid after a series of dives when Tufted Ducks rested and digested Zebra Mussels *Dreissena polymorpha*. Common Eiders also use heat generated from digestion of Blue Mussels *Mytilus edulis* for thermoregulation (Nehls 1995) and probably, like Tufted Ducks, delay recovery from body cooling from diving until they begin a rest bout. Thus, when estimating *diving costs* for Common Eider, adjustments for low winter temperatures should be made when calculating resting metabolic rate. The multiplication factor used to derive diving costs need not be adjusted further.

Although sample size in most diving physiology experiments has been limited to six or seven birds (Woakes and Butler 1983; Stephenson *et al.* 1989; Bevan and Butler 1992; Bevan *et al.* 1992; Stephenson 1994), several studies have documented individual variation in oxygen consumption during diving and pausing. Mean oxygen consumption during diving in the Tufted Duck ranged from 0.38 to 0.68 ml/sec (Woakes and Butler 1983) in six individuals whose mean diving duration varied between 9 and 22 seconds. For each duck, oxygen consumption was closely related to dive duration. In contrast, Stephenson (1994) found that resting rate of oxygen consumption varied little within and between six Lesser Scaup, but that the ratio of diving oxygen consumption to resting oxygen consumption varied from 3.2 to 4.5 among individuals. Although Bevan and Butler (1992) do not report individual values for oxygen consumption in six Tufted Ducks, they do give a range for diving heart rate as 143 to 167 beats/min at winter temperatures, and heart rate has been shown to be a good indicator of oxygen consumption in this species (Bevan *et al.* 1992). These studies suggest that individuals can significantly differ in their capacity or strategy of oxygen regulation, or in their total oxygen stores.

Birds hyperventilate before and after a dive; this may fully load oxygen stores by increasing oxygen tension in the air sacs and in the venous blood (Butler and Woakes 1979). Penguins probably dive after inspiration (Kooyman *et al.* 1971) but most diving ducks dive upon expiration (Butler and Woakes 1979), probably to reduce buoyancy. When resting or swimming vigorously, Pochards breathe at rates of 17 and 27 breaths/min, respectively (Butler and Woakes 1979). Before the first dive in a series, respiratory frequency of Pochards increased up to 48 breaths/minute just before submerging. Respiratory frequency was high upon resurfacing, about 39 breaths/min but decreased steadily, although it did not usually reach resting levels before it rose again in anticipation of the next dive. Consequently, for the second or subsequent dives in a series, the respiratory frequency was at even higher levels, for example, up to 56 breaths/min one second before dives. Tufted Ducks showed a very similar pattern. The only significant difference was a higher respiratory frequency by Tufted Ducks in the last second before the first dive of a series (Butler and Woakes 1979). Respiratory frequency upon surfacing was similar in both species. Breathing rates may give some indication of the amount of time required to replenish oxygen stores (Butler 1982; Kooyman *et al.* 1980) and will be discussed more later in reference to tissue oxygenation.

Oxygen stores

In birds, oxygen is stored in three major body tissues: lungs, blood and muscle (Kooyman 1989, Stephenson *et al.* 1989). However, not all of this stored oxygen is available to a bird during a dive; the proportion which is actually usable determines the aerobic dive limit. The respiratory system of birds consists of lungs and air sacs. Air sacs are poorly vascularized and cannot be considered a primary respiratory organ (Welty 1982) but the air contained in the sacs provides buoyancy and this may be why penguins, which are close to neutral buoyancy, have a larger proportion of air stored in the air sacs when compared to ducks. It is assumed that birds use at least some of the oxygen in their lungs while underwater, although the mechanism by which they do so is not well understood. However, because air in the lungs is comprised of about 79% nitrogen, nitrogen is also taken up from the lungs into the blood along with oxygen (Williams 1995). This may be a problem for deep divers like Emperor or King Penguins which dive to 200 m or more (Kooyman 1989) because it could cause direct narcotic effects as well as decompression sickness or "the bends" as a bird ascends and nitrogen expands to form bubbles in the blood (Kooyman and Ponganis 1990). Thus, a conflict arises because the bird should maximize blood flow to the lungs in order to maximize oxygen uptake but, on the other hand, should minimize blood flow to lungs to minimize uptake of nitrogen. Kooyman and Ponganis (1990) suggested that penguins reduce nitrogen problems by reducing the exchange of gas between the respiratory and circulatory systems at depths greater than 100 m. Only 2% of cardiac output could exchange freely with lung and air sac gases to maintain blood nitrogen below that which caused bubble formation. In Adelie and Gentoo Penguins forced to dive to simulated depths of 68 m (Kooyman *et al.* 1973), high blood nitrogen tensions existed only briefly and appeared to pose no danger to the birds. For the depths at which most free-ranging penguins dive, the amount of nitrogen uptake that may occur does not seem to be a problem. Therefore, it seems likely that for ducks such as the Common Eider which routinely dive to depths less than 20 m, nitrogen uptake is not a concern.

The amount of oxygen in the blood depends on hematocrit (the percentage of blood volume comprised of red blood cells), hemoglobin concentration and blood volume. Flying birds generally have high oxygen carrying capacity, whether they dive or not, and there is little difference in hematocrit and hemoglobin concentrations between diving and non-diving birds (Bond and Gilbert 1958; Balasch et al. 1974). The few data available for blood volume indicate more variation among species. Adelie Penguins and terrestrial Rock Doves (domestic pigeons) *Columba livia* have similar blood volumes (9.3% of body mass; Kooyman 1989) but both have less than Thick-billed Murres (12.3%; Croll *et al.* 1992) or Redthroated Loons *Gavia stellata* (13.2%; Bond and Gilbert 1958). Tufted Ducks had 25% greater blood volume than Mallards *Anas platyrhynchos*, and dive-trained Tufted Ducks which had to dive farther and deeper for food had greater blood volume than control ducks (Stephenson *et al.* 1989). Among a variety of diving ducks, there was little difference in blood parameters related to oxygen-carrying capacity (Table II-1) and Common Eider blood indices are expected to be similar to these.

The importance of myoglobin in muscles as an oxygen store is apparent in the increased concentrations of this pigment in relation to diving performance among species. For example, aquatic birds have myoglobin concentrations 10-30 times higher than terrestrial birds (Kooyman 1989) and, among diving birds, pectoral muscles of alcids such as Common and Thick-billed Murres and Atlantic Puffins *Fratercula arctica* have one-third to one-half the amount found in Little Penguins *Eudyptula minor* and Adelie Penguins (Davis and Guderly 1987, Croll *et al.* 1992). Among penguins, species which dive deepest have the highest myoglobin content of the penguin group (Kooyman 1989). Tufted Ducks forced to dive for longer durations to reach food had higher myoglobin concentrations in the pectoralis and leg muscles than control ducks (Stephenson *et al.* 1989).

Table II-2 provides mean values of respiratory, circulatory and muscle variables for several diving bird species. Estimates of total usable oxygen stores vary from 58 ml O_2 /kg in the King Penguin (Kooyman 1989) to 45 ml O_2 /kg in Thick-billed Murres (Croll *et al.* 1992) and 42 ml O_2 /kg in the Tufted Duck (Keijer and Butler 1982). Dive-trained Tufted Ducks which had to dive farther and deeper for food had similar total usable oxygen stores to control ducks, although the two groups differed in the relative quantities of oxygen in each storage site (Stephenson *et al.* 1989).

Costs of locomotion

Recent studies have focused on the mechanics of underwater locomotion in ducks (Lovvorn *et al.* 1991; Wilson *et al.* 1992; Stephenson 1994; Stephenson 1995) and highlighted the importance of buoyancy to the energetic costs of diving in ducks. Factors affecting buoyancy such as respiratory and plumage air volumes should therefore be considered in calculating dive costs, especially since small changes in air volume have large effects on buoyancy (Lovvorn 1991). Since the respiratory system can contribute as much as 52% of initial buoyancy (Stephenson 1995), ducks may be able to influence diving costs by reducing buoyancy through exhaling before diving. Loons and grebes which can submerge until only the head or bill show above the water (Cramp and Simmons 1977) must be actively controlling buoyancy. Active regulation of the respiratory volume is indicated by lower end expiratory volume in Tufted Ducks trained to dive longer distances for food (Stephenson *et al.* 1989). Flattening of feathers (ptilosuppression) could also decrease plumage air volume (Lovvorn and Jones 1991a), however,

Table II-1. Oxygen carrying parameters of the blood in diving ducks.

Species	Hc[a]	Hb[b]	RBC[c]	PCV[d]	MCV[e]	Reference
Pochard	43.7	14.6	3.25		134.3	Balasch *et al.* 1974
Tufted Duck (control)	43.1	15.6	2.38		182.8	Stephenson *et al.* 1989
Tufted Duck (dive-trained)	45.3	15.5	2.17		209.7	Stephenson *et al.* 1989
Lesser Scaup			2.45	57.1		Kocan 1972
Lesser Scaup *	45.8	16.0	5.0		99.7	M. Pokras, pers. comm.
Ring-necked Duck			2.50	49.1		Kocan 1972
Bufflehead			2.64	54.3		Kocan 1972
Redhead *	44.4		3.2		140	M. Pokras, pers. comm.
Canvasback			2.56	52.2		Kocan 1972
Canvasback *	46.1	15.6	3.2		144	M. Pokras, pers. comm.
Redhead and Canvasback	37	18.0	3.2			Bond and Gilbert 1958
Ruddy Duck *	46.2	13.9	2.9		159	M. Pokras, pers. comm.

[a] Hematocrit, %

[b] Hemoglobin, g/100ml

[c] Red blood cell count, x 10^6

[d] Packed cell volume, %

[e] Mean corpuscular volume, u^3

* captive zoo population

Table II-2. Mean values of blood, muscle and respiratory variables related to oxygen storage capacity for selected diving birds (adapted from Kooyman 1989, with additions).

Species	Hct[a]	Hb[b]	Blood O^{2}[c]	Blood vol.[d]	Mb[e]	Resp. vol.[f]	References
Ducks							
Tufted Duck	43.1	15.6	20.9	107 ml/kg	0.73	180	Stephenson *et al.* 1989
	48.8	18.4	24.6	114 ml/kg	5.5		Keijer and Butler 1982
	45.9						Woakes and Butler 1986
Penguins							
Adelie Penguin	46.2	16.5	22.4 ml/100g	9.3	3.0	165	Kooyman 1989
	49	17.5		12.3			Chappell *et al.* 1993
Chinstrap Penguin	52.8	19.6	26.3				Kooyman et al. 1989
Gentoo Penguin	43.4	16.4			4.4		Kooyman 1989
Little Blue Penguin	40	18	24.6		2.8		Kooyman 1989
Emperor Penguin	47.0	16.9	23.1		4.3		Kooyman 1989
King Penguin	53	19.8	26.2		4.3		Kooyman 1989
Alcids							
Thick-billed Murre	52.8	18.0		12.3	1.9		Croll et al. 1992
Common Murre					1.4		Davis and Guderly 1987
Atlantic Puffin					1.3		Davis and Guderly 1987
Rhinoceros Auklet	37.0						Stephenson *et al.* 1992

[a] Hematocrit, %
[b] Hemoglobin, g/100 ml
[c] Blood oxygen capacity, ml O_2/100 ml, except where otherwise specified
[d] Blood volume, % of body mass, except where otherwise specified
[e] Myoglobin, g/100g
[f] Respiratory volume, ml/kg

- changes in body composition, such as lipid reserves, in ducks (*Aythya* spp.) had negligible effects on overall dive costs (Lovvorn and Jones 1991b).

Buoyancy has been estimated in several species by the volumetric displacement method which involves immersing restrained birds or cadavers and calculating buoyancy as a function of water mass displaced (Lovvorn *et al.* 1991; Wilson *et al.* 1992). Water displacement experiments showed that Common Eiders had higher buoyancies (Lovvorn and Jones 1991a) and faced greater upthrust force (Wilson *et al.* 1992) when underwater than smaller diving ducks. However, values generated from restrained or dead birds may not be applicable to wild birds. Stephenson (1994) monitored air pressure changes to indirectly measure buoyancy at the start and end of a dive in freely diving Lesser Scaup. This technique yielded a significantly higher buoyancy at the start of a dive than that measured by the volumetric displacement method and demonstrated that plumage air volume can decrease by as much as 32% over the course of a dive as air escapes from the plumage under hydrostatic pressure. Because plumage air volume influences buoyancy and, therefore, energetic costs of diving, compression of the air spaces in the plumage can lead to decreased energetic costs as the dive progresses or depth increases. Indeed, a few studies have documented a negative relationship between mean dive duration and mean oxygen consumption (Woakes and Butler 1983, Bevan *et al.* 1992). Air lost from the plumage during a dive is probably replaced immediately upon resurfacing (Stephenson 1995).

Because of the relationship between depth and plumage air volume, buoyancy has a greater effect on the locomotor costs of shallow divers than deep divers (Lovvorn and Jones 1991b). Although Common Eiders can dive to depths of 42 m (Guillemette *et al.* 1993) where buoyancy must be greatly reduced (Lovvorn and Jones 1991b), they prefer depths of 3-12 m (Nilsson 1970, Player 1971, Ryan 1985, Goudie and Ankney 1988, Guillemette *et al.* 1993, Brager *et al.* 1995). In shallow water, Common Eiders ascending passively without use of the wings (Tinbergen 1958, Humphrey 1958) have obviously not become negatively buoyant. Therefore, it is probably safe to assume that i) diving costs of eiders do not decrease dramatically over the course of a shallow dive, and ii) diving costs measured in other ducks in laboratory settings are relevant to shallow-diving eiders.

Aerobic dive limit

Diving animals only incur physiological debt when dive duration extends beyond the capacity of body oxygen stores, resulting in anaerobic metabolism. This process produces lactic acid (lactate) which must be metabolized later at the surface. In terms of a diving bird's physiology, then, the surface interval has two functions: i) tissue reoxygenation, and ii) metabolism of lactate. Kooyman *et al.* (1983) first coined the term aerobic dive limit (ADL) to describe "the maximum breath-hold that is possible without any increase in lactic acid concentration during or after the dive". These authors monitored lactic acid levels in the blood of immature Weddell Seals and, from a graph of post-dive lactate concentration in relation to dive duration, they designated the ADL as the dive duration at which post-dive lactate levels rose above resting levels. Any dives of shorter duration were considered completely aerobic. Although no studies have monitored post-dive lactate concentration in any other free-diving species, many authors have calculated ADL for diving birds and mammals using the following formula:

$$\text{ADL} = \frac{\text{available oxygen stores (i.e., usable oxygen in blood, lungs \& air sacs, muscle)}}{\text{oxygen consumption rate during dive}}$$

However, the values used in this formula are rarely measured and the precision of calculated ADL can vary widely because of the numerous assumptions involved in estimating the various parameters (see below). They particularly depend on estimates of metabolic rate which, as discussed earlier, vary widely between species and among techniques. Even when oxygen stores are measured, the amount of oxygen actually available to an animal during a dive is rarely known.

Tissue oxygenation

Even for dives within ADL, birds must replenish oxygen stores upon surfacing through hyperventilation, vasodilation and tachycardia. Oxygen uptake at the surface slows over time as partial pressures decline and rate of oxygen gain is decreased by lower diffusion rates (Kramer 1988). Consequently, there is diminishing oxygen return as surface time increases past a certain point and the optimal oxygen store may not be the maximum (Kramer 1988). Generalized oxygen gain curves have been used in several modelling exercises (Kramer 1988; Houston and Carbone 1992) but empirical data are not available for time required to replenish oxygen stores in birds (de Leeuw, pers. comm.). Several authors merely state that oxygen stores are recharged "quickly" or "over several breaths" (Culik *et al.* 1996; Kooyman *et al.* 1980). Rapid reloading of oxygen stores is indicated by the brevity of pauses recorded for several species of birds. Wanless *et al.* (1988) reported that Common Murres, Razorbills and Atlantic Puffins all preformed dives in quick succession with short pauses. In one dramatic example, a puffin made 194 dives in 84 minutes with a median pause time of only 3 seconds. It is unlikely that an oxygen debt was carried for such an extended period. It is presumed that hyperpnoea (hyperventilation) lasts as long as is needed after aerobic dives to replace the oxygen stores (Butler 1980; Kooyman *et al.* 1980). As discussed earlier, mean respiratory frequency in Pochards and Tufted Ducks was initially high after surfacing from a voluntary dive of 8-9 second duration (Butler and Woakes 1979). It then declined steadily during the surface interval and increased again just a second before the next dive. From a graph of mean respiratory frequency in Pochards, it appears that a minimum of about 24 breaths/min was reached at 10 seconds after surfacing (Butler and Woakes 1979). This may indicate the point at which oxygen stores are replenished. For unrestrained Lesser Scaup diving for a mean duration of 12 seconds, about 20 seconds at the surface was required for full equilibration of the respiratory system and a return to normal blood gas tensions (Stephenson 1995). Even after forced submersions of 2 minutes, blood gas tensions returned to normal within 20 seconds of surfacing (ref). Restoring oxygen in muscles probably requires additional time beyond respiratory equilibration but this has not been confirmed. The above suggests that the surface interval required to replenish oxygen stores after an aerobic dive is probably less than 10 seconds.

It is possible that handling prey during a surface interval affects the rate at which a bird is able to recharge its oxygen stores. Manipulating and eating food has an energetic cost in itself; the average incremental cost of manipulating and ingesting food in birds is about 11% above that of perching (Robbins 1993). Eiders handling urchins at the surface were moving their heads and necks and appeared to be exercising more strenuously than when pausing (personal observation). Guillemette *et al.* (1992) estimated handling costs for an eider as 23.1 J/sec as opposed to 21 J/sec for pausing. Birds handling prey can probably breathe while they handle urchins with their bills but some of the oxygen being taken up at the surface is, presumably, used to support this activity and, therefore, birds engaged in handling may not be replenishing oxygen as fast as a diver which merely sits during a pause. However, given the widely accepted notion that diving birds reload oxygen stores within seconds of surfacing, the degree to which replenishment may be slowed by handling is not likely to greatly extend the surface interval. At most, handling time may be added to pause time to give an upper estimate for surface interval after dives within ADL.

Anaerobic metabolism

Some birds dive for durations much longer than calculated ADL and undoubtedly use anaerobic metabolism (Ydenberg and Forbes 1988; Croll *et al.* 1992). Although anaerobiosis is energetically expensive, i.e., 18 mol of glucose is expended to yield 36 mol of ATP, the same amount of ATP can be generated aerobically with only 1 mol of glucose (Ydenberg and Clark 1989), it may be the only solution if obtaining more oxygen is even more costly or is impossible. Anaerobic metabolism produces lactic acid in muscles as a by-product. Lactic acid must be metabolized before it accumulates to a threshold which incapacitates locomotory muscles through muscle fatigue. Processing lactate requires more time than simply loading oxygen-carrying pigments so exceptionally long surface times often follow dives or forced submersions which exceed ADL (Butler and Jones 1982; Castellini *et al.* 1988). The only freely-diving animal in which post-dive blood lactate has been monitored, however, is the Weddell Seal (Kooyman *et al.* 1980; Kooyman *et al.* 1983; Castellini *et al.* 1988). When Weddell Seals dived for durations twice that of ADL of 26 minutes, lactic acid levels in the blood only returned to normal levels after 40 minutes of recovery, whereas seals typically surfaced for about 5 minutes after an aerobic dive (Kooyman *et al.* 1980). Castellini *et al.* (1988) suggested that short dives after exceptionally long dives may function as recovery periods since lactate concentration declined as rapidly during subsequent short dives as if the seal remained on the surface. However, this happened only rarely; usually, seals performed no dives immediately after one which exceeded ADL. Kooyman *et al.* (1992) also speculated that King Penguins were metabolizing lactate while diving when long periods of shallow dives occurred between deep, long dives. If Common Eiders incur physiological "debt" and delay recovery to maximize foraging time, it would be predicted that this would involve recovery from anaerobic metabolism when a bird exceeds ADL, and not simply replenishment of oxygen stores.

COMMON EIDER - LOCOMOTION, OXYGEN CONSUMPTION, ADL

There is little published on the underwater movements of Common Eiders, although most authors describe them as mainly foot-propelled but also employing partially-opened wings for underwater locomotion (Humphrey 1958; Tinbergen 1958; Lovvorn 1991). A detailed description of the diving of a captive eider is provided by Humphrey (1958). To submerge, a female eider leapt forward, pulling itself under with the wings (wing-lunge) while thrusting with the feet. She descended by flapping the half-open wings and alternately stroking the feet. This is in contrast to most diving birds which use synchronous stroking when underwater and use alternate stroking of the feet when swimming (Lovvorn 1991). When travelling along the bottom, the eider used only its feet and held the wings half-open and motionless, apparently to act as hydroplanes and counteract the bird's buoyancy. It ascended passively through positive buoyancy, again with wings held slightly away from the body and motionless.

Alternate stroking of the feet by eiders probably involves less acceleration, less inertial work and lower body drag costs than sychronous stroking (Lovvorn 1991). However, it is possible that pitching and yawing which may occur from alternate stroking increase hydrodynamic drag and offset these benefits (Lovvorn 1991). In addition, the use of wings may reduce inertial work and be more efficient than foot propulsion alone (Lovvorn 1991). Thus, it appears possible that Common Eiders have lower locomotory costs, and hence lower diving costs, than other diving birds, but resolving this question requires more biomechanical data than is available. It may be that eiders need to use their wings in addition to foot propulsion as an aid in diving partly to counteract the lower efficiency of small paddles. Raikow (1973) developed a paddle index as a ratio of foot surface area to body weight for several species of dabbling and diving ducks. Three eider species (Spectacled *Somateria fischeri*, King *S. spectabilis* and Common Eiders) had paddle indices which were lowest among the diving ducks measured and more comparable to those of dabbling ducks.

Although an aerobic dive limit has not been measured in the Common Eider, ADL can be estimated using values for oxygen stores and diving oxygen consumption measured in other diving birds. As described above, estimated ADL will depend on a) total body oxygen stores available and b) rate of utilization of these oxygen stores which, in turn, will be directly related to metabolic rate (oxygen consumption rate). The amount of oxygen available for use during a dive may be calculated using the following assumptions (Kooyman 1989; Stephenson *et al.* 1989; Croll *et al.* 1992, and refs. therein):

1) all birds hyperventilate before voluntary dives; ducks dive on expiration, penguins, on inspiration
2) the oxygen concentration in the anterior and posterior air sacs is 16% and 19.5%, respectively
3) posterior air sacs represent 45% of total respiratory volume
4) mean oxygen concentration in the respiratory system before diving is 17.6%
5) Up to 75% of oxygen in respiratory system is available during the dive
6) oxygen-binding capacity of hemoglobin is similar to that measured in the Black-headed Gull, *Larus ridibundus* and the Rock Dove *Columba livia*: 1.2 ml O_2/g pigment
7) oxygen-binding capacity of myoglobin is 1.24 ml O_2/g pigment
8) blood volume is 70% venous, 30% arterial
9) arterial blood is 98% saturated and venous blood, 70%
10) up to 96% of oxygen in blood is available for use during a dive
11) concentration of myoglobin (5.5g/g muscle in Tufted Ducks) is similar in all muscle tissues
12) skeletal muscle is 25% of total body mass

Oxygen stores in Lesser Scaup (42 ml O_2/kg, Stephenson 1994) and Tufted Duck (43 ml O_2/kg, Keijer and Butler 1982; Stephenson *et al.* 1989) were similar to levels estimated in Adelie Penguins (43 ml O_2/kg; Lenfant *et al.* 1969) and Gentoo Penguins (46 ml O_2/kg; Kooyman *et al.* 1973). Given that mass-specific oxygen stores are so similar between these species, and that body oxygen stores are directly related to body mass ($M^{1.0}$, Kooyman and Kooyman 1995), I can reasonably assume Common Eiders have oxygen stores similar to the above birds. However, the diving ducks used in the aforementioned studies were restrained physically or pharmacologically (with anesthesia). Stephenson (1995) showed that these methods underestimate respiratory volume, which represents up to 64% of total oxygen stores. Thus, he concluded that the total oxygen stores of unrestrained Lesser Scaup were 57.7 ml O_2/kg. As shown in Table II-1, most diving ducks have similar blood parameters and, therefore, most likely have similar blood oxygen stores, which further supports the assumption that eiders have similar mass-specific oxygen storage capacity as Tufted Ducks and Lesser Scaup. Thus, using an average weight of 1.865 kg for adult male and female eiders at Cape St. Mary's (R.I. Goudie, unpubl. data) and an estimate of total body oxygen stores of 57.7 ml O_2/kg, I calculated total oxygen stores for Common Eiders as 107.6 ml O_2.

Diving oxygen consumption rates are available for several duck species: Lesser Scaup, (Stephenson 1994) 3.6 x basal metabolic rate (BMR), Tufted Duck, 2.3 x BMR (Bevan *et al.* 1992) and 3.5 x BMR

(Woakes and Butler 1983). Metabolic rate scales as body mass$^{0.75}$ (Kleiber 1961; Peters 1983) and diving costs appear to be inversely related to body mass within other groups of diving birds (Cooper 1986). For example, among alcids of the *Uria* genus, for example, heavier Common Murres (0.836 kg) exhibited a diving metabolic rate 1.8 times resting metabolic rate (RMR) while smaller Thick-billed Murres (0.803 kg) showed an increase of 2.4 x RMR (Croll and McLaren 1993). Common Eiders are 2.3-3.3 times heavier than Lesser Scaup or Tufted Ducks. In addition, unlike most other diving ducks, eiders stroke their feet alternately and use their wings while underwater, which may incur lower drag costs than synchronous stroking (Lovvorn 1991). Even considering that eiders may be more buoyant than Lesser Scaup or Tufted Ducks, eiders probably have lower diving costs than these species and I used an estimate of 2.5 x BMR for eider diving costs. Heat production in winter-acclimatized eiders resting on water below thermoneutrality (lower critical temperature in water = 15 °C) can be determined by the equation H_{BMR} (W/kg) = 5.48 - $0.09T_w$, where T_w = water temperature in °C (Jenssen *et al.* 1989). At Cape St. Mary's, water temperature in winter is approximately -1° C, and resting costs were, therefore, 5.57 W/kg. Using a multiplication factor of 2.5 x BMR, eider diving costs were calculated to be 13.93 W/kg. For an eider weighing 1.865 kg, diving would cost 25.98 W. The equivalent of 1 W is 0.05 ml O_2/sec (Peters 1983); thus, diving by eiders requires 1.30 ml O_2/sec.

Therefore, an eider with total body oxygen stores of 107.6 ml O_2 and using oxygen at a rate of 1.30 O_2/sec while underwater, would have an aerobic dive limit of 83 seconds. Individual variation, e.g., in body mass, may result in higher or lower ADL for some birds, but this difference is not expected to be large. Given the assumptions necessary to calculate this theoretical ADL, it is an estimate but, nonetheless, a conservative one. If, for example, large body mass of an eider (> 3 times as large as a Tufted Duck) conferred even more of an advantage to eiders than I have allowed, and/or I used the lowest dive costs measured for Tufted Ducks (2.3 x BMR; Bevan *et al.* 1992) as a reference point, then metabolic costs of diving for eiders may be as low as 1.5 x BMR. This would give an ADL of 138 seconds. If, on the other hand, buoyancy or method of propulsion of eiders led to higher diving costs than for Tufted Ducks, i.e., 3.5 x BMR, ADL would be 60 seconds.

COMPARISON OF ADL AND DIVING DURATION

As shown in Figure II-1, only 1.4% of dive durations by eiders at Cape St. Mary's were above the estimated ADL of 83 seconds, assuming diving costs of 2.5 x BMR. Such a small proportion suggests that my ADL calculation is not an underestimate. More than 90% of dives were less than 70 seconds and 83% were less than 60 seconds which could indicate I have overestimated ADL. A plot of dive duration versus pause duration (Fig. II-2) provides some insight into the range of true ADL. While some birds may be expected to pause at times for longer than necessary after dives of a given duration, the lowest points on the graph should indicate the minimum time needed to replenish oxygen stores and/or

Figure II-1. Frequency distribution of dive duration by Common Eiders.

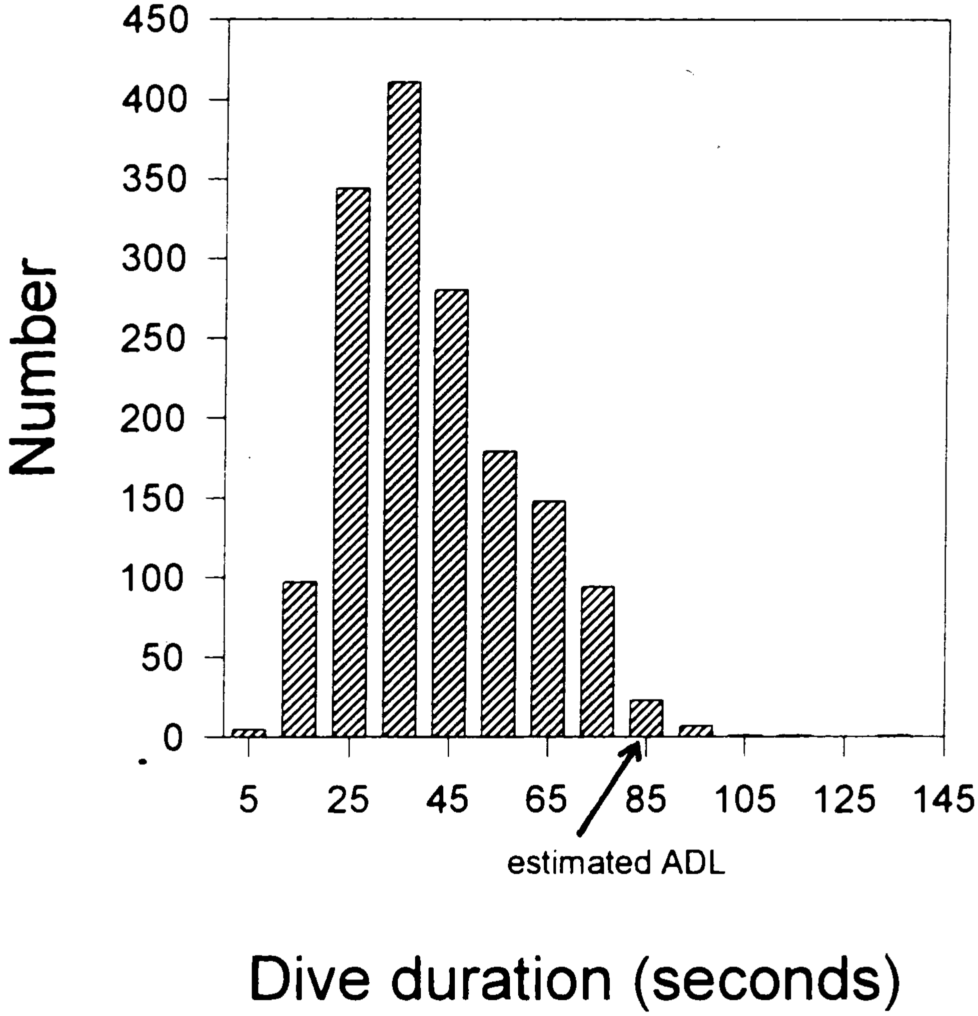
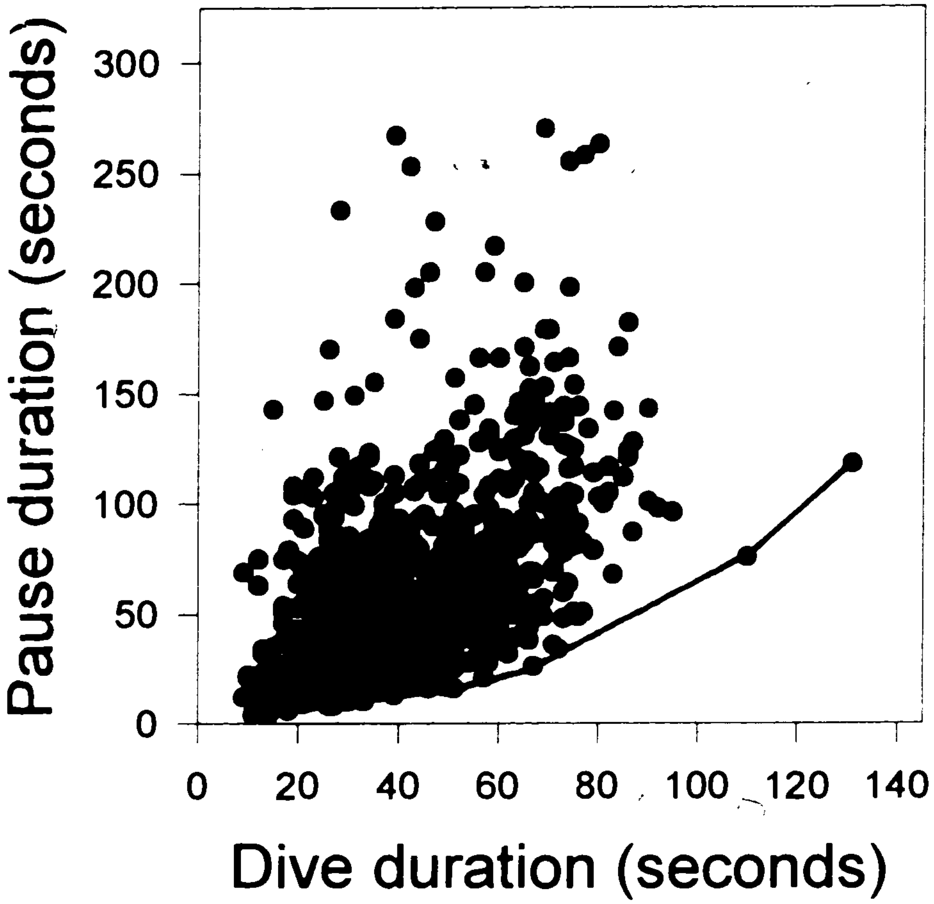

450
400
350
300
250
200
150
100
50
0
Number
5
25
45
65
85
105
125
145
estimated ADL
Dive duration (seconds)

Figure II-2. Relationship between dive and pause duration of Common Eiders. The line joining the lowest points on the graph indicates a possible minimum duration needed for oxygen replenishment.


Pause duration (seconds)
300
250
200
150
100
50
0
0
20
40
60
80
100
120
140
Dive duration (seconds)

metabolize lactate (Kooyman and Kooyman 1995). Pause duration increased with dive duration and appeared to increase at a slightly steeper slope when dive duration was about 70 seconds, suggesting perhaps that longer recovery is required at this point. However, given that I assumed similar oxygen stores as smaller diving ducks, and lowered diving costs by a conservative margin, overestimation of ADL by almost 20 seconds is not likely. Furthermore, many eiders dived for durations of 60-70 seconds in several consecutive dives without lengthy pauses at the surface, and it seems unlikely that all these individuals were routinely surpassing ADL. For example, Figure II-3 illustrates a series of dives and pauses by an adult female eider. She performed the longest dive of 131 seconds, after which she paused for no longer than she had after previous shorter dives. She then surpassed the ADL a second time during the same feed bout. Successive dives and pauses by an adult male are shown in Figure II-4. Although all dives by this male were less than 50 seconds, he paused at the surface for a few extended intervals. It is doubtful that pauses of this duration were required for physiological recovery after 40-second dives, especially given that birds can sustain such underwater times for an extended period. For example, an immature male (Figure II-5) dove for an average of 45 seconds for 27 consecutive dives separated by a mean pause duration of 48 seconds. Eiders which exceeded ADL varied in sex and age, and included 8 males (4 adults, 4 immatures) and 5 females (2 adults, 3 unknown age). Of the 22 dives which exceeded ADL, only 14 could be identified as prey type and these were all urchin dives; half of these urchin dives were successful.

Dive durations at this site were greater than reported elsewhere. For example, Eliassen (1960) reported mean dive duration of eiders in Norway as 30 seconds and maximum observed dive as 90 seconds. Gulf of St. Lawrence eiders dived longest when feeding on crabs but the average was still only 35.0 ± 9.3 seconds (Guillemette *et al.* 1992) with the longest dives recorded as 72 sec (Ydenberg and Guillemette 1991). In the Wadden Sea, almost all dives by eiders were less than 40 seconds and none was higher than 53 seconds (Nehls 1995).

Thus, it appears that eiders at Cape St. Mary's usually dived well within their ADL. This is not an unexpected result, since it is widely accepted that most voluntary dives by birds in the wild are for durations that are shorter than calculated ADL (Butler 1988, Butler 1989, Jones 1990, Wilson 1990) as demonstrated for the following species: Atlantic Puffins, Common Murres and Razorbills (Wanless *et al.* 1988), Japanese cormorants *Phalcrocorax capillatus* (Watanuki *et al.* 1996), Pied Shags *Phalacrocorax v. varius* and White-throated Shags *P. melanoleucus brevirostris* (Stonehouse 1967) Although ADL was not calculated for Surf Scoters or Barrow's Goldeneyes *Bucephala islandica* (Beauchamp 1992), the majority of dives were less than 35 and 25 seconds, respectively and, thus, below calculated ADL of 51 seconds for the much smaller Tufted Duck (Woakes and Butler 1983). In diving mammals, too, typical

Figure II-3. Sequential dive and pause durations by adult female Common Eider #571.

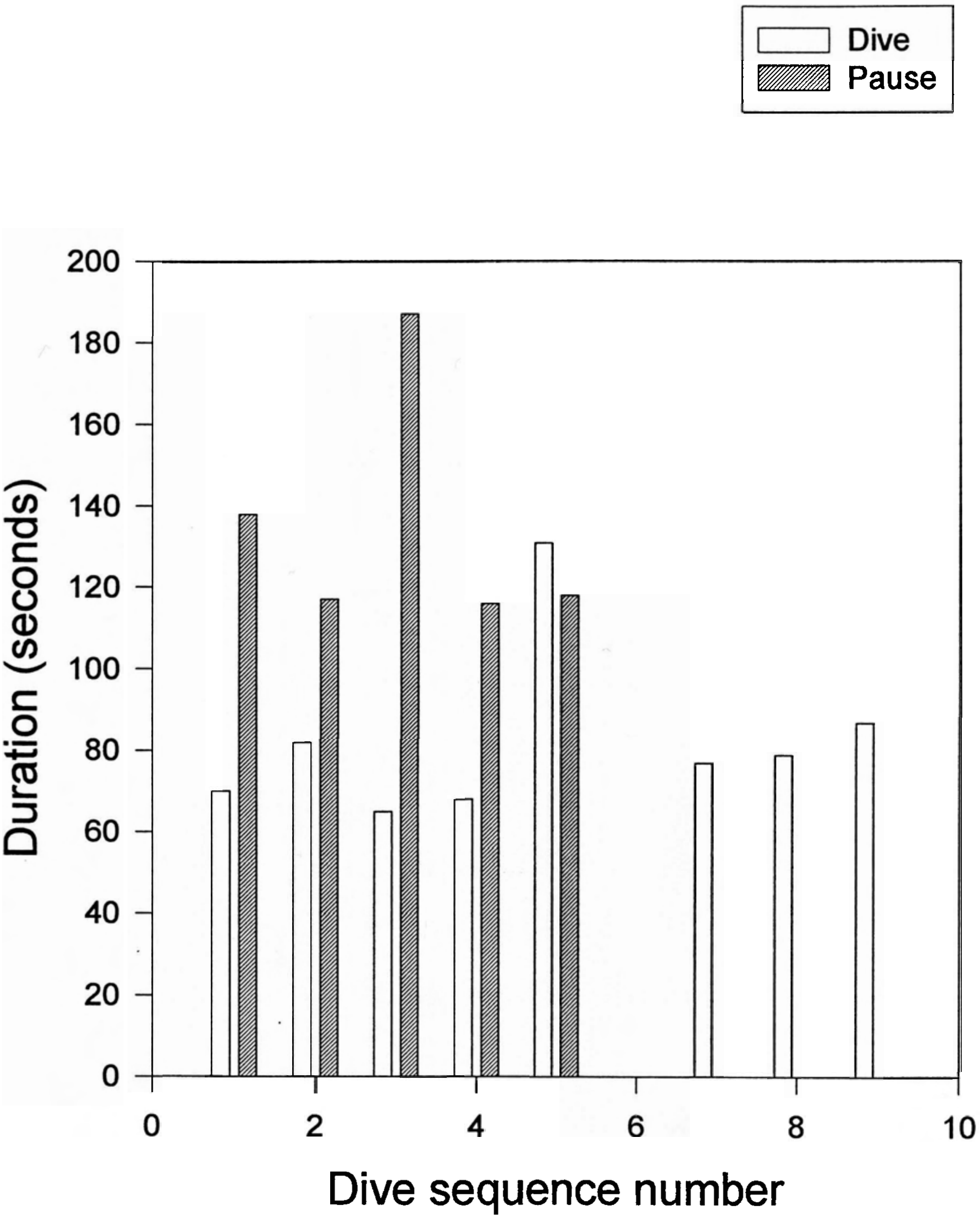

Dive
Pause
Duration (seconds)
200
180
160
140
120
100
80
60
40
20
0
0
2
4
6
8
10
Dive sequence number

Figure II-4. Sequential dive and pause durations by adult male Common Eider #233.

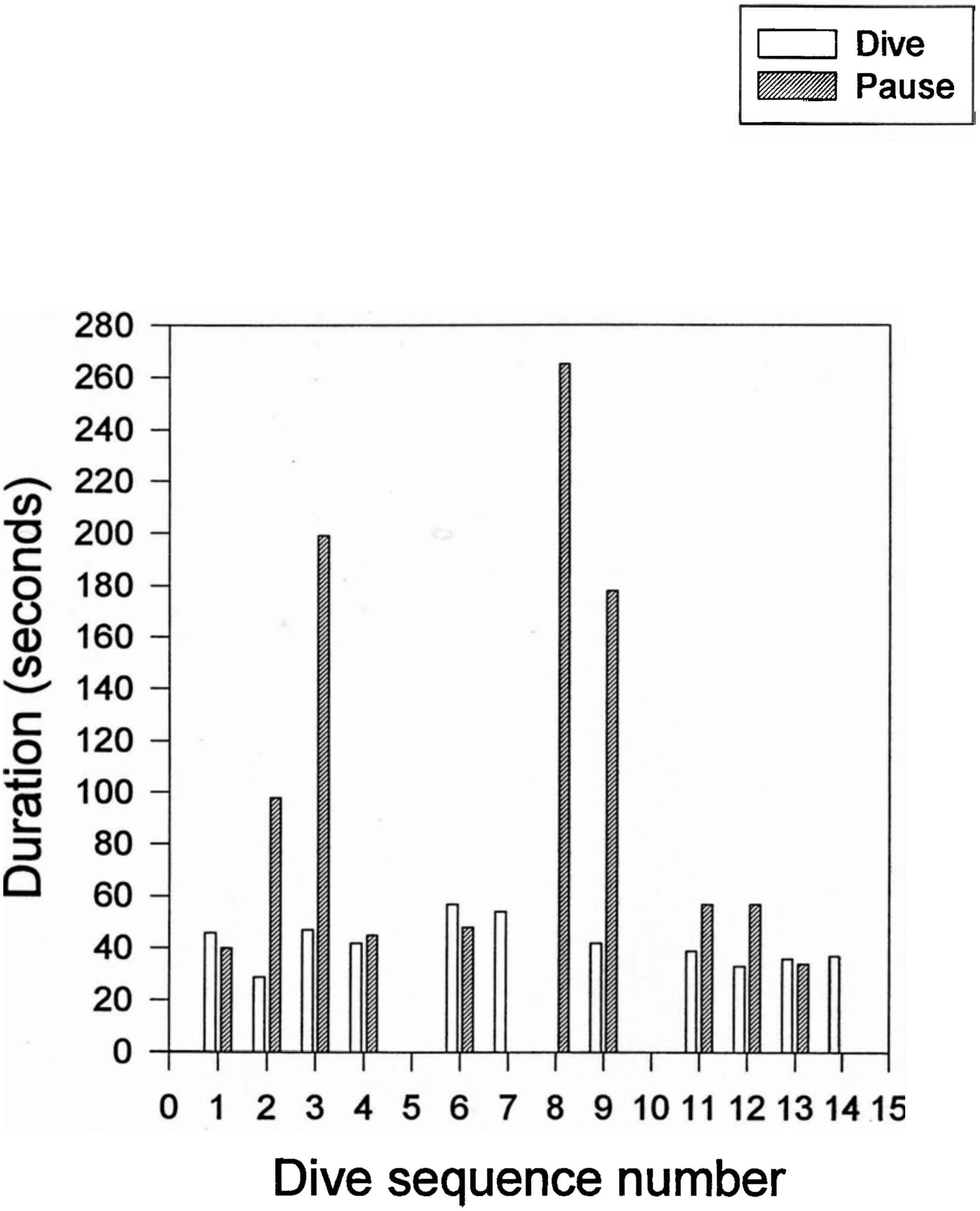
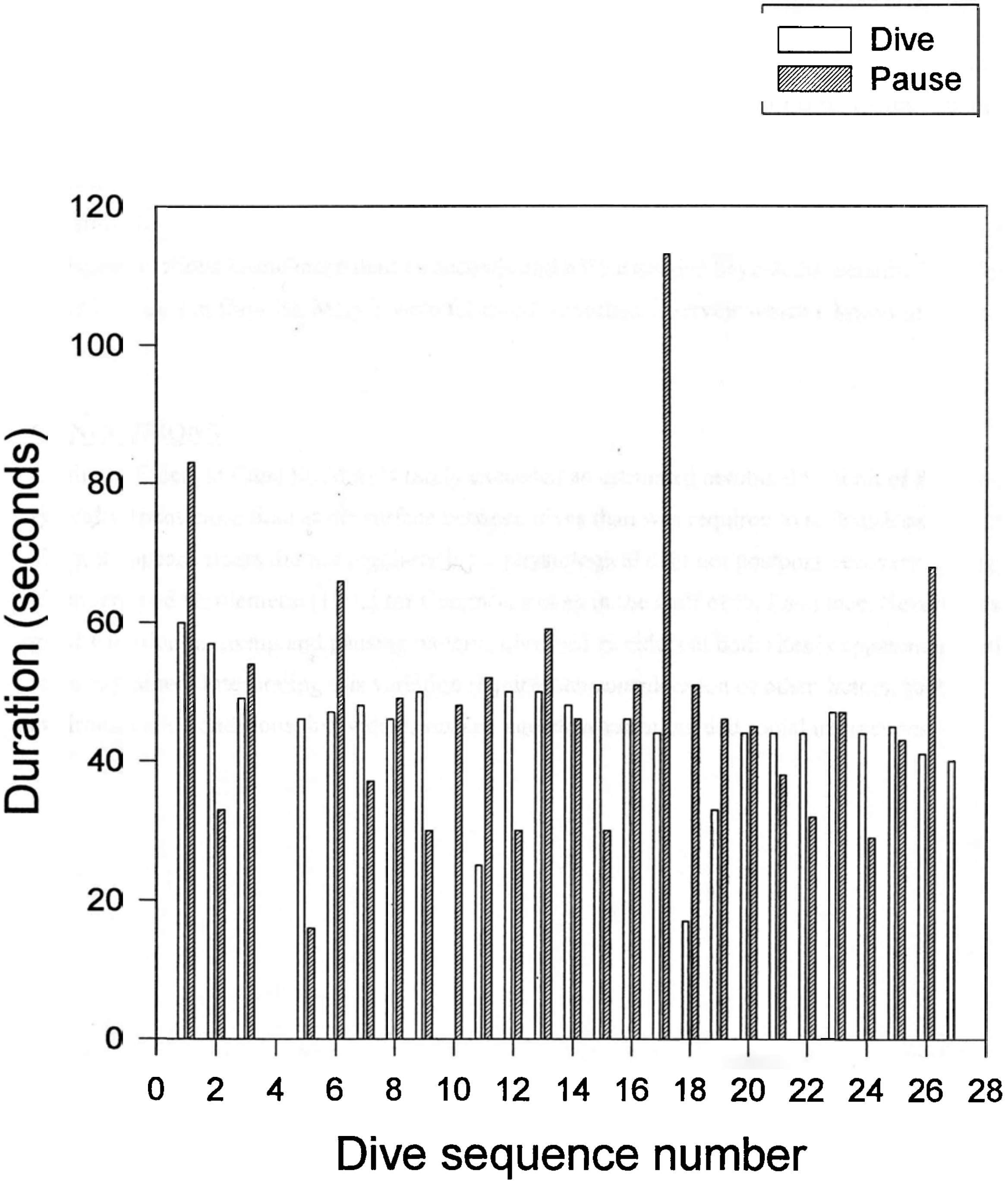

Dive
Pause
Duration (seconds)
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
Dive sequence number

Figure II-5. Sequential dive and pause durations by immature male Common Eider #564.


Dive
Pause
Duration (seconds)
0
20
40
60
80
100
120
Dive sequence number
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28

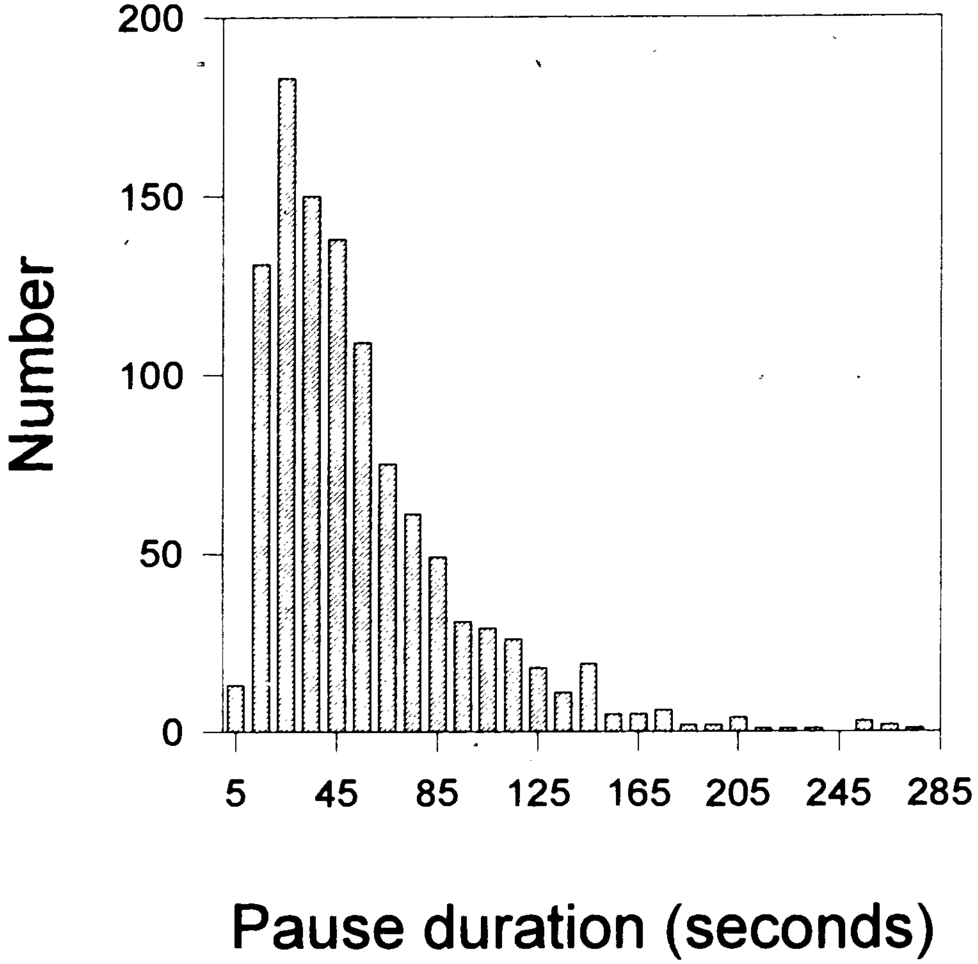
dive durations are moderate in relation to their ability: Humpback Whales *Megaptera novaeangliae* (Dolphin 1987), Weddell Seals (Kooyman *et al.* 1980), Ringed Seals *Phoca hispida* (Kelly and Wartzok 1996), Antarctic Fur Seals *Arctocephalus gazella* (Boyd *et al.* 1995b), various fur seal and sea lion species (Kooyman 1989) and Otters *Lutra lutra* (Nolet *et al.* 1993) usually dive within their maximum aerobic limits.

If Common Eiders do not routinely exceed ADL, then they do not generally incur physiological debt (in terms of increased blood lactate), and recovery during the pause phase of the dive cycle should involve no more than reloading of oxygen stores. Although the amount of time required for oxygen replenishment has not been measured in diving animals, it is probably less than 10 seconds and, almost certainly, less than 20 seconds. A frequency distribution of pause duration (Figure II-6) shows that 99% of pause durations lasted more than 10 seconds and 85% extended beyond 20 seconds. Therefore, most dives by eiders at Cape St. Mary's were followed by surface intervals which allowed full oxygen recovery.

CONCLUSIONS

Common Eiders at Cape St. Mary's rarely exceeded an estimated aerobic dive limit of 83 seconds and typically spent more time at the surface between dives than was required to replenish oxygen stores. Thus, it appears eiders did not regularly incur physiological debt nor postpone recovery, as suggested by Ydenberg and Guillemette (1991) for Common Eiders in the Gulf of St. Lawrence. Nevertheless, the great variation in diving and pausing patterns observed in eiders at both sites is apparent and still needs to be explained. Interpreting this variation requires the consideration of other factors, such as environmental conditions, individual, sex and age class variation, and social interactions.

Figure II-6. Frequency distribution of pause duration by Common Eiders.


200
150
100
50
0
Number
5
45
85
125
165
205
245
285
Pause duration (seconds)

Chapter III
Diving and Foraging Patterns in Wintering Common Eiders

INTRODUCTION

Diving has historically been considered a costly foraging method and time spent at the surface between dives as necessary recovery time (MacArthur 1984). While numerous studies of diving vertebrates have noted a positive relationship between dive and subsequent pause duration at the surface (Stonehouse 1967; Cooper 1986; Nolet *et al.* 1993), most voluntary dives by free-living birds are probably aerobic in nature (Butler 1989; Jones 1990; Wilson 1990) and recovery simply involves replenishment of oxygen stores. After a completely aerobic dive, no extra time is required to restore blood and muscle lactic acid levels to pre-dive concentrations (Kooyman and Davis 1987). In Chapter II, I showed that wintering Common Eiders *Somateria mollissima* typically dive well within a theoretical aerobic dive limit (ADL) of 83 seconds. Nevertheless, whether physiological debt is incurred or not, it is clear that Common Eiders (Ydenberg and Guillemette 1991; this study), as well as other species of diving birds, show marked variation in dive and pause duration.

Size differences related to age and sex may result in some variation in diving performance, since maximum dive depth and duration are related to body mass (Butler and Jones 1982; Burger 1991; Wilson 1991; Kelly and Wartzok 1996; Schreer and Kovacs 1997). Sexual differences in diving behaviour have been reported in several species. For example, in Japanese Cormorants *Phalcrocorax capillatus* (Watanuki *et al.* 1996) and South Georgian Shags *P. georgianus* (Wanless *et al.* 1995), larger males dive for longer than females. Dive duration and depth increases with age in Elephant (Le Boeuf *et al.* 1996) and Weddell Seals (Kooyman *et al.* 1983). Greater body size of adult males compared to females (seven percent difference; R.I. Goudie, unpubl. data) or of adult Common Eiders compared to immatures (three percent difference between adult and immature males; nine percent for females; R.I. Goudie, unpubl. data) may allow increased dive duration or decreased pause duration in these cohorts.

Some of the observed variability in diving patterns may be understood through re-examination of basic assumptions of diving research. Throughout the literature concerning diving vertebrates, pause duration is considered to be determined by the dive which immediately preceded it. However, Kramer (1988) put forth an optimal breathing model based on diminishing oxygen return at the surface which suggested that divers should load oxygen at the surface to maximize underwater time in an upcoming dive. Lea *et al.* (1996) tested this model in several species of cormorants (*Phalcrocorax* spp.) and used the terms "reactive" breathers to describe those which showed a greater correlation between surface interval and preceding dive and "anticipatory" breathers for those in which the correlation was stronger with the following dive. Whether a species exhibited one or both breathing patterns appeared to be a function of prey type and foraging style. Common Eiders feeding on Green Sea Urchins *Stronglyocentrotus droebachiensis* and returning to the surface with each one are clearly not maximizing bottom time and may be functioning as reactive breathers. However, one might expect Common Eiders swallowing multiple Blue Mussels *Mytilus edulis* underwater to extend bottom time as this would allow a greater number of mussels to be gathered per dive. A Common Eider may be better able to predict the duration of an upcoming dive when consuming mussels than when searching for a single urchin. Therefore, an eider may switch to anticipatory breathing when feeding on mussels.

Several recent studies of diving birds have suggested that dive and pause duration may be influenced by ecological conditions such as food availability, as well as physiological factors. For example, the Western Grebe *Aechmophorus occidentalis* may spend very short periods at the surface between dives when in contact with a school of fish (Ydenberg and Forbes 1988), presumably to maximize capture of prey before the school disperses. In a year of low food abundance, Common Murres *Uria aalge* spent less time at the surface between dives than they did after dives of similar duration in a good food year (Monaghan *et al.* 1994).

Factors other than food availability, such as risk of starvation or predation, may effect changes in foraging behaviour of many avian species. Oystercatchers *Haematopus ostralegus* varied their intake rate in response to time stresses imposed by irregular tidal cycles (Swennen *et al.* 1989). Great Tits *Parus major* gained body mass when exposed to shortened or unpredictable daylength (Bednekoff and Krebs 1995) or cold overnight temperatures (Lilliendahl *et al.* 1996). In the cold, Redheads *Aythya americana* fed more and also minimized energy expenditure by foraging during low tides and in shallow water (Michot *et al.* 1994). Birds expecting negative energy budgets may engage in risk-prone behaviour. For example, Yellow-eyed Juncos *Junco phaeonotus* exposed to cold temperatures (Caraco *et al.* 1990) and underweight Common Eiders (Guillemette *et al.* 1992) may select prey or habitat types associated with a high variance of energy return. Birds may also adjust feeding behaviour in the presence of predators or kleptoparasites. Great Tits adjusted their body mass in association with changes in the population of their principal predator, the Sparrowhawk *Accipiter nisus*, increasing fat loads as Sparrowhawks decreased and decreasing fat as the predators became more common (Gosler *et al.* 1995). Surf Scoters *Melanitta perspicillata* swamped kleptoparasitic gulls by increasing diving and surfacing synchrony (Schenkveld and Ydenberg 1985).

In the present study, I examined the ecological factors that might affect the diving behaviour of wintering Common Eiders, which may be exposed to many of the above ecological circumstances and may react by adjusting foraging effort. Foraging adjustments may take place at one or both levels of foraging (as outlined in Ch. I): i) dive and pause duration during a feed bout and ii) overall feed bout duration and offshore rest bout duration. An eider's ability to modify dive and pause time will be limited to some degree by the consumption and replenishment of oxygen stores. As well, an eider may only be able to extend feed bouts or truncate rest bouts within bounds set by digestive processes. However, these physiological constraints do allow for some variation in bout duration, as documented in previous studies of Common Eiders (Guillemette *et al.* 1992; Nehls 1995), and potential adjustments could be important to survival. For example, because Common Eiders are diurnal foragers (Nilsson 1970; Goudie and Ankney 1986) and tend to feed at low tide (Bent 1926; Player 1971; Nehls 1995), impending darkness or rising tide may represent a foraging time horizon beyond which diving is less profitable or even impossible. Under these circumstances, eiders may alter feeding behaviour either by shortening pause duration or lengthening feed bout duration to make the most of foraging time remaining. Urchins and mussels do not grow or reproduce during the winter (Steele 1983) and may become depleted through predation by diving ducks (Guillemette *et al.* 1996). Consequently, eiders may decrease pause duration late in the season as prey populations decline and they have to work harder to find food. Common Eiders are at risk from human predators (Goudie *et al.* 1994), and kleptoparasites (mainly gulls; Ingolfsson 1969) and it is possible that adjustments in diving patterns decrease their vulnerability. For example, an eider feeding close to shore at a site where hunting occurs could shorten pause duration between dives, thereby increasing feeding intensity within a feed bout and decreasing overall time spent inshore within range of hunters. An eider could minimize the chances of losing its urchin to a gull by choosing smaller urchins which could be handled quickly at the surface. At one site at Cape St. Mary's, almost 25% of urchins were too big or too small to be utilized by Common Eiders (Ryan 1985). A narrowing of size selection criteria would likely be associated with an increase in search time and, hence, dive duration. In addition, a Common Eider may compensate for the lower energy gain from smaller urchins by intensifying feeding rate, i.e. spending less time on the surface between dives. In this chapter, I examine responses of eiders to environmental and ecological conditions in the context of feeding behaviour.

Predictions

I tested the following predictions regarding the diving and foraging behaviour of wintering Common Eiders:

Dive, handling and pause duration

i) *Reactive/anticipatory breathing*: eiders may be reactive breathers when feeding on urchins and returning to the surface with each prey item, and anticipatory breathers when feeding on mussels and swallowing numerous underwater during each dive.

ii) *Sex and age characteristics*: Greater body mass may allow males to dive for longer and/or pause for shorter durations than females. For the same reason, adult eiders may dive for longer and/or pause for shorter durations than immature eiders.

iii) *Food availability*: a) *time of day* - Eiders may decrease pause duration at dusk and dawn because they feed intensively before and after the overnight fast; b) *tide level* - Eiders may decrease pause duration at low and falling tides to take advantage of decreased travel distance to bottom; c) *time of season* - eiders may increase dive duration and decrease pause duration late in the season as prey depletion occurs.

iv) *Disturbance effects*: a) *predation* - Eiders may decrease pause duration at sites where predation is possible (i.e. at sites accessible by hunters) in order to shorten overall time spent inshore. b) *kleptoparasitism* - Eiders may decrease pause duration in the presence of kleptoparasitic gulls. Common Eiders may choose smaller urchins which can be handled quickly and, in order to maintain energy intake, spend less time at the surface between dives. Increased selectivity by eiders in the presence of gulls may lead to increased dive duration.

Feed and rest bout duration

i) *Food availability* - Eiders may increase feed bout duration and decrease rest bout duration at dusk and dawn, and at low and falling tides. Eiders may increase feed bout duration and decrease rest bout duration as the winter progresses and prey populations decline.

ii) *Disturbance effects: a) kleptoparasitism* - Eiders may decrease rest bout duration in the presence of kleptoparasitic gulls as eiders choosing smaller urchins or losing urchins to gulls must increase feeding time in order to maintain energy intake.

METHODS

Study Area

Common Eiders were observed in the Cape St. Mary's Ecological Reserve (46° 17' N, 54° 12' W) in southeastern Newfoundland during February - March 1995 and January - April 1996. The terrestrial and marine topography of the reserve contribute its suitability as a wintering site for approximately 3000 Common Eiders. The reserve is composed of numerous steep-sided headlands and coves which offer protection from extreme winds. Although hunting of seaducks is prohibited within the reserve, some illegal activity does occur, but only at a few sites where the water is accessible to hunters. Bedrock ledges taper into the water at shoreline and provide habitat for dense aggregations of mussels, an important prey item for Common Eiders (Player 1971; Ryan 1985; Nehls 1995). Urchins, another major prey type (Goudie and Ankney 1986), are ubiquitous, especially adjacent to bedrock slabs. Turbulent conditions limit major predators of mussels, the dog whelks (*Thais* and *Buccinum* spp.), and also prevent the formation of landfast ice which can damage intertidal fauna. Tides and currents do not bring pack ice to the area in winter so feeding by eiders is not restricted by ice cover. Common Eiders usually feed within 60m of land and water is relatively shallow in this zone: <15 m within 150 m of shore (Goudie and Ankney 1986). Tides are semi-diurnal and tidal amplitude averages about 1.5 m, but the intertidal zone is broader because of heavy sea swells and shallow inshore water. Steep cliffs and heavy seas made it impossible to mark individual Common Eiders for identification. From clifftop vantage points where I could view large areas of coastline, I used a 30x telescope to distinguish focal individuals by their plumage and/or position within a feeding flock.

Measurement of Foraging Behaviour

Feed and rest bouts of flocks

Common Eiders are social birds which congregate in flocks of 30 - 3000 or more and synchronize foraging and resting activity in well-defined, alternating *feed and rest bouts* (Figure I-1). To feed, birds in a flock swam inshore together and dived and surfaced synchronously. After feeding, the flock moved offshore by 50-100 m to rest, preen, loaf or court. Feed and rest bout durations for whole flocks were timed to the nearest minute with a wristwatch. At the start of a feed bout, most birds dived together or one after the other in a rapid fashion so that the whole flock was submerged within a matter of seconds. I began timing the bout when 50% of the birds in a flock were submerged on the first dive. I stopped timing the feed bout and began timing the rest bout when at least 50% of the individuals regrouped to swim out. Again, this usually took place over just a few seconds and the flock generally moved as a whole. I followed some flocks through several feed bouts and considered each bout to be independent since eider flocks often switched prey types or locations between bouts, and variables such as tide level and time of day were different for each bout. Factors such as flock size, temperature, and presence/absence of gulls also varied between bouts. Occasionally while feeding, a whole flock rushed out in an apparent panic. Any such feed bouts which ended abruptly, as well as the rest period which followed them, were dropped from the dataset.

Dive, handling and pause durations of individuals

Each feed bout consisted of successive dive cycles, and each complete dive cycle, regardless of prey choice, included a *dive and pause phase* (Fig. I-1). Dive duration was defined as the period of time between submergence and surfacing. When eiders dived for mussels or unsuccessfully for urchins, pause duration began when the bird surfaced and ended when it dived again. When successfully diving for urchins, eiders brought one urchin per dive back to the surface for handling before swallowing. Common Eiders rolled each urchin around in their bills, to flatten or break off the spines before swallowing them whole. Thus, each successful dive cycle for urchins also included a handling phase. The emergence of an eider with an urchin marked the start of the handling phase; the swallowing of the urchin marked the end of the handling phase and the start of the pause phase. Any pauses during which an eider engaged in an activity which may have extended the pause duration, such as swimming or preening, were dropped from the analyses, as were any dives which appeared to be in response to breaking waves. Duration of dive, handling and pause were recorded (in seconds) using a stopwatch. I followed each individual through as many dive cycles as possible, until it was no longer identifiable from its neighbours or until the flock moved out of sight or swam out to rest. Some individuals could be followed through several feed bouts and I assumed each feed bout by an individual to be independent.

Determination of prey type

Dives were classified regarding prey type according to the bird's location, behaviour and whether the eider surfaced with prey. Eiders generally fed on one prey type per bout (personal observation) and prey were somewhat segregated at this site according to water depth and microhabitat. Mussels were abundant on sunkers and bedrock ledges where water was < 3 m deep (Goudie and Ankney 1988) and were rarely found in water > 9 m deep (Ryan 1985). Urchins were more common adjacent to bedrock slabs where water was deeper, increasing gradually from 3 m up to 10 m at about 100 m offshore (Ryan 1985; Goudie and Ankney 1988). I categorized eiders positioned near inshore, kelp-covered rocks and surfacing repeatedly without visible prey as feeding on mussels. Common Eiders collected at these sites by Goudie (1984) and Ryan (1985) had mussels in their gizzards and stomachs. When feeding on mussels, eiders swallowed several mussels while underwater and every dive for mussels was considered successful. When a flock fed on urchins, all individuals surfaced regularly with urchins, and any dives resulting in no visible prey were considered unsuccessful dives. At some sites, both prey were available and it was occasionally unclear which prey eiders were eating. In these cases, prey type was classified as unknown and these dive cycles were excluded from the analysis, as were a small number of dive cycles in which eiders captured crabs. While feeding on urchins, Common Eiders spread out and synchrony was somewhat less marked than when when feeding on mussels. Kleptoparasitic gulls (Herring Gull *Larus argentatus*, Iceland Gull *L. glaucoides*, Glaucous Gull *L. hyperboreus* and, occasionally, Greater Black-backed Gull *L. marinus* Gulls) were often present, attempting to steal urchins as eiders surfaced. Groups of eiders feeding on mussels were more cohesive and exhibited even tighter synchrony than groups feeding on urchins. Gulls rarely attended eiders that were feeding on mussels; if they did arrive, they remained for only a dive or two.

I therefore collected information regarding the following foraging parameters: 1) dive duration, 2) pause duration, 3) handling duration (if applicable), 4) prey type, 5) feed bout duration and 6) rest bout duration.

Environmental Conditions

Since distance from shore and water depth are highly correlated at Cape St. Mary's (Goudie and Ankney 1986), I used a visual estimate of a Common Eider's distance from shore as an index of water depth. I also recorded relevant environmental, temporal and ecological variables: time of day, time of year, temperature, sea swell, cloud cover, precipitation, wind speed and direction, flock size and presence/absence of kleptoparasitic gulls. Tide levels were obtained from Tide and Current Tables published by the Department of Fisheries and Oceans.

Analyses

Dive, handling and pause duration

I analysed diving data using the SAS (SAS Institute 1990) program. Sample size varies in some sections because complete dive cycles were not available for each of the 731 individuals observed. All tests were 2-tailed and results were considered significant below probability level $\alpha = 0.05$. The overall relationship between dive and pause was calculated using all dive cycles for all individual birds. Dive, handling and pause duration were averaged per bout per bird and these mean values were used in subsequent analyses. Dive cycles were analysed separately according to prey type because of the great differences in dive cycle duration exhibited by eiders when feeding on urchins vs. mussels. Dive cycle data for eiders feeding on mussels is restricted to 1996 because I did not record Common Eiders feeding on mussels in 1995. Ecological variables were entered along with previous dive duration into a stepwise multiple regression with pause duration as the dependent variable. Dive duration, julian date, distance from shore, count, and flock size were entered as continuous variables. Categorical variables such as sex, year, predation (hunting present vs. absent), time of day (dusk and dawn (0500-0859 and 1630-2100) vs. midday (0900-1629)), tide level (low and ebbing vs. high and flooding) were coded as dummy variables. The regression model provided partial r^2 values for each independent variable, indicating the amount of variation in pause duration explained by a particular factor, after controlling for the effect of all other variables. Except where otherwise specified, statistics and values presented in all figures, therefore, apply to residual values of continuous variables.

Feed and rest bout duration

As for dive/pause data, I examined the relationship between feed and rest bout duration using all bouts for all flocks feeding on urchins and mussels. Each feed and rest bout was considered independent and all were used to generate overall average feed and rest bout duration for each prey type. Mean rest bout durations were used in multiple regression models of feed bout duration and ecological factors on rest bout duration.

RESULTS

i) Dive, handling and pause duration

The role of handling time in oxygen replenishment

I assumed Common Eiders could breathe while handling urchins in their bills. The considerable length of handling time by some Common Eiders (maximum of 203 seconds; Figure III-1), in addition to the preceding dive, supports this conclusion; it is doubtful birds could postpone breathing for such extended periods. If oxygen stores are being reloaded during the handling phase of a successful dive cycle, should handling time and pause time be added together and considered as an overall surface interval? In order to test whether handling time in Common Eiders should be added to pause duration or not, I compared 2 regression equations of dive on pause, one of which represented the relationship between dive and pause, the other the relationship between dive and "total pause", which was the sum of handling time and pause time. The r^2 for the former equation was higher ($r^2 = 0.22$) than for the latter ($r^2 = 0.15$), indicating that more variation in pause duration was explained by dive duration when pause excluded handling time. Consequently, although the slopes of the two regression equations were significantly different (ANCOVA, dive*group $F_{[1,534]} = 42.62$, $P = 0.0001$), I did not consider handling time as a component of pause duration.

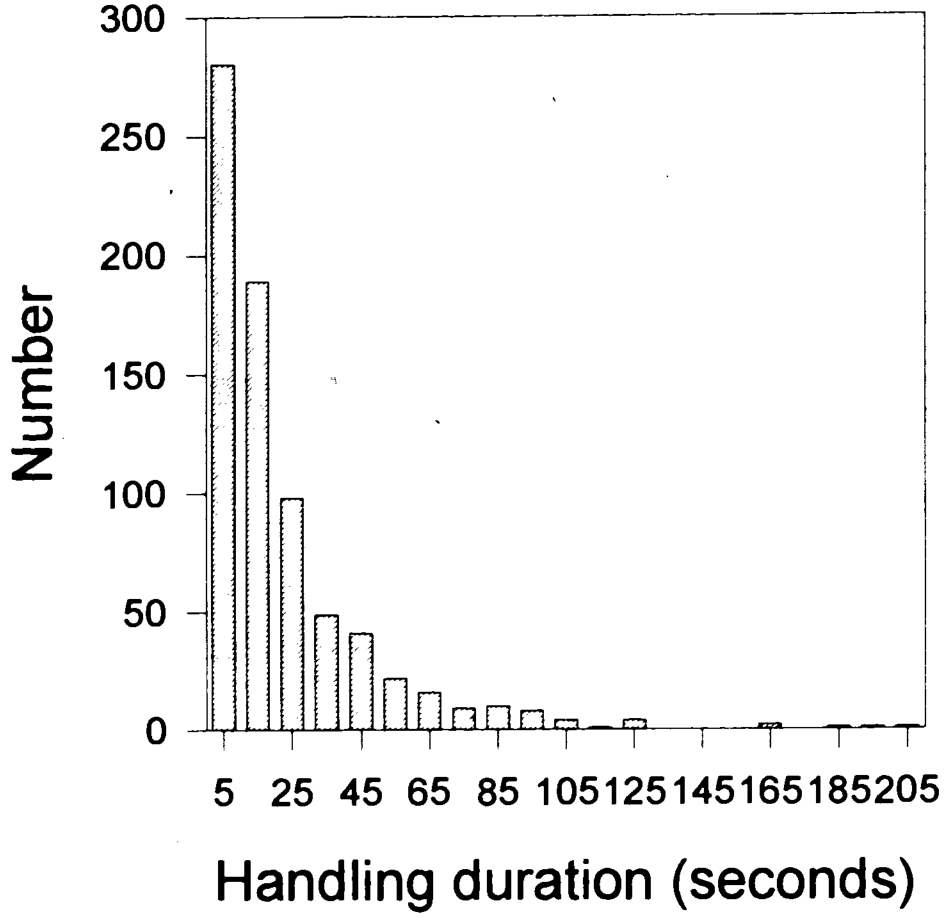
Reactive vs. anticipatory breathing

For all individual dives, I compared two regression equations of dive on pause which differed in whether the dive preceded or followed the pause. Using the following dive slightly increased the explanatory power of the equation by zero and two percent for dives for urchins and mussels, respectively. Such a small increase is not convincing evidence of anticipatory breathing in Common Eiders. The slopes of the regression lines were not significantly different for either prey type (ANCOVA; urchin: dive*group $F_{[1,874]} = 0.27$, $P = 0.60$, group $F_{[1,874]} = 0.12$, $P = 0.73$; mussel: dive*group $F_{[1,353]} = 0.13$, $P = 0.72$, group $F_{[1,353]} = 0.04$, $P = 0.84$). Based on these results, I considered Common Eiders reactive breathers when feeding on mussels and urchins and, consequently, I used previous dive duration as one of the independent variables in the multiple regression analyses.

Use of mean values, and independence of bouts

Within flocks of synchronously diving Common Eiders, I could follow individual birds for an average of 3 (range 1-35) partial or complete dive cycles. To avoid pseudoreplication by including all dive cycles recorded for each eider, I used mean durations per individual per feed bout. To determine whether mean values were representative of an individual's behaviour during a feed bout, I examined dive and pause

Figure III-1. Frequency distribution of handling duration of urchins by Common Eiders. Mean handling duration was 22.3 ± 23.9 seconds.


Number
300
250
200
150
100
50
0
5
25
45
65
85
105
125
145
165
185
205
Handling duration (seconds)

duration in sequences of 5-10 dive cycles (Figure III-2). In general, dive and pause duration did not change over a series of dive cycles (i.e. the interaction was not significant in 3/4 cases and there was no effect of sequence number on either phase of the dive cycle). I, therefore, concluded that dive and pause duration remained relatively constant throughout a feed bout and that mean values were representative of an eider's behaviour during that bout. The significant individual effect in most series is probably due to the variation in conditions under which each individual was observed: eg., date, time, tide, weather conditions, depth.

Since success rate for Common Eiders feeding on urchins was only 55%, many dive cycles had no handling phase and it was difficult to obtain sequences in which sample size was sufficient to test for changes in handling duration. For series of 5 dives, handling time did not change (Figure III-3) and I concluded that mean handling time was also representative of an individual's behaviour within a feed bout.

Thus, mean durations per individual per feed bout were used to generate overall mean dive and pause durations of dive cycles for urchins and mussels shown in Figures III-4 and III-5, respectively. When eiders fed on urchins, successful dives (42.7 ± 15.9 sec) were significantly shorter than unsuccessful dives (50.3 ± 16.1 sec; t-test P= 0.0001), but there was no difference in pause duration for successful dive cycles (71.8 ± 47.5 sec) versus unsuccessful dive cycles (65.0 ± 36.5 sec; t-test P= 0.18). Eiders handled urchins for an average of 22.3 ± 23.9 seconds. Dive (25.9 ± 7.4 sec) and pause durations (26.4 ± 11.8 sec) by eiders for mussels were the shortest dive cycles observed and were significantly shorter than dives (t-test $P < 0.0001$) and pauses (t-test $P < 0.0001$) by eiders feeding on urchins. I combined all dives for urchins by an individual in a bout when calculating a mean per individual per bout for use in the multiple regression models.

Sex and age effects

I was able to look for age effects only within males because of the difficulty in aging female Common Eiders in the field. Male Common Eiders take 3-4 years to mature and gain adult plumage (Palmer 1976, Madge and Burn 1988) so I divided males into immature (1-2 years) and adult (3^+ years) cohorts. About 50% of dives for urchins by immature males were successful whereas 57% of dives by adult males were successful. There were no significant differences between the male age classes for any phase of urchin or mussel dive cycles (Table III-1; t-test with Bonferroni adjustment; Rice 1989). Table III-1 also presents mean dive, handling and pause durations for female Common Eiders. It seemed reasonable to assume that, like males, females showed no effects of age on diving performance and I, therefore, combined age classes within each sex to examine foraging differences between males and females within the multiple regression model. There were no significant differences in dive, handling or pause duration between male and female

Figure III-2. Mean dive (A and B) and pause (C and D) duration (with standard error bars) during series of 5-10 dive cycles by Common Eiders. Sequence number denotes the position of the dive phase in a consecutive series of dive cycles. Sample size is in upper right corner of graphs. Analysis of covariance demonstrated no significant effect of sequence number on dive or pause duration: **A**. Individual P = 0.0001, sequence no. P = 0.63, individual*sequence no. P = 0.02; **B**. Individual P = 0.0001, sequence no. P = 0.47, individual*sequence no. P = 0.59; **C**. Individual P = .77, sequence no. P = 0.29, individual*sequence no. P = 0.96; **D**. individual P = 0.02, sequence no. P = 0.40, individual*sequence no. P = 0.19.

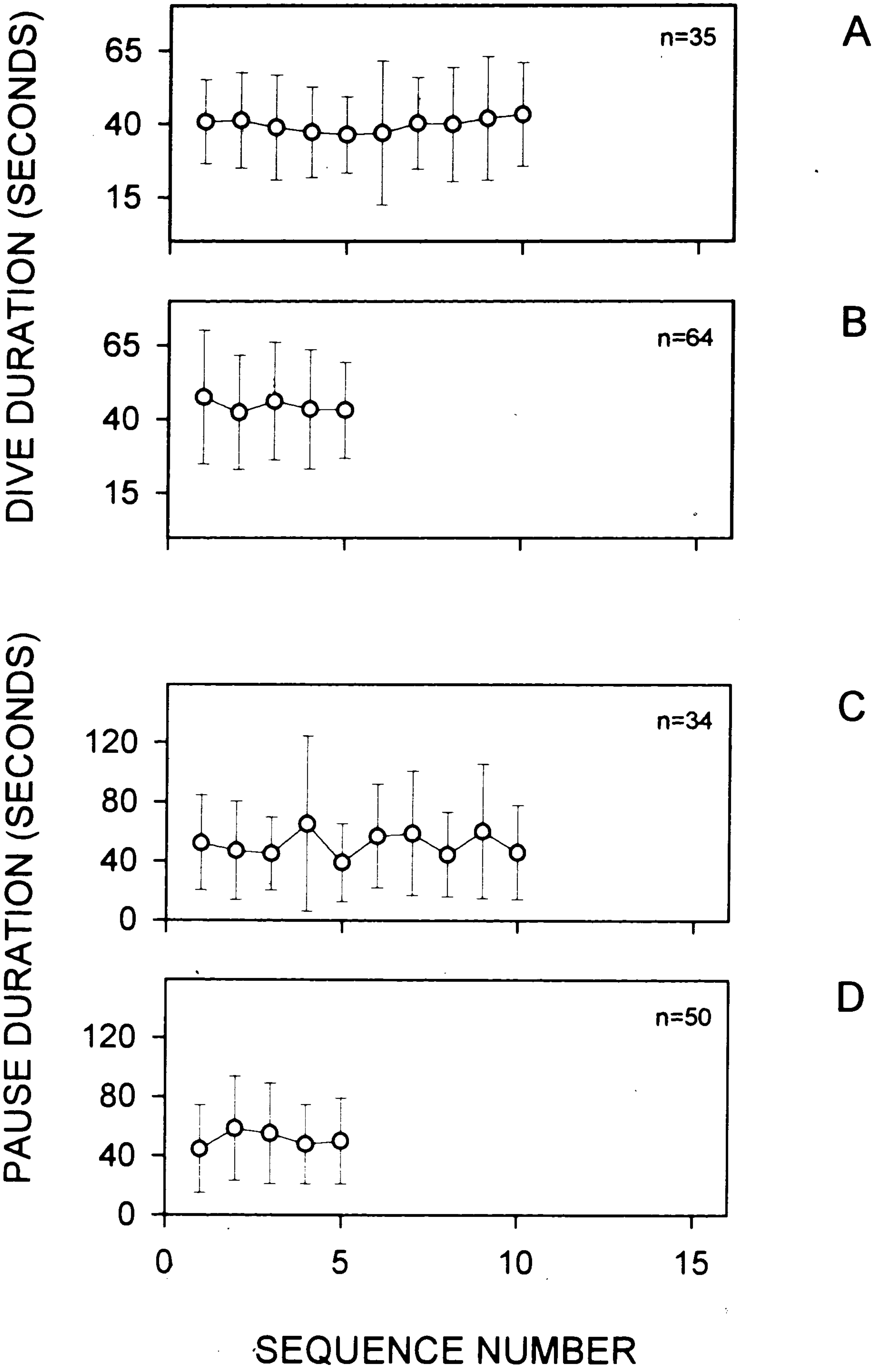

DIVE DURATION (SECONDS)
PAUSE DURATION (SECONDS)
A
n=35
65
40
15
B
n=64
65
40
15
C
n=34
120
80
40
0
D
n=50
120
80
40
0
0
5
10
15
SEQUENCE NUMBER

Figure III-3. Mean handling duration (with standard error bars) during series of 5 dive cycles by Common Eiders. Sequence number denotes the position of the dive phase in a consecutive series of dive cycles. Sample size is in upper right corner of graph. Analysis of covariance demonstrated no significant effect of sequence number on handling duration (Individual P = 0.96, sequence no. P = 0.57, individual*sequence no. P = 0.98).

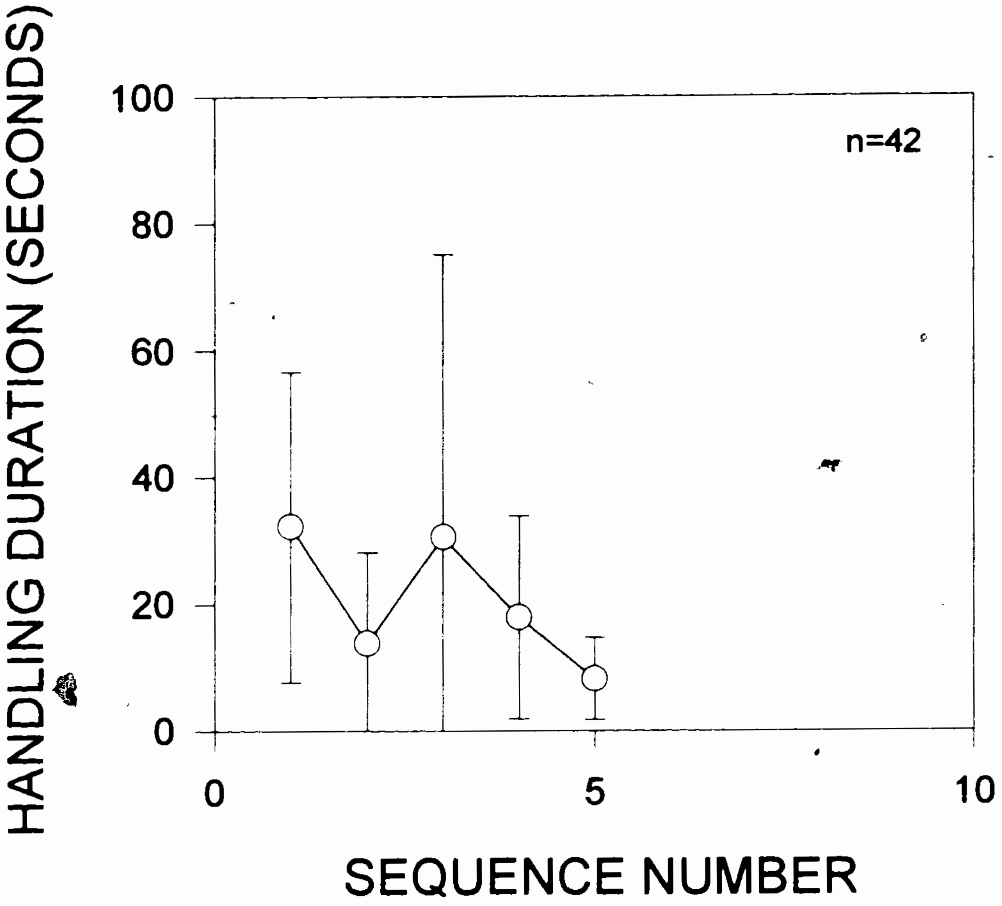

HANDLING DURATION (SECONDS)
100
80
60
40
20
0
n=42
0
5
10
SEQUENCE NUMBER

Figure III-4. Mean duration (± 1 s.d.) of each phase of the dive cycle (dive, handling and pause) by Common Eiders feeding on urchins. Sample size (number of feed bouts for which mean durations were obtained) is at top of bars.

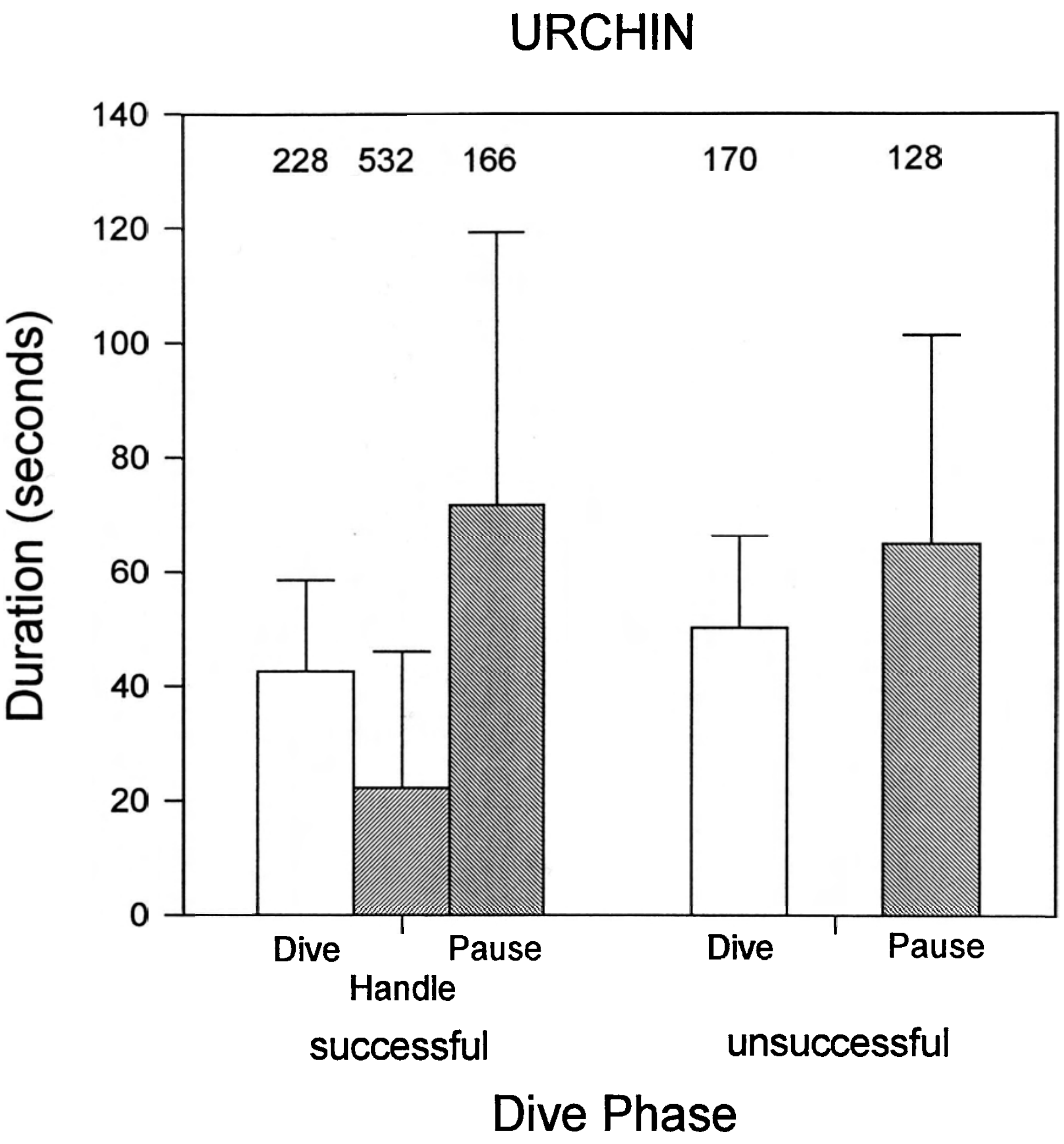

URCHIN
Duration (seconds)
0
20
40
60
80
100
120
140
228
532
166
170
128
Dive
Handle
Pause
Dive
Pause
successful
unsuccessful
Dive Phase

Figure III-5. Mean duration (± 1 s.d.) of each phase (dive and pause) of dive cycles by Common Eiders feeding on mussels. Sample size (number of feed bouts for which mean durations were obtained) is at top of bars.

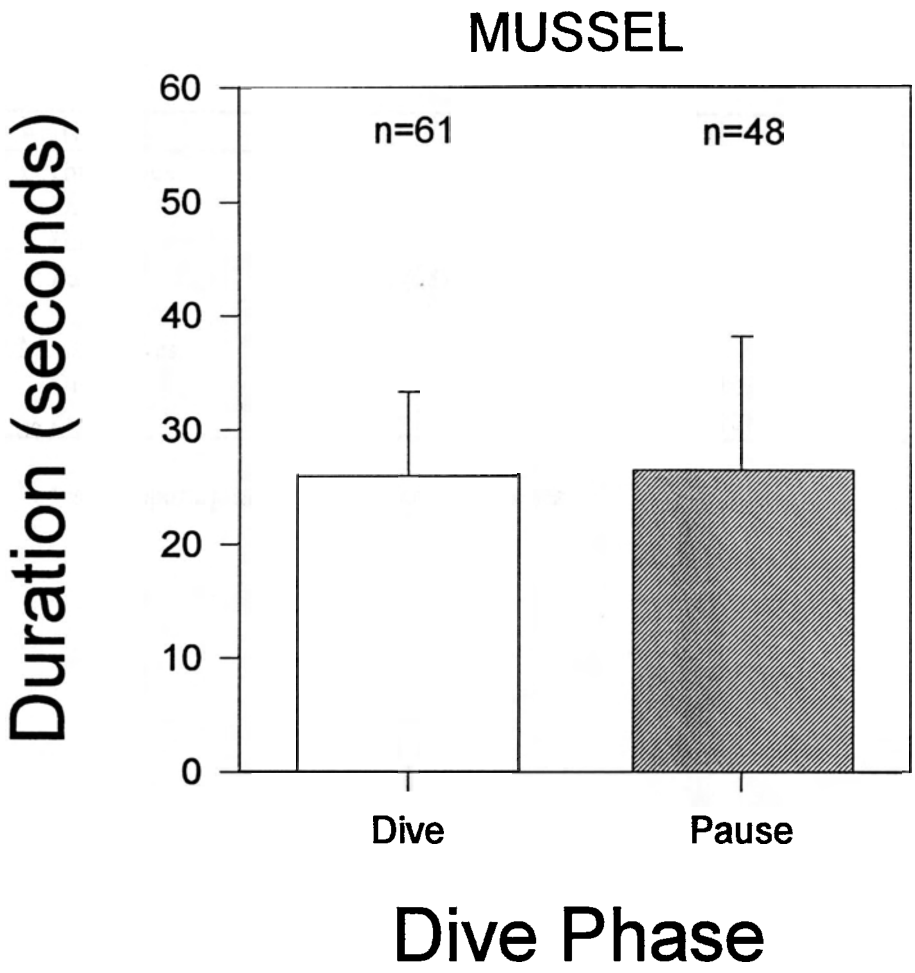

MUSSEL
Duration (seconds)
60
50
40
30
20
10
0
n=61
n=48
Dive
Pause
Dive Phase

Table III-1. Average duration in seconds (± 1 s.d.) of dive, handle and pause phases of female, adult male and immature male Common Eiders feeding on urchins and mussels. Number of individuals observed is given in brackets. There were no significant differences between male age classes for any type of dive phase at a table-wide significance level of α=0.01 (sequential Bonferroni t-test).

Activity	Female	Adult Male	Immature Male	P[a]
Urchin Dives				
Dive	49.7 ± 17.0 (85)	47.1 ± 16.2 (120)	43.8 ± 13.0 (95)	0.11
Handle	19.5 ± 22.2 (235)	25.0 ± 26.1 (206)	23.7 ± 23.0 (86)	0.66
Pause	74.2 ± 45.3 (68)	71.8 ± 44.5 (91)	67.7 ± 41.1 (72)	0.45
Mussel Dives				
Dive	26.4 ± 9.1 (16)	29.2 ± 6.1 (10)	24.8 ± 7.2 (29)	0.09
Pause	31.8 ± 19.6 (7)	30.8 ± 12.7 (10)	23.7 ± 8.7 (26)	0.14

[a] t-test comparing males of different age classes

Common Eiders for either prey type (Table III-2) (for urchin, n=163 males, 68 females; for mussel, n=36 males, 7 females).

Relationship between dive and pause duration

The overall relationship between dive and subsequent pause was positive and linear for dives by individuals for urchins and mussels (using all dive/pause pairs from all individuals). For eiders feeding on urchins, the relationship was described by the equation Pause = 13.00 + 1.24(Dive) ($r^2 = 0.22$, n = 529, P = 0.0001). For individual eiders preying on mussels, the equation was Pause = 5.84 + 0.73(Dive) ($r^2 = 0.136$, n=197, P = 0.0001). Longer pauses followed longer dives of both prey types but there was no evidence of acceleration over the range of dives observed. A quadratic term was entered into both regression equations but was only significantly different from zero for dives for urchins (P = 0.013). However, the inclusion of the quadratic term only increased the r^2 value by about 1% and, therefore, was not included in the final regression equations. The lack of acceleration in this relationship and the fact that pause duration was not affected by the number of dives in a bout (Table III-2) indicated that eiders were not becoming exhausted. The stepwise multiple regression models confirmed the significant relationship between dive and pause duration of dive cycles for urchins and mussels (Table III-2). Figure III-6 illustrates this relationship between dive and pause after controlling for 10 other factors. Dive duration explained 28% and 9% of the total variation observed in pause duration for urchins and mussels, respectively.

Ecological factors affecting pause and handling duration

Ecological factors affecting pause duration differed according to prey type and are summarized in Table III- 2. Distance from shore (depth) and year accounted for about 6% of the total variation observed in urchin pause duration, while time of year and tide level together accounted for 34% of the variation observed in mussel pause duration by individual eiders. The specific effects of environmental variables are discussed below according to prey type.

Urchin pause duration

Food availability

There was little annual variation in pause duration.; year accounted for less than three percent of the variation in pause duration. Pauses were shorter in 1996 than in 1995 (Figure III-7). Time of day and tide level had no effect on pause duration when eiders fed on urchins (Table III-2). As distance from shore (depth) increased, Common Eiders increased pause duration (Figure III-8). Again, only three percent of the variation in pause duration was due to water depth.

Table III-2. Results of stepwise multiple regression models for pause duration by Common Eiders feeding on urchins (n=218) and mussels (n=40).

	Urchin		Mussel	
Variable	r^2	*P*	r^2	*P*
dive duration	0.283	0.0001	0.088	0.014
distance from shore (depth)	0.030	0.003	<0.03	NS
year [a]	0.028	0.001	---	---
sex	<0.01	NS	<0.01	NS
julian date	<0.01	NS	0.235	0.0001
tide level	<0.01	NS	0.103	0.01
time of day	<0.01	NS	<0.05	NS
flock size	<0.01	NS	<0.03	NS
gull [b]	<0.01	NS	---	---
predation	<0.01	NS	<0.01	NS
number of dives in sequence	<0.01	NS	<0.02	NS

[a] Dive cycles for mussels only recorded in 1996.

[b] Gulls did not attend flocks feeding on mussels.

Figure III-6. Relationship between dive and pause duration of Common Eiders feeding on urchins and mussels. Values used for both variables are residuals provided by multiple regression model after controlling for ecological factors.

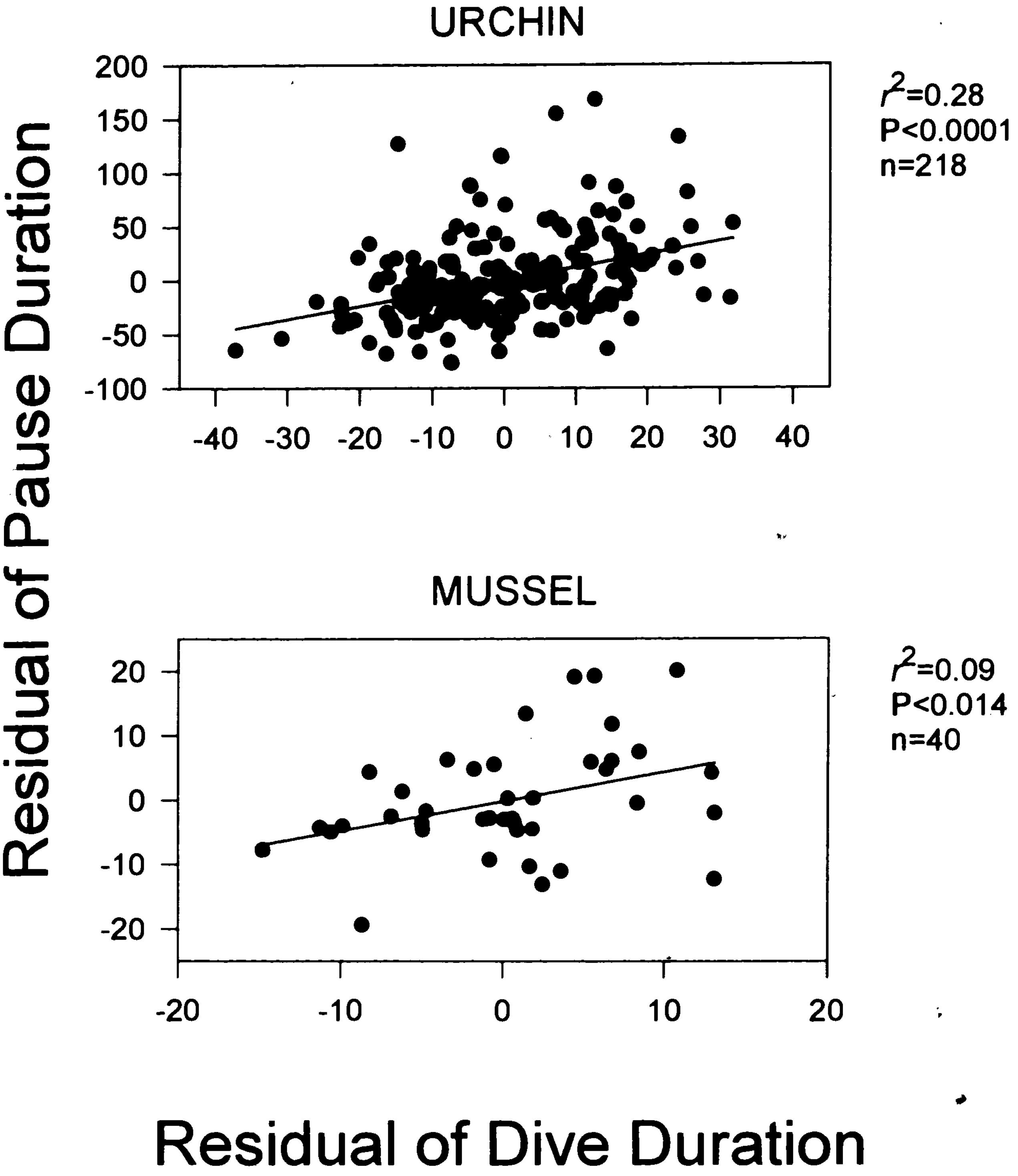

URCHIN
200
150
100
50
0
-50
-100
-40
-30
-20
-10
0
10
20
30
40
r^2=0.28
P<0.0001
n=218
MUSSEL
20
10
0
-10
-20
-20
-10
0
10
20
r^2=0.09
P<0.014
n=40
Residual of Pause Duration
Residual of Dive Duration

Figure III-7. Annual variation in pause duration of Common Eiders feeding on urchins. Values used for pause duration are residual provided by multiple regression model after controlling for ecological factors.

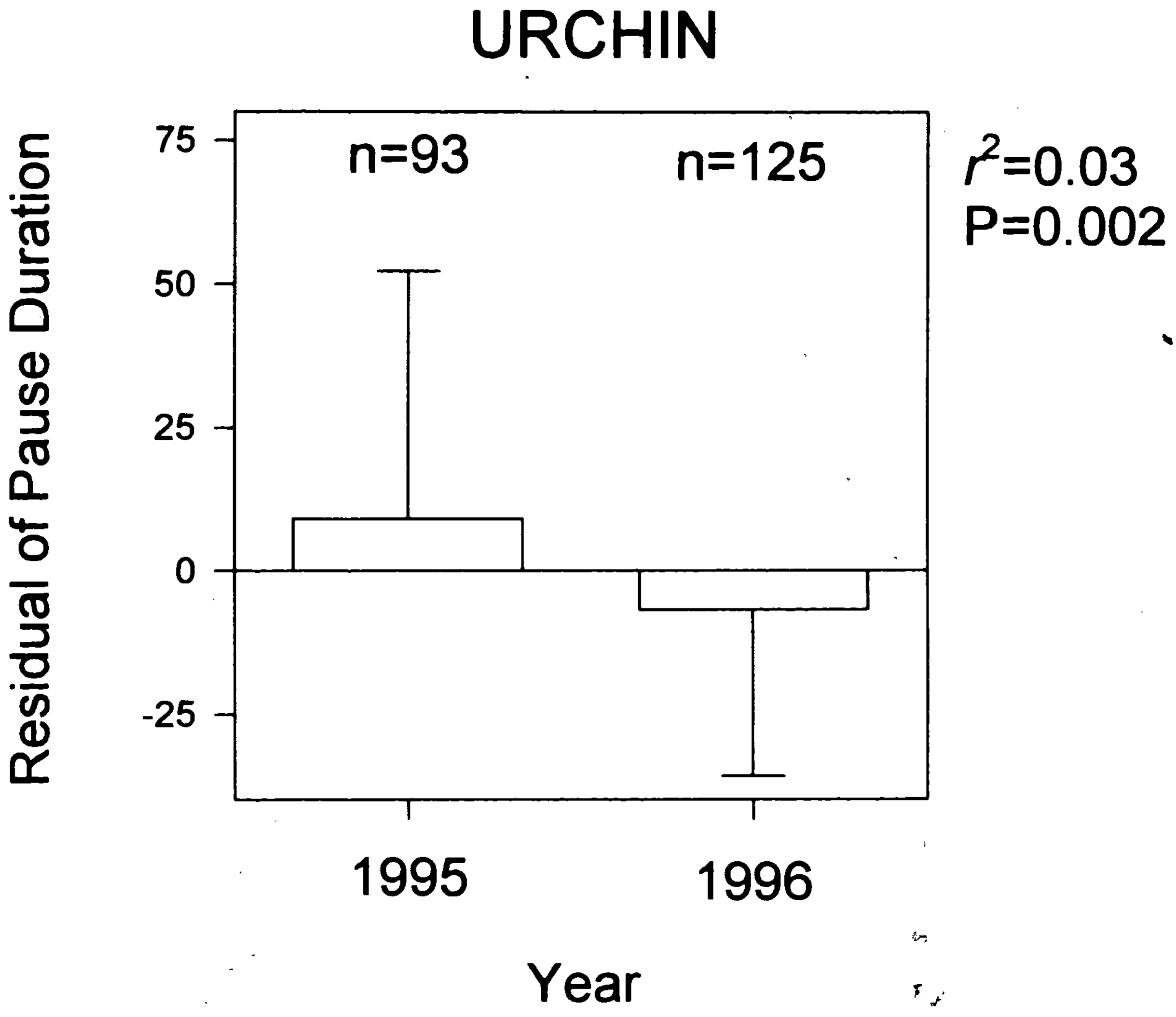
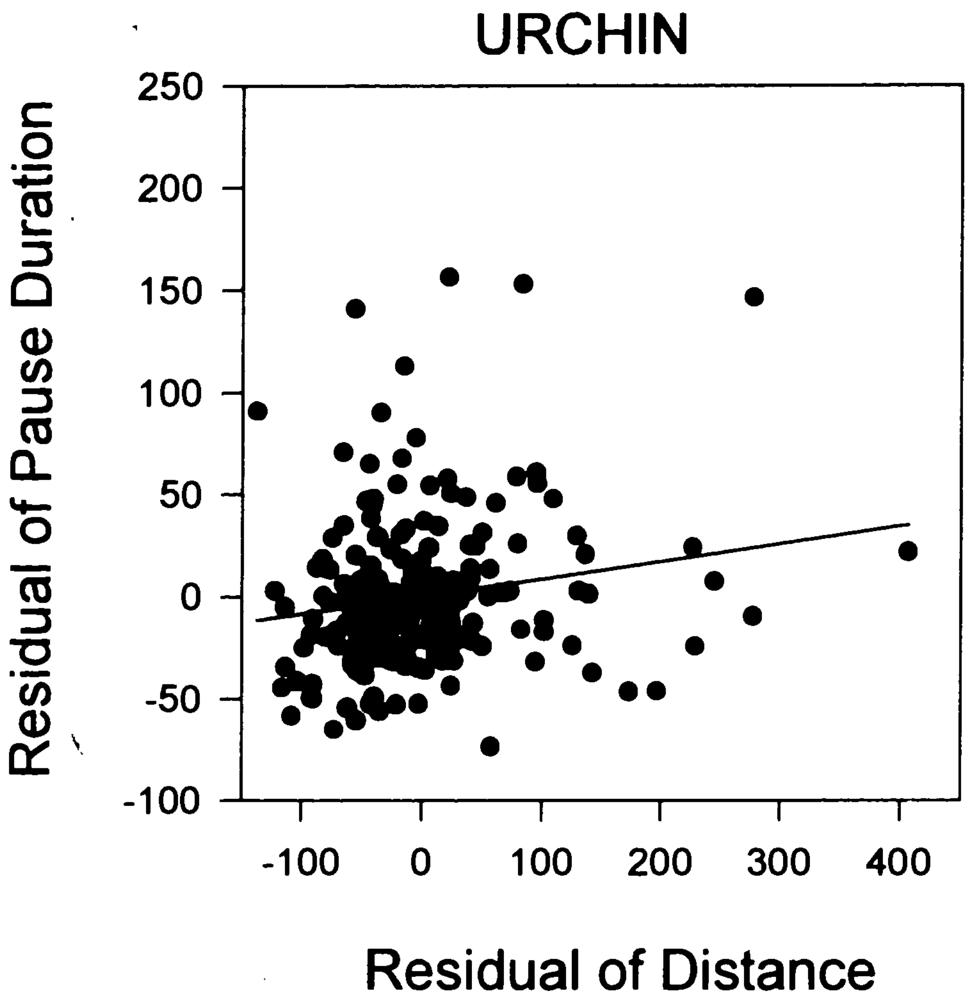

URCHIN
n=93
n=125
r^2=0.03
P=0.002
75
50
25
0
-25
Residual of Pause Duration
1995
1996
Year

Figure III-8. Relationship between pause duration and distance from shore (water depth) at which Common Eiders fed on urchins. Values used for pause duration are residuals provided by multiple regression model after controlling for all other factors.



r^2=0.02
P=0.01
n=218

Disturbance effects

Eiders did not adjust pause duration in the presence of kleptoparasitic gulls or at sites accessible to hunters (Table III-2).

Urchin handling duration

Results of the multiple regression involving handling duration are presented in Table III-3. Handling time decreased with increasing dive duration (Figure III-9). There was a barely significant effect of time of season on handling time (Figure III-10). As the winter progressed, Common Eiders spent less time handling urchins. Contrary to prediction, eiders did not adjust handling time when kleptoparasitic gulls were present.

Mussel pause duration

Food availability

Eiders feeding on mussels decreased pause duration as the winter progressed at a rate of almost 0.25 second per day (Figure III-11). Time of season was the principle factor influencing pause duration, accounting for even more variation in pause time than even dive duration. As predicted, when tides were low or ebbing, Common Eiders spent less time on the surface between dives (Figure III-12), however, there was no effect of water depth on pause duration when eiders fed on mussels (Table III-2). There was no effect of time of day on mussel pause duration (Table III-2).

Disturbance effects

Risk of predation by hunters did not influence eider pause duration (Table III-2). Because gulls did not attend flocks feeding on mussels, kleptoparasitism was not considered in this model.

ii) Feed and rest bout duration

Relationship between feed and rest bout duration

As presented in Table III-3, feed bouts were longer and rest bouts were shorter when eiders fed on urchins than when they fed on mussels. There was no significant relationship between the length of time eiders spent feeding and the subsequent time spent resting when prey was urchin (Table III-4). However, when feeding on mussels, eiders increased rest duration with increasing feed duration (Figure III-13). The ecological factors influencing rest bout duration for each prey type are discussed below.

Ecological factors affecting rest bout duration

Distance from shore (depth) was the only factor which had an effect on rest bout duration of eiders feeding on urchins, accounting for about four percent of variation in rest duration (Table III-5). Time of year and

Table III-3. Results of stepwise multiple regression model for handling duration by Common Eiders feeding on urchins (n=215).

Variable	r^2	P
dive duration	0.058	0.002
distance from shore (depth)	<0.01	NS
year	<0.01	NS
sex	<0.01	NS
julian date	0.017	0.049
tide level	<0.01	NS
time of day	<0.01	NS
flock size	<0.01	NS
gull	<0.01	NS
predation	<0.01	NS
number of dives in sequence	<0.01	NS

Figure III-9. Relationship between handling duration and dive duration by Common Eiders feeding on urchins. Values used for each variable are residuals provided by multiple regression model after controlling for all other factors.

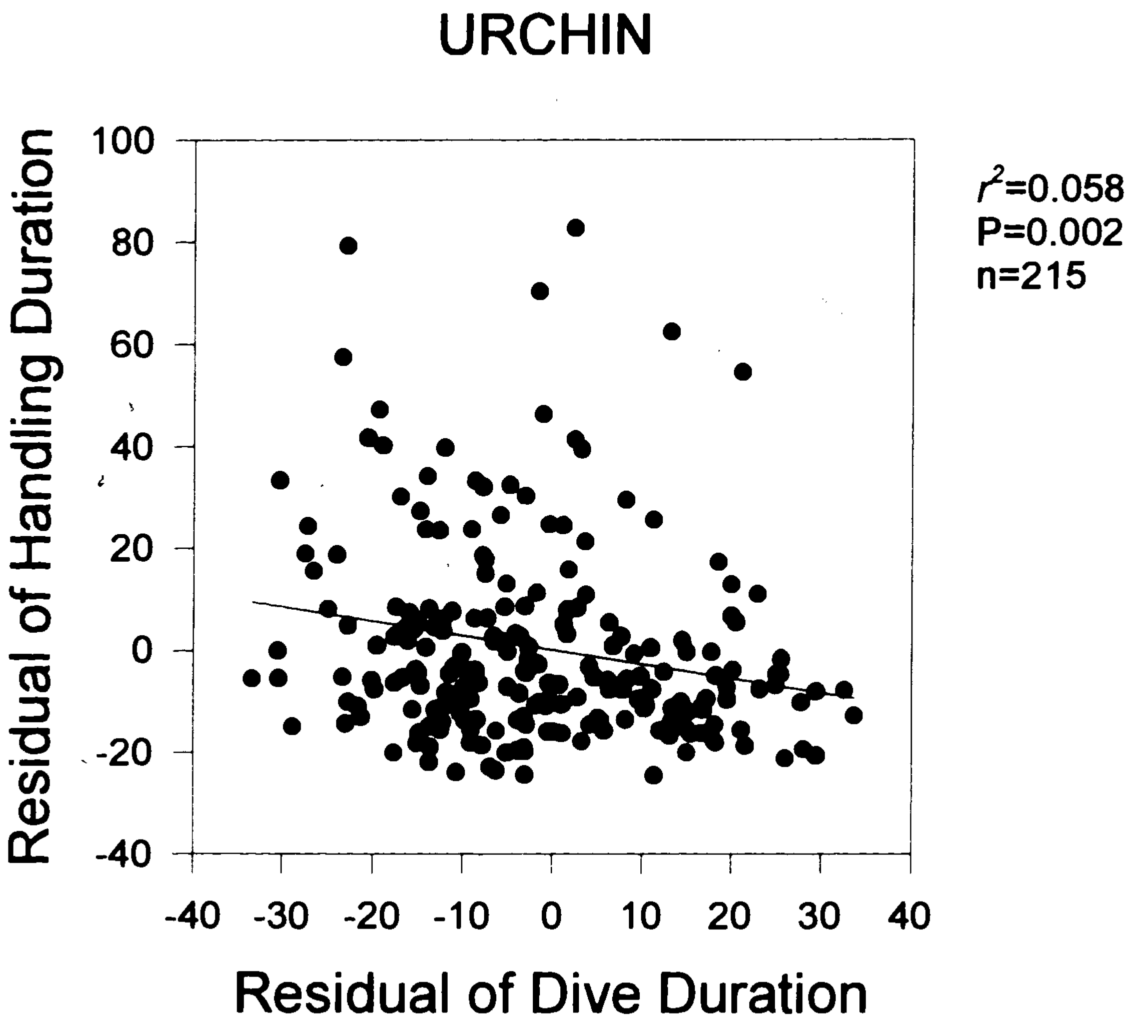
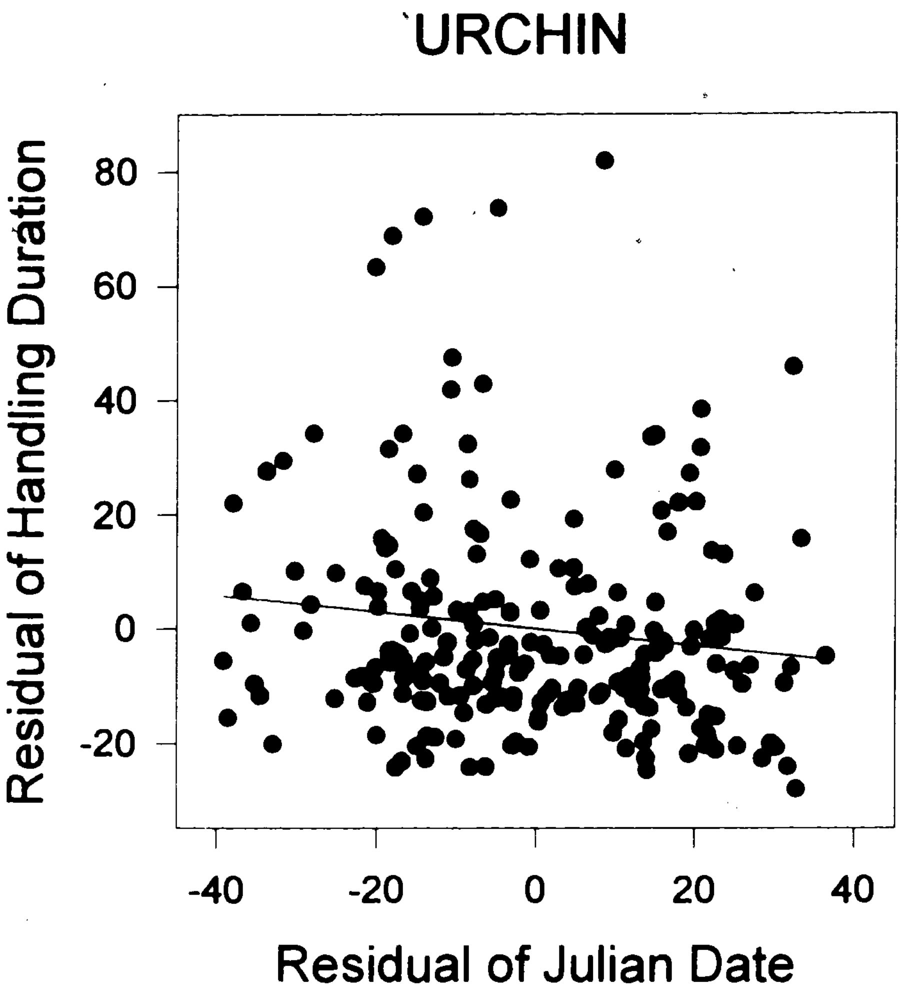

URCHIN
r²=0.058
P=0.002
n=215
Residual of Handling Duration
100
80
60
40
20
0
-20
-40
-40
-30
-20
-10
0
10
20
30
40
Residual of Dive Duration

Figure III-10. Relationship between handling duration and time of year by Common Eiders feeding on urchins. Values used for each variable are residuals provided by multiple regression model after controlling for all other factors.



URCHIN

r^2=0.017
P=0.049
n=215

Figure III-11. Relationship between time of year and pause duration of Common Eiders feeding on mussels. Values used for pause duration are residuals provided by multiple regression model after controlling for all other factors.

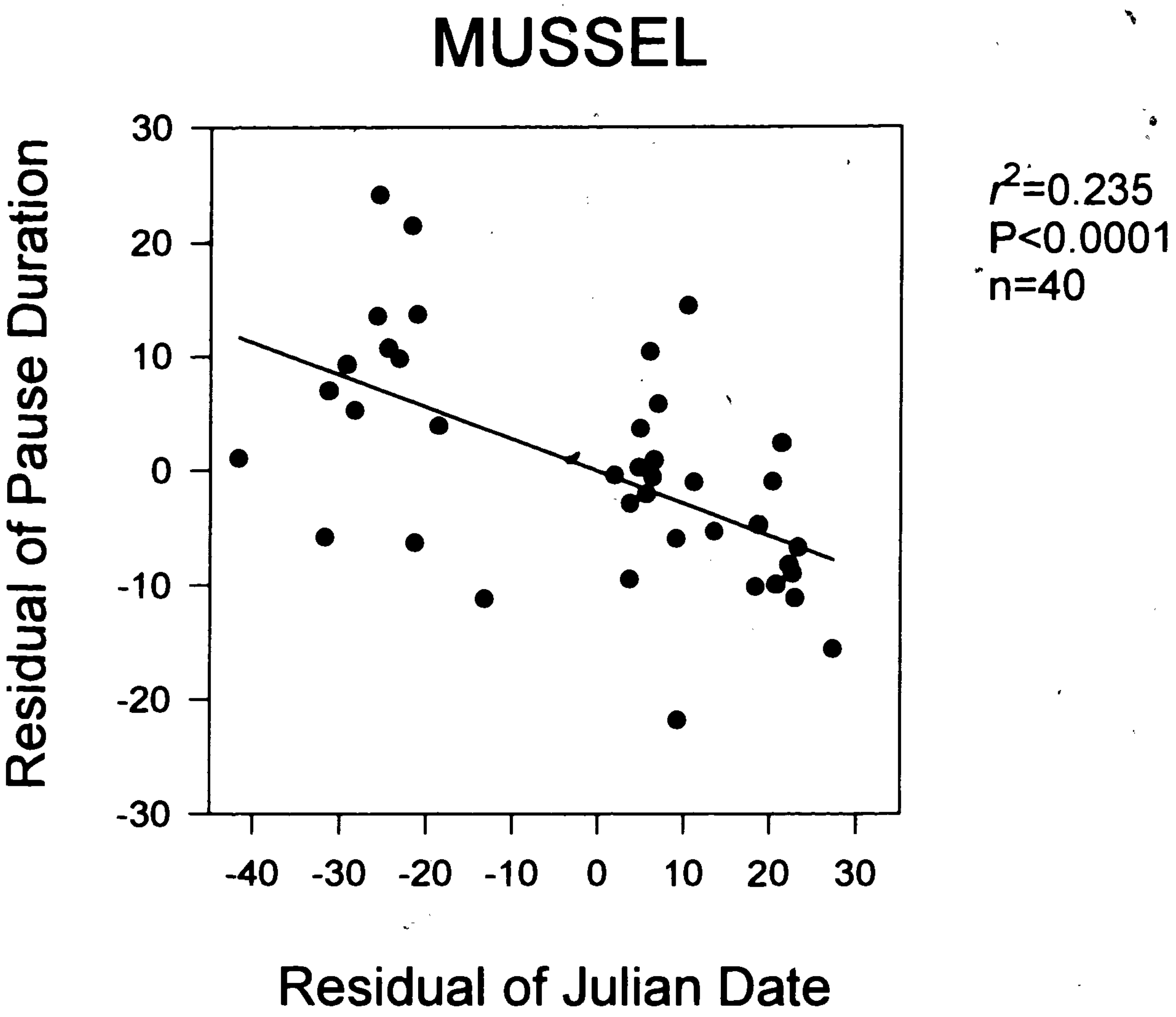

MUSSEL
Residual of Pause Duration
30
20
10
0
-10
-20
-30
-40
-30
-20
-10
0
10
20
30
Residual of Julian Date
r²=0.235
P<0.0001
n=40

Figure III-12. Relationship between pause duration of Common Eiders feeding on mussels and tide level. Values used for pause duration are residuals provided by multiple regression model after controlling for all other factors.

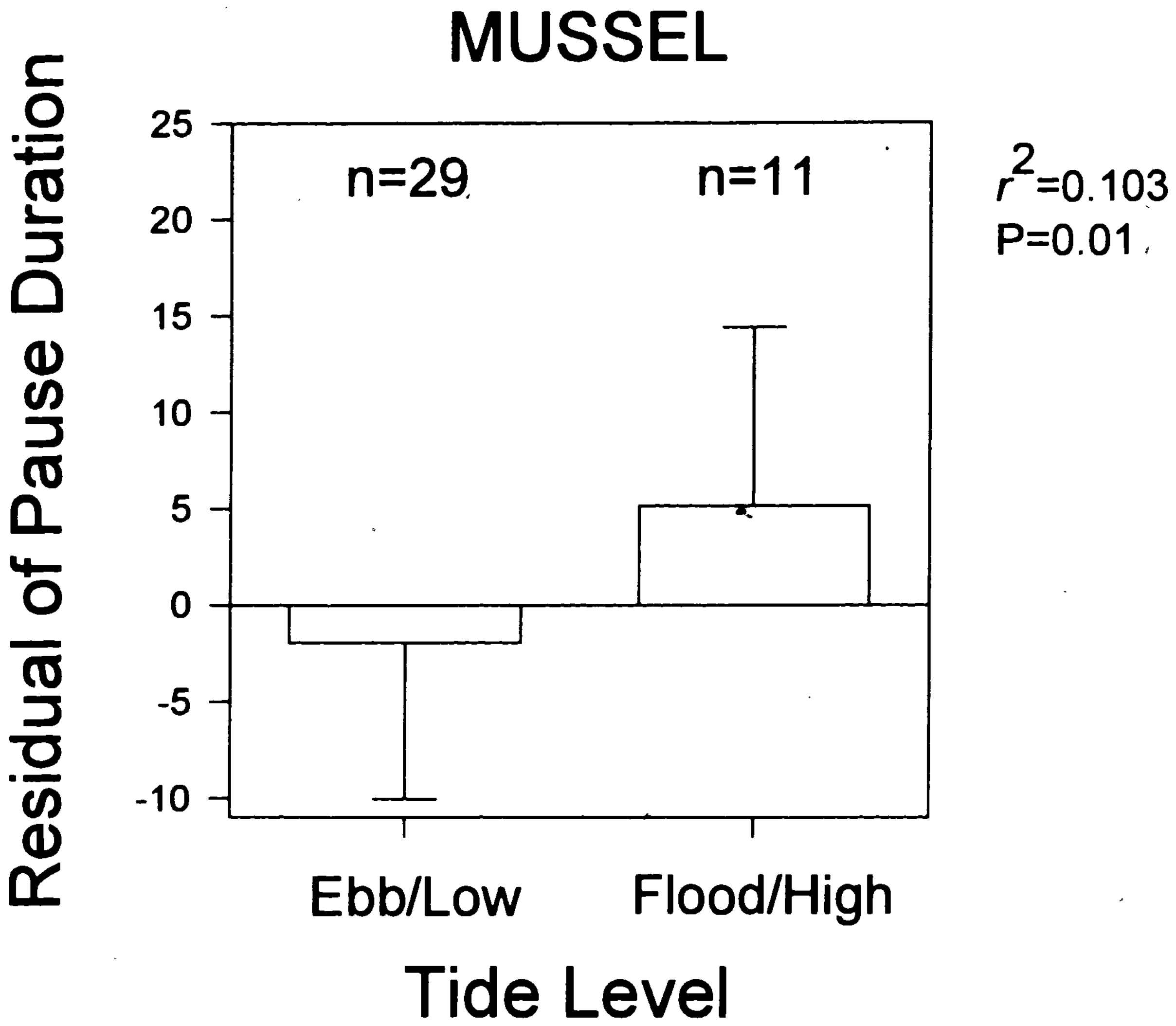
MUSSEL
Residual of Pause Duration
25
20
15
10
5
0
-5
-10
n=29
n=11
r^2=0.103
P=0.01
Ebb/Low
Flood/High
Tide Level

Table III-4. Average feed and rest bout duration in minutes (± 1 s.d.) of Common Eider flocks feeding on urchins and mussels. Sample size is given in brackets.

Bout	Urchin	Mussel	P [a]
Feed	23.6 ± 13.0 (146)	10.4 ± 4.9 (128)	<0.0001
Rest	10.5 ± 5.7 (154)	17.7 ± 8.1 (119)	<0.0001

[a] t-test between bouts of different prey types

Figure III-13. Relationship between rest and feed bout durations of Common Eiders feeding on mussels. Values used for pause duration are residuals provided by multiple regression model after controlling for all other factors.

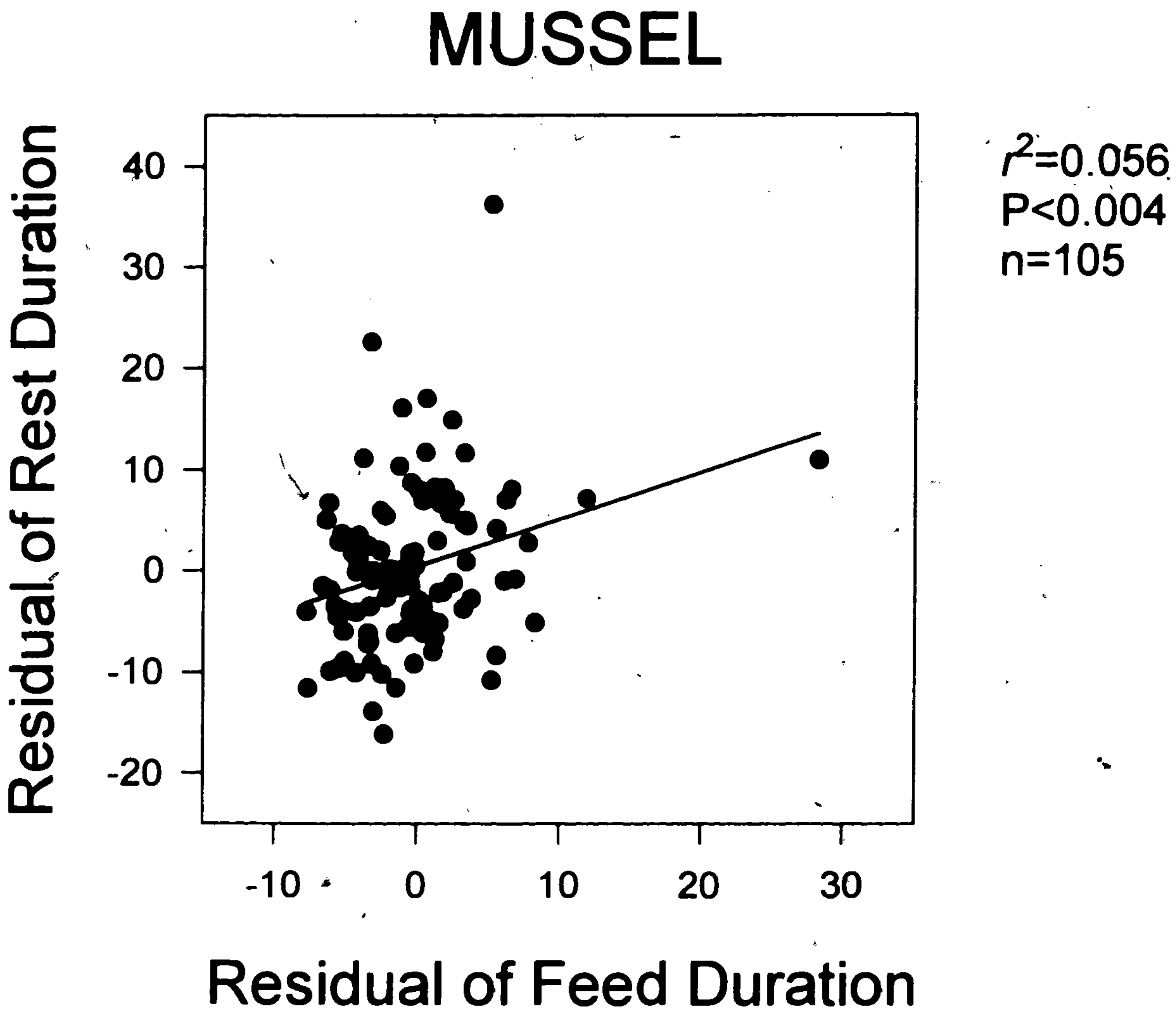

MUSSEL
Residual of Rest Duration
40
30
20
10
0
-10
-20
-10
0
10
20
30
Residual of Feed Duration
r^2=0.056
P<0.004
n=105

Table III-5. Results of stepwise multiple regression models for offshore rest bout durations by Common Eider flocks feeding on urchins (n=154) and mussels (n=104).

	Urchin		Mussel	
Variable	r^2	P[a]	r^2	P[a]
feed bout duration	<0.01	NS	0.056	0.008
distance from shore (depth)	0.043	0.012	<0.01	NS
year	<0.03	NS	x	x
sex[a]	---	---	---	---
julian date	<0.01	NS	0.070	0.002
tide level	<0.04	NS	<0.01	NS
time of day	<0.01	NS	<0.01	NS
flock size	<0.01	NS	0.038	0.054
gull[b]	<0.04	NS	---	---
predation	<0.01	NS	<0.05	NS
number of bouts in sequence	<0.01	NS	<0.02	NS

[a] All birds in a flock observed as a unit

[b] Gulls only attended flocks feeding on urchins

flock size together explained 11% of variation in mussel rest durations (Table III-5), although flock size was marginally non-significant. The specific effects of ecological parameters are discussed below according to prey type.

Urchin rest bout duration

Distance from shore (depth)

Eiders rested for shorter durations when they had been feeding in deeper water (Fig. III-14).

Mussel rest bout duration

Food availability

As the season progressed, eiders increased time spent resting after they fed on mussels (Fig. III-15). Seven percent of the variation in rest duration could be attributed to time of year.

Flock size

There was a trend towards increased time spent resting as flock size increased (Fig. III-16).

Disturbance effects

There was no evidence that eiders adjusted rest duration when feeding on mussels at a site accessible to hunters (Table III-5).

iii) Dive duration

When eiders fed on urchins, dive duration increased with increasing depth (Table III-6). Dive duration also increased as the season progressed.

iv) Feed bout duration

When foraging for urchins, eiders fed for shorter durations in 1996 than in 1995 (Table III-7). When feeding on mussels, eiders fed for longer durations at low and falling tides and for shorter durations later in the season. Risk of predation was associated with shorter mussel feed bout durations.

DISCUSSION

Relationship between dive and pause duration

Common Eiders wintering at Cape St. Mary's foraged for urchins and mussels, and varied diving patterns according to prey type. When feeding on urchins and returning to the surface with each one, eiders dived and paused for longer durations on average than when they swallowed several mussels underwater. When diving for urchins, unsuccessful birds dived longer than successful birds, as predicted by Beauchamp *et al.*

Figure III-14. Relationship between rest bout duration and distance from shore at which Common Eiders fed on urchins. Values used for pause duration are residuals provided by multiple regression model after controlling for all other factors.

Figure III-15. Relationship between rest bout duration of Common Eiders feeding on mussels and time of year. Values used for pause duration are residuals provided by multiple regression model after controlling for all other factors.

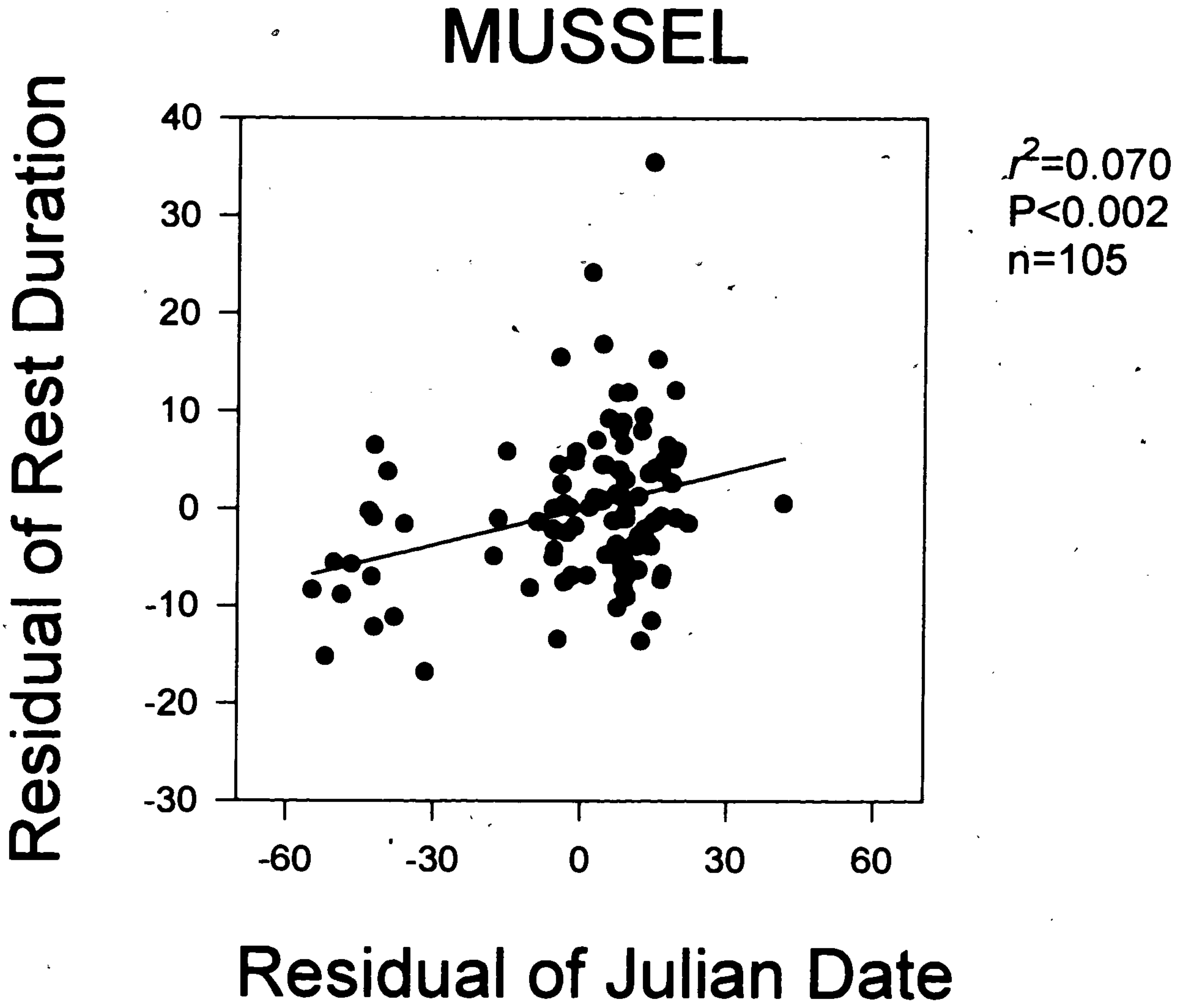

MUSSEL
Residual of Rest Duration
40
30
20
10
0
-10
-20
-30
-60
-30
0
30
60
Residual of Julian Date
r^2=0.070
P<0.002
n=105

Figure III-16. Relationship between rest bout duration and flock size of Common Eiders feeding on mussels. Values used for pause duration are residuals provided by multiple regression model after controlling for all other factors.

Table III-6. Results of stepwise multiple regression models for dive duration by Common Eiders feeding on urchins (n=300) and mussels (n=46).

	Urchin		Mussel	
Variable	r^2	*P*	r^2	*P*
distance from shore (depth)	0.293	0.0001	<0.01	NS
year [a]	<0.01	NS	---	---
sex	<0.01	NS	<0.01	NS
julian date	0.02	0.004	<0.01	NS
tide level	<0.01	NS	<0.01	NS
time of day	<0.01	NS	<0.01	NS
flock size	<0.01	NS	<0.01	NS
gull [b]	<0.01	NS	---	---
predation	<0.01	NS	<0.02	NS
number of dives in sequence	<0.01	NS	<0.02	NS

[a] Dive cycles for mussels only recorded in 1996

[b] Gulls only attended flocks feeding on urchins

Table III-7. Results of stepwise multiple regression models for feed bout durations by Common Eider flocks feeding on urchins (n=146) and mussels (n=128).

	Urchin		Mussel	
Variable	r^2	P[a]	r^2	P[a]
distance from shore (depth)	<0.01	NS	<0.01	NS
year	0.046	0.018	<0.01	NS
sex [a]	---	---	---	---
julian date	<0.01	NS	0.219	0.0001
tide level	<0.01	NS	0.044	0.005
time of day	<0.01	NS	<0.01	NS
flock size	<0.02	NS	<0.01	NS
gull [b]	<0.01	NS	---	NS
predation	<0.01	NS	0.025	0.039
number of bouts in sequence	<0.01	NS	<0.01	NS

[a] All birds in a flock observed as a unit

[b] Gulls only attended flocks feeding on urchins

(1992), but only by an average of 7 seconds. That handling duration declined with dive time suggested eiders became less choosy as a dive progressed and took a smaller urchin rather than surface with none at all, also as predicted by Beauchamp *et al.* (1992). The difference in mean dive duration between prey types, may reflect, in part, the greater range of depths over which urchins were found (Ryan 1985) and, thus, the greater travel distance associated with some dives for urchins. Even in shallow zones where both prey were available, greater dive duration by eiders feeding on urchins may have resulted from search time required to find an urchin of appropriate size which could be handled and swallowed without risk of injury. More than 20% of urchins sampled between 3 and 12 m depths at Cape. St. Mary's were outside the range typically eaten by eiders (Ryan 1985) and, since urchins grew progressively larger with decreasing depth, search time may have been greater in depths < 6 m. In contrast, mussels were small (< 10 mm in length) and all size classes would have been available to eiders capable of ingesting mussels up to 40 mm in length (Player 1971; Nehls 1995; Guillemette *et al.* 1996). Guillemette *et al.* (1992) observed Common Eiders wintering in the Gulf of St. Lawrence and recorded mean dive durations of less than 20 seconds for eiders feeding on mussels and urchins in depths generally < 6 m. Guillemette *et al.* (1992) suggested that gathering several mussels per dive led to the slightly longer duration of dives for mussels. The large difference between duration of dives for urchins at this site and my own study site may have been due to greater depths at which eiders fed on urchins at Cape St. Mary's.

Common Eiders rarely exceeded or even approached an estimated ADL range of 70-105 seconds, whether searching unsuccessfully for urchins or swallowing numerous small mussels underwater. Since anaerobic metabolism yields only one-eighteenth of the energy that may be derived from aerobic metabolism (Ydenberg and Clark 1989; Boyd 1997), it would only be an efficient strategy when an animal is making use of a rich, and perhaps temporary, food source that would compensate for the additional energetic demands of anaerobiosis (Boyd 1997), eg. Western Grebes in contact with a school of fish (Ydenberg and Clark 1989). Sessile prey such as urchins and mussels would probably not warrant such a costly method of foraging. The relationship between dive and pause duration was positive and linear but showed no acceleration. Although Ydenberg and Guillemette (1991) found a curvilinear relationship between dive and pause duration, it was very slight and numerous studies have found linear relationships between dive and surface time of diving animals, eg., Western Grebes (Ydenberg and Forbes 1989), cormorants *Phalacrocorax* spp. (Stonehouse 1967; Croxall et al. 1991; Hustler 1992), Darters *Anhinga melanogaster* (Hustler 1992), Tufted Ducks (Draulans and De Bont 1990), Common Murres (Monaghan *et al.* 1994), Gentoo Penguins *Pygoscelis papua* (Williams *et al.* 1992), Bowhead Whales *Balaena mysticetus* (Wursig *et al.* 1984) and Otters *Lutra lutra* (Nolet *et al.* 1993). Even the longest dives of 90-131 seconds by eiders at Cape St. Mary's were not followed by unusually lengthy pauses at the surface, indicating that even dives of this length did not require recovery beyond replenishment of oxygen stores. As well, dive and pause duration did not change over series of 5-10 dives and pause duration was unrelated to the number of dives in a series. Thus, there was no evidence of postponed recovery or exhaustion within the range of dive durations observed, supporting the conclusion that ADL was not exceeded. I am confident that the lack of change over series of 5-10 dives is representative of typical foraging bouts because, even though I could not often follow individual eiders through complete feed bouts, I used mean duration of dive cycles and feed bouts to calculate an average number of dives per bout: 11.3 dives/bout for eiders feeding on urchins and 13.8 dives/bout for eiders feeding on mussels. Previous dive duration accounted for less than 30% and 9% of the variation observed in pause duration when eiders fed on urchins and mussels, respectively, which suggests that pause is not strictly determined by recovery from diving. Ydenberg and Guillemette's (1991) regression equation for dive on pause for eiders feeding mainly on mussels explained approximately 31% of the variation in pause.

Reactive vs. anticipatory breathing

Common Eiders did not appear to be anticipatory breathers (Lea *et al.* 1996), as per Kramer's (1988) optimal breathing model. Lea *et al.* (1996) tested this model in several species of foot-propelled diving cormorants and suggested that reactive and anticipatory breathing was related to diet in these birds. The European Shag (*Phalacrocorax aristotelis*), feeding on small sandeels *Ammodytes* which could be swallowed underwater, appeared to be an "anticipatory" breather with a positive correlation between pause and subsequent dive duration within a feed bout. The Little Shag (*P. melanoleucus*), in contrast, showed reactive breathing, which may have been the only feasible strategy for a bird which usually swallowed small prey underwater but surfaced when larger prey were found. Two other species which switched between foraging techniques and habitats, the Cormorant (*P. carbo*) and Pied Shag (*P. varius*), showed evidence of both types of breathing patterns. Despite prey-switching between urchins and mussels, Common Eiders did not appear to switch between reactive to anticipatory breathing. This suggests that eiders were not maximizing bottom time or diving near ADL and that factors other than physiological concerns, i.e. ecological factors, influenced the diving patterns of Common Eiders at least within the range of dive duration observed in this study.

Separation of handling from pause duration

Previous studies of diving behaviour in birds which handle prey at the surface have varied in the way handling time was addressed. Guillemette *et al.* (1992) considered handling time separately from pause duration in Common Eiders and Hobson and Sealy (1985) only analyzed pauses in Pelagic Cormorants (*Phalcrocorax pelagicus*) during which no handling occurred. In most studies of cormorants and shags (*Phalacrocorax* spp.), however, authors included all surface activity as part of pause duration (Wanless *et al.* 1993; Watanuki *et al.* 1996), whether handling was considered typical (Wilson and Wilson 1988), unusual (Cooper 1986) or not always necessary (Croxall *et al.* 1991). Handling time was also included as part of pause duration in Western Grebes (Ydenberg and Forbes 1988), Surf Scoters and Barrow's Goldeneyes *Bucephala islandica* (Beauchamp *et al.* 1992). In my study of Common Eiders, there was no increase in the amount of variation in pause duration explained by dive duration when pause included handling time and, therefore, using total surface time as a dependent variable would not have improved the regression models.

Individual, sex and age differences

Differences between individual Common Eiders accounted for 74% of the variation in dive duration (nested ANOVA) and 38% of variation in pause duration. The analysis of sequential dive and pause duration also showed a significant individual effect, however, it is difficult to interpret these results since virtually all individuals were observed under different conditions, i.e., feeding at different depths or at different times during the season. Because such uncontrolled factors undoubtedly affected diving performance, it is difficult to separate variation due to differences between *individuals* from that due to differences between *conditions* under which those individuals were observed. Although individual differences probably do exist in diving ability and performance, a more meaningful quantification of this variation would require simulataneous observation of marked indivduals within the same flock. Unlike solitary foragers in which individual variation has been documented (Boyd *et al.* 1991; Williams *et al.* 1992; Boyd *et al.* 1994; Monaghan *et al.* 1994), eiders are social foragers which synchronize diving and pausing activity. This coordination must have limited individual variation to some degree as activity of all flockmates was generally dictated by the group (see Chapter IV).

I observed no significant sex differences in diving behaviour among Common Eiders at Cape St. Mary's. This finding is consistent with other studies of wintering Common Eiders (Guillemette *et al.* 1992; Nehls 1995). Nilsson (1972) found that wintering female Common Goldeneyes had similar diving abilities to males. Nilsson (1970) did not mention any sexual differences in eight species of diving waterfowl he studied, including the Common Eider. Alexander and Hair (1980) found no differences in dive duration between sexes in wintering Canvasbacks, Ring-necked Ducks, Lesser Scaup or Redheads. A few studies have found differences in diving behaviour of males and females of sexually dimorphic species (Le Boeuf 1994; Wanless *et al.* 1995; Watanuki *et al.* 1996). For example, male Japanese Cormorants (*Phalacrocorax capillatus*), which are 26% heavier than females, dived 13 seconds longer on average and about 8 m deeper (Watanuki *et al.* 1996) than females. Among South Georgia Shags, mean dive duration of males, which are 16% heavier than females, was 20 seconds greater than that of females (Wanless *et al.* 1995). These differences may be relate to the greater body mass and, hence greater ADL (Kooyman *et al.* 1983), of the larger sex.

Similarly, older animals may exhibit increased diving performance over juveniles as a result of increased body size (Kooyman *et al.* 1980). In another benthic diving bird, the Olivaceous Cormorant *Phalacrocorax olivaceus*, immature (first-year) birds showed no differences from adults in dive or pause time, although they did have lower foraging success (by 8%) and fed for longer and rested for less time than adults. Young Adelie Penguins also catch prey less successfully than adults (Ainley and Schlatter 1972). Age had no effect on diving performance of male Common Eiders. It is possible that size differences among eider sex (7%) and age classes (3-9%) were not sufficient to result in observable differences in diving ability. On the other hand, the lack of variation between these cohorts may be further indication that eiders at Cape St. Mary's did not routinely approach the limits of their diving ability.

Feed and rest bout duration

On average, eiders feeding on mussels fed for 13 minutes less and then rested for 7 minutes longer than when they fed on urchins. When eiders fed on mussels, the amount of time spent resting increased as time spent feeding increased, whereas there was no relationship between these parameters when eiders fed on urchins. Assuming that initiation and termination of feeding is somewhat related to the amount of food in the gut (Guillemette 1994) and that an eider could only feed until its esophagus was full, this threshold may have been reached in less time when eiders fed on mussels as opposed to urchins. My assumptions that every dive for mussels was successful and that eiders gathered several mussels per dive were likely valid since eiders fed on dense aggregations of mussels, of which they could ingest all available size classes. In contrast, only 57% of dives for urchins were successful and birds sometimes lost urchins to gulls upon surfacing. Longer rest bout durations after feeding on mussels may have been related to mechanical processing. Mussel shells are obviously thicker than urchin tests and averaged 67% of total body mass whereas urchin tests were 62% of total body mass (Guillemette *et al.* 1992). Bustnes and Eriskstad (1990) found that eiders selected mussels of certain size classes to minimize daily shell intake. Flesh content of mussels was highest in smaller size classes and shell weight increased more than flesh weight with increasing mussel length. The energetic costs of mussel shell crushing by Common Eiders increased exponentially with mussel length (Nehls 1995). While it unclear whether a meal is processed in the gizzard during both feeding and resting or only during resting (Guillemette *et al.* 1994), it is clear that digestion of mussels takes substantial time. Swennen (1976) determined mean transit time (from ingestion to defecation) for Common Eiders feeding on mussels as 62.5 minutes. Grandy (1972) found that it took 30-40 minutes for blue mussels to pass to the terminal portion of a Black Duck's digestive system. Unfortunately, I have no information on digestion of urchins.

Rest bouts are probably necessary for thermoregulation as well as for digestion. Birds diving in cold water must cope with increased thermal conductance (Jenssen *et al.* 1989) and hydrostatic compression of plumage (Wilson et al. 1992) while underwater, both of which increase heat loss. However, diving animals do not appear to use their limited oxygen stores to maintain body temperature while diving (MacArthur 1984; Bevan and Butler 1992; de Leeuw 1996) but, rather, recover from body cooling during a rest bout after foraging (de Leeuw 1996). Preening and grooming activities during rest bouts (MacArthur 1984; Stephenson *et al.* 1988; Croll and McLaren 1993; de Leeuw 1996) are important to maintain waterproof pelage or plumage but also to generate heat which can contribute to recovery from thermoregulatory costs of diving. Heat production from digestion itself may be valuable, as Nehls (1995) demonstrated for wintering Common Eiders. Eiders feeding on mussels used as much as 10% of ingested energy to heat mussels when temperatures were low but crushing of shells and digestion of flesh contributed to thermoregulation. However, longer rest bout duration of eiders feeding on mussels as opposed to urchins at Cape St. Mary's was probably related less to the thermoregulatory function of a rest bout than to its digestive function, since eiders spent less time underwater (6.0 minutes) during an average feed bout for mussels than they did while feeding on urchins (8.8 minutes).

Gulf of St. Lawrence eiders feeding on urchins and mussels showed a different pattern than those at Cape St. Mary's. Eiders there fed for 13 minutes and rested for 8 minutes when feeding on mussels and fed and rested for equal durations of 17 minutes when feeding on urchins (Guillemette *et al.* 1992). While eiders in the Gulf ate larger mussels (average shell of 9.7mm; Guillemette *et al.* 1992) than eiders at Cape St. Mary's (6.4mm; Ryan 1985) and would have been expected to fill up and quit eating sooner, the difference in feed bout duration between the two sites is not great. The larger size of urchins eaten by Gulf eiders (mean test diameter 29.8 mm; Guillemette *et al.* 1992) may have been the reason they fed for shorter durations than Cape St. Mary's eiders taking smaller urchins (20.1 mm; Ryan 1985).

Ecological factors affecting pause and rest bout duration

Time of season

When feeding on mussels, Common Eiders spent less time pausing between dives as the season progressed, probably as a result of prey depletion. Since mussel growth and reproduction is slow or negligible over the winter (Steele 1983; Craeymeersch *et al.* 1986), thousands of Common Eiders feeding on mussels over several months would likely reduce the biomass available. An average biomass of 0.4 kg/m^2 of mussels within 3-9 m depths was reported at a headland site called Brierly in the Cape St. Mary's Ecological Reserve (Ryan 1985). Ryan (1985) estimated that 200 Common Eiders feeding at this site would remove 60 kg/day of invertebrates, of which a minimum of 20 kg/day would be mussels. Although average biomass of mussels was much higher in the Gulf of St. Lawrence (2.8 g/m^2) (Guillemette *et al.* 1996), prey depletion was believed to determine Common Eider movement between reefs after they had consumed an estimated 48-69% of the mussel biomass available at each reef. Similarly, there is no winter recruitment among sea urchins and annual growth is very slow (Himmelman *et al.* 1983) so they may also decline in numbers over the season. But eiders probably remove far less of the available biomass since they avoided urchins and actively selected mussels (Ryan 1985). In the Gulf of St. Lawrence, eiders removed only 3-6% of the urchin biomass. Common Murres also reduced pause duration between dives when prey was scarce (Monaghan *et al.* 1994) and other diving animals have been shown to adjust foraging effort when prey populations declined, eg., Antarctic Fur Seals (Boyd *et al.* 1994) and Adelie Penguins (Watanuki *et al.* 1993).

As the season progressed, eiders feeding on mussels increased rest bout duration. It is possible that more time was needed for digestion if the smallest and most easily digested mussels had been taken early in the season. The trend, albeit non-significant, toward increasing rest bout duration with increasing size of flocks feeding on mussels, supports the idea that depletion of mussels of optimal size leads to increase in time required for digestion during rest bouts.

Handling duration

The decline in handling duration over the season suggested that urchins of optimal size may also have become scarcer as winter progressed. Without a measurement of urchin size, I assumed that handling time reflected urchin size, and that a lower handling duration indicated a smaller urchin. This seems to be a valid assumption since handling time by eiders in Gulf of St. Lawrence was 39 seconds for urchins averaging 30 mm in diameter (Guillemette et al. 1992) whereas eiders at my study site took 22 seconds (Figure III-4) to handle urchins that were 20mm in diameter (Ryan 1985). The increase in dive duration which occurred over the season is consistent with the theory of prey depletion since eiders probably had to spend more time searching for urchins of appropriate size later in the winter.

Tide level and water depth

Several studies have documented that Common Eiders (Player 1971; Cantin *et al.* 1974; Nehls 1995) and other diving ducks (Michot *et al.* 1994) dive in greater numbers at low rather than at high tide, suggesting that diving ducks prefer feeding when travel time to the bottom is decreased. This study is the first, however, to provide evidence that Common Eiders intensify their diving efforts to take maximum advantage of lower water depths during low tide. By decreasing time spent at the surface between dives for mussels, Common Eiders maximize underwater time and, presumably, energy intake during a feed bout. Although tidal amplitude at Cape St. Mary's is relatively low (< 1.5 m), mussels occur in shallow water zones (< 3 m) where tidal shifts would have more marked effects on water depth than in deeper water (3-10 m) where urchins are common (Goudie 1984). I found no effect of water depth (distance from shore) on pause duration when eiders fed on mussels, possibly because mussels occurred in shallow water (< 3 m) close to shore and not over the same range of depths in which urchins are found. Ydenberg and Guillemette (1991) found no effect of depth on the dive-pause relationship of Common Eiders feeding mainly on mussels at depths of 12 m or less. Because of frequent heavy sea swells, shallow zones were not always accessible to Common Eiders. The energy content of mussels (kJ/g wet mass) is twice as high as that of urchins (Goudie and Ankney 1986; Guillemette *et al.* 1992) and a Common Eider's ability to adjust foraging behaviour to maximize mussel intake during the periods when they are available may be an important adaptive strategy. Campbell (1978) suggested that eiders showed marked tidal activity patterns only in estuaries where extreme hydrological conditions make feeding difficult at certain tide levels, and that diurnal routines should be the norm in marine areas (see below). However, since eiders at Cape St. Mary's do not always have access to inshore mussel beds, diurnal routines may be overridden by tidal activity. Eiders did not decrease rest bout duration when feeding on mussels at low tide, possibly because of digestive constraints, as discussed above.

Increased depth at which Common Eiders fed on urchins was associated with an increase in pause duration but a decrease in rest bout duration. The effect of depth on diving costs is unclear since compression and loss of air from plumage decreases the cost of overcoming buoyancy but increases heat loss (de Leeuw 1996), thereby affecting hydrodynamic and thermoregulatory costs in different directions. Nevertheless, pause duration has been shown to increase with depth in some other benthic foragers, including Tufted Ducks (de Leeuw 1996) and Shags *Phalcrocorax aristotelis* (Wanless *et al.* 1993). Shags making longer dives in deep water spent more time on the surface afterwards than when making long dives in shallow water, suggesting that deep dives cost more than shallow dives (Wanless *et al.* 1993).

Time of day

As referenced in Player (1971), Pethon (1967) found that Common Eiders in summer fed between daybreak and sunset with a midday rest which shortened in duration as daylight decreased with the onset of winter. Player (1971) found that eiders wintering in Scotland showed peaks in feeding activity early and late in the day and that very few birds fed at midday even when tides were low, although low tide was preferred at other times of the day. Feeding intensity (percent birds feeding) of eiders wintering at another site in Scotland was high towards dusk, regardless of tide level (Campbell 1978). Eiders at Cape St. Mary's fed all day long and there was no association with time of day for any of the foraging parameters recorded. Eiders did increase rest bout duration after feeding on mussels late in the season. It is possible that this change was associated with increased daylength in spring, however, if this was the case, a similar change would be expected in rest bouts by eiders feeding on urchins, and it was not.

Disturbance effects

Kleptoparasitism by gulls of diving birds, including Common Eiders, has been previously observed (Sage 1962, Ingolfsson 1969) and may be associated with changes in foraging behaviour of diving ducks (Schenkeveld and Ydenberg 1985). Surf scoters feeding in flocks showed greater surfacing synchrony when attended by Glaucous-winged Gulls *(Larus glaucescens)*. Schenkeveld and Ydenberg (1985) suggested that improved synchrony swamped potential kleptoparasites and decreased the chances that an individual scoter would lose its mussel. In contrast, Beauchamp (1992) found no effect of gull presence on diving or surfacing synchrony in Surf Scoters or Barrow's Goldeneyes. Gulls which attended flocks of Common Eiders feeding on urchins at Cape St. Mary's tried to steal urchins by rushing at eiders as they surfaced. Gulls were often successful as eiders usually dropped the urchin immediately or after diving briefly in an escape attempt. While I had no quantitative measure of foraging synchrony, I expected changes in dive duration if Common Eiders altered urchin selection criteria in the presence of gulls and chose smaller urchins which could be handled faster. However, dive duration did not increase, as would be expected if Common Eiders became choosier. Nor did Common Eiders shorten pause time when attended by gulls, suggesting either that eiders were not choosing smaller prey or that they did not need to compensate for smaller prey. That handling time did not change supports the former. Eiders did not spend less time handling urchins; perhaps the potential cost of injury from an improperly handled urchin may have been greater than the loss of an urchin to a gull. I did not consider the level of potential kleptoparasitism (i.e., the number of gulls present versus the number of eiders in a flock) in the analyses, however, usually only one gull attended each flock. As has been noted elsewhere (Ingolfsson 1969), gulls actively defended eider rafts by driving away other gulls which landed nearby. Schenkeveld and Ydenberg (1985) found that the presence of any gull was sufficient to increase foraging synchrony in Surf Scoters; the number of gulls present and their activity (resting or actively robbing scoters of mussels) did not affect the level of synchrony.

At sites where predation by hunters was possible, eiders foraging for mussels decreased overall time spent feeding. The lack of associated changes in dive and pause durations at these sites suggests that eiders did not compensate for decreased feeding time by feeding more intensively, and may have experienced decreased energy intake. Eiders are long-lived birds and the local population probably consisted of birds which returned repeatedly to this site to overwinter. Many would have had previous experience with hunters and, indeed, eiders at Cape St. Mary's were very wary of human presence and flushed easily at any location at the sight of a person on the cliffs above or a boat on the water. However, eiders likely experienced a greater number of incidents at sites where hunters had access to the water and probably associated a greater level of risk with these areas.

I did not examine potential effects of weather on eider foraging, however, other studies have shown that foraging by diving ducks may be influenced by temperature and wind velocity and direction (Paulus 1984; Goudie and Ankney 1986; Bergan *et al.* 1989; Michot et al. 1994). Goudie and Ankney (1986) examined 2 temporal and 5 environmental variables in relation to time spent feeding by Common Eiders at Cape St. Mary's. Feeding increased with higher tide level and sea swell and decreased with decreasing temperature. Wind direction also affected foraging behaviour in that eiders fed less when in a crosswind and more when in the direct path of the prevailing winds. However, these environmental variables explained only 18% of the variation in time spent feeding. If I consider that some of the variation in the foraging parameters I observed were due to weather (< 18%, given that I have already accounted for daylength and tide level), it still leaves a substantial proportion of variation unexplained.

Year

Eiders spent less time pausing after dives for urchins in 1996 than in 1995, although year only accounted for three percent of the variation in pause duration. This suggests that eiders fed more intensively when feeding on urchins in 1996 than in 1995. Unfortunately, I have no data on prey abundance in either year. Other diving animals have shown changes in foraging behaviour in association with prey abundance, California Sea Lions *Zalopus californianus* feeding on mid-water schooling fish and squid increased feed bout durations in a poor food year (Feldkamp *et al.* 1989). In a year when their main prey was very low in abundance, Common Murres feeding on fish made shorter pauses for a dive of given duration, made longer foraging trips (which were a good indicator of number of dives/bout), and spent more time diving when at sea (Monaghan *et al.* 1994). Breeding Adelie Penguins feeding on Antarctic Krill *Eupahusia superba* and several species of fish extended foraging trip duration in a year of poor food availability and dived deeper and longer (Watanuki *et al.* 1993). However, total diving effort per day did not increase; it appeared extra time was spent travelling and searching for food but once a prey patch was found, the amount of time spent underwater did not increase. Blue-eyed shags *Phalcrocorax atriceps* feeding on bottom-dwelling fish foraged with more frequent and shorter duration feed bouts in a bad year (Kato *et al.* 1991). Clearly, low food abundance was associated with major changes in foraging patterns in all these species. I observed annual variation only in pause duration after dives for urchins. If the urchin population had been affected by environmental factors, I would have expected changes between years associated with feeding on mussels, either because eiders were more dependent on mussels in 1996 or because other marine invertebrates such as mussels were affected as well. To a human observer, 1996 was a milder winter with higher temperatures and less precipitation. Given the lack of annual variation in other foraging parameters and the lack of convincing evidence of a decline in urchin populations, it is difficult to attribute the annual variation in pause duration to low prey abundance.

CONCLUSIONS

Common Eiders wintering at Cape. St. Mary's intensified foraging efforts for mussels in response to tidal changes and seasonal prey depletion by reducing the amount of time spent on the surface between dives. However, there was no evidence of exhaustion or postponed recovery within the range of dives recorded and Common Eiders rarely exceeded an estimated aerobic dive limit. Dive duration and ecological factors explained only 35% and 43% of the observed variation in urchin and mussel pause duration, respectively. If Common Eiders were not maximizing foraging time at the bottom or optimizing breathing at the surface, what determined dive and pause duration? Part of the answer might be found in examining coordination of individual Common Eiders with their flockmates. Common Eiders form huge rafts in winter, feeding and resting together, even synchronizing diving and surfacing with flockmates. Flocking may an anti-predatory strategy (Hamilton 1971; Fox *et al.* 1994) and/or a way to increase the probability of finding patchy prey (Guillemette *et al.* 1993). I witnessed several incidents in which flocks were flushed by boats or planes and the few individuals who surfaced late found themselves in a group of only 2-3 birds when they had dived with a hundred or more. Each time, the stragglers were visibly alarmed and immediately stopped feeding to swim offshore. Whatever the reason for flocking, Common Eiders must gain a benefit from feeding in groups; diving and surfacing together would maintain cohesion while foraging underwater. A Common Eider unsuccessful at finding an urchin would, thus, terminate a dive in order to maintain contact with the flock rather than extend the dive duration. To date, foraging in diving vertebrates has been explained in terms of risk-sensitivity (Guillemette *et al.* 1992), breathing optimization (Kramer 1988), reduction in body heat loss (Nolet *et al.* 1993) and maximization of a currency such as energy intake (Ydenberg and Clarke 1989). However, diving in social foragers such as wintering Common Eiders may be more easily understood in terms of social interactions than currency maximization. In Chapter 4, I discuss diving by groups of Common Eiders and the possible benefits of social foraging.

Chapter IV
Diving in Groups: the Benefits of Social Foraging by Common Eiders

INTRODUCTION

Many animals are social and congregate with conspecifics at some point during their life cycle. For example, seabirds breed in large colonies (Jones 1992) and geese (Frederick and Klaas 1982) and shorebirds (Skagen and Knopf 1994) concentrate in staging areas during migration. Flocking behaviour associated with foraging is common in avian species (Carrascal and Moreno 1992; Poysa 1994; Benkman 1997) and, in diving birds, individuals within a group may not only feed and rest at the same time but synchronize the very movements associated with feeding, i.e., they submerge and surface as a group. Highly synchronized or progressive diving has been observed in many diving birds, including Common Eiders *Somateria mollissima* (Mudge and Allen 1980; Campbell 1978; Guillemette 1994), Steller's Eiders *Polysticta stelleri* (McKinney 1965), Oldsquaw *Clangula hyemalis* (Stewart 1967), Tufted Ducks *Aythya fuligula* (Pedroli 1982), Surf Scoters *Melanitta perspicillata* (Schenkeveld and Ydenberg 1985, Beauchamp 1992), Common Goldeneyes *Bucephala clangula* (Beauchamp 1992), Cormorants *Phalcrocorax carbo sinensis* (Van Eerden and Voslamber 1995), Red-breasted Mergansers *Mergus serrator* (Hending *et al.* 1962; Des Lauriers and Battstrom 1965) and Jackass Penguins *Spheniscus demersus* (Broni 1985; Wilson et al. 1986).

Several hypotheses have been proposed to explain social foraging and/or synchronized diving. For diving animals feeding on mobile prey, communal herding of prey by the group may increase foraging success (Des Lauriers and Brattstrom 1965). A switch to this type of foraging from almost exclusively solitary foraging in Cormorants *Phalacrocorax carbo sinensis* was associated with increased density of smaller prey and decreasing water visibility in a lake in the Netherlands (Van Eerden and Voslamber 1995). Synchrony may also develop in birds feeding on sessile prey when individuals in a flock follow each other to extremely localized food resources (McKinney 1965). Guillemette *et al.* (1993) suggested that such an information-sharing mechanism was behind the flocking of wintering Common Eiders. Eiders were subject to drift by currents and winds but maintained position over mussel beds by virtue of the fact that a portion of the flock was always diving and surfacing over the patch. Flocking may also serve to swamp potential kleptoparasites (Schenkeveld and Ydenberg 1985) or to increase detection and avoidance of predators (Hamilton 1971; Kenward 1978; Lazarus 1979; Fox *et al.* 1994). Finally, in the specific case where ice cover may threaten access to food by diving birds, the presence of a large number of birds can maintain open water (Sayler and Afton 1981).

The flocking and synchronized diving behaviour of Common Eiders wintering at Cape St. Mary's may be related to one or more of the above functions of social foraging, and in turn may explain some of the remaining 70% of variation in dive and pause patterns not explained by the ecological factors considered in Chapter III. Their preferred prey, mussels, exists in localized patches (Ryan 1985) and high winds and heavy seas common at this site may cause drift from the food patch. Avian predators are present, including Peregrine Falcons *Falco peregrinus*, Gyrfalcons *Falco rusticolus* and Bald Eagles *Haliaeetus leucocephalus* (personal observation), and kleptoparasitic gulls *Larus* spp. attempt to steal urchins as eiders surface from dives.

Synchrony in Common Eiders appeared to be most pronounced when eiders fed on mussels. This marked synchrony allowed me to time dive and pause durations of the flock as a whole. I was then able to test some of the hypotheses investigated for individual eiders, generally that eiders are anticipatory breathers when feeding on mussels and that eiders adjust pause and rest bout durations in response to ecological conditions. Because flocks were measured in a different way than individual activity, I have analysed dive cycle data collected on a flock level separately from data on individuals. The specific predictions tested were:

Predictions

Dive, handling and pause duration

i) *Reactive anticipatory breathing*: Eiders in flocks may exhibit anticipatory breathing when feeding on mussels and swallowing numerous mussels underwater during each dive.

ii) *Food availability*: a) *time of day* - Eider flocks may decrease pause duration at dusk and dawn because they feed intensively before and after the overnight fast; b) *tide level* - Eider flocks may decrease pause duration at low and falling tides to take advantage of decreased travel distance to bottom; c) *time of season* - Eider flocks may increase dive duration and decrease pause duration late in the season as prey depletion occurs.

iv) *Disturbance effects*: a) *predation* - Eider flocks may decrease pause duration at sites where predation is possible (i.e., at sites accessible by hunters) in order to shorten overall time spent inshore.

METHODS

Study Area

Common Eiders were observed in the Cape St. Mary's Ecological Reserve in southeastern Newfoundland. Detailed descriptions of the terrestrial and marine topography of the reserve are provided in Chapters I and III. I recorded group dives of Common Eiders only in 1996.

Measurement of Foraging Behaviour

Foraging behaviour of Common Eiders and determination of prey type was discussed in detail in Chapters I and III and will not be repeated here. The measurement of group dive cycles differs from that of individuals in that the submersion of the whole flock was timed. When feeding, most birds dived together or one after the other in a rapid fashion so that the whole flock was submerged within a matter of seconds. I began timing the start of a group dive when 50% of the flock submerged and started timing the pause when 50% reappeared at the surface. Duration of dive and pause were recorded (in seconds) using a stopwatch. This method has been used for other synchronously diving ducks such as Surf Scoters and Barrow's Goldeneye *Bucephala islandica* (Beauchamp 1992). All group dives were recorded in flocks feeding on mussels and, thus, there was no handling phase. Any dives or pauses which terminated in a panicked rush from the feeding site were not included in the analyses. I followed each flock through as many dive cycles as possible, until it moved out of sight or swam out to rest. Some flocks could be followed through several feed bouts and I considered each bout to be independent. Eider flocks often switched prey types or locations between bouts, and variables such as tide level, time of day, temperature and flock size also varied between bouts.

Environmental Conditions

Distance from shore and water depth are highly correlated at Cape St. Mary's (Goudie and Ankney 1986). I visually estimated distance from shore of the centre of a flock as an index of water depth. Flocks of 30 to several hundred eiders formed a tight, circular or elliptical mass over a mussel bed whereas large flocks of >800 birds formed long lines, about 10-20 birds in width, that ran parallel to shore. I also recorded relevant environmental, temporal and ecological variables: time of day, time of year, temperature, sea swell, cloud cover, precipitation, wind speed and direction and flock size. Tide levels were obtained from Tide and Current Tables published by the Department of Fisheries and Oceans.

Analyses

I analysed diving data using the SAS (SAS Institute 1990) program. All tests were 2-tailed and results were considered significant below a probability level of a = 0.05. The overall relationship between dive and pause was calculated using all dive cycles for all flocks. Dive and pause duration were averaged per bout per flock and these mean values were used in subsequent analyses. Ecological variables were entered along with previous dive duration into a stepwise multiple regression with pause duration as the dependent variable. Dive duration, time of year, distance from shore, count, and flock size were entered as continuous variables. Categorical variables such as predation (hunting present vs. absent), time of day (dawn, 0500-0859, and dusk, 1630-2100, vs. midday, 0900-1629) and tide level (low and ebbing vs. high and flooding) were coded as dummy variables. The regression model provided partial r^2 values for each independent variable, indicating the amount of variation in pause duration explained by a particular factor, after controlling for the effect of all other variables. Except where otherwise specified, statistics and values presented in all figures apply to the residual values of continuous variables.

RESULTS

Use of mean values, and independence of flocks and bouts

To determine whether mean values were representative of a flock's behaviour during a feed bout, I examined dive and pause duration in sequences of 5 or 10 dive cycles. There was no difference among flocks regarding changes in pause duration with sequence number (ANCOVA for 10 cycles, flock*seq. no. $F_{[15,77]} = 1.8$, $P = 0.050$; for 5 cycles, flock*seq. no. $F_{[19,31]} = 0.3$, $P = 0.998$) and pause duration remained constant throughout bouts (ANCOVA, for 10 cycles, seq. no. $F_{[1,77]} = 2.0$, $P = 0.159$; for 5 cycles, seq. no. $F_{[1,31]} = 0.02$, $P = 0.887$). Although dive duration did change in different ways among flocks (ANCOVA for 10 cycles, flock*seq. no. $F_{[16,123]} = 3.1$, $P = 0.0002$; for 5 cycles, flock*seq. no. $F_{[25,88]} = 1.8$, $P = 0.030$), overall, dive duration did not change with sequence number (ANCOVA, for 10 cycles, seq. no. $F_{[1,123]} = 2.8$, $P = 0.096$; for 5 cycles, $F_{[1,88]} = 1.0$, $P = 0.310$). The significant flock effect for both dive duration (ANCOVA, for 10 cycles, flock $F_{[16,123]} = 17.8$, $P = 0.0001$; for 5 cycles, $F_{[25,88]} = 12.7$, $P = 0.0001$) and pause duration (ANCOVA, for 10 cycles, flock $F_{[15,77]} = 8.6$, $P = 0.0001$; for 5 cycles, $F_{[19,31]} = 2.6$, $P = 0.008$) was probably due to the variation in conditions under which each flock was observed: e.g., date, time, tide, weather conditions, depth. Therefore, I concluded that dive and pause duration remained relatively constant throughout a feed bout and that mean values were representative of a flock's behaviour during that bout.

Mean durations per flock per feed bout were used to generate overall mean dive and pause durations of dive cycles. Group dives by eiders feeding on mussels were 26.8 ± 4.6 seconds and group pauses were 32.0 ± 12.4 seconds (Fig. IV-1).

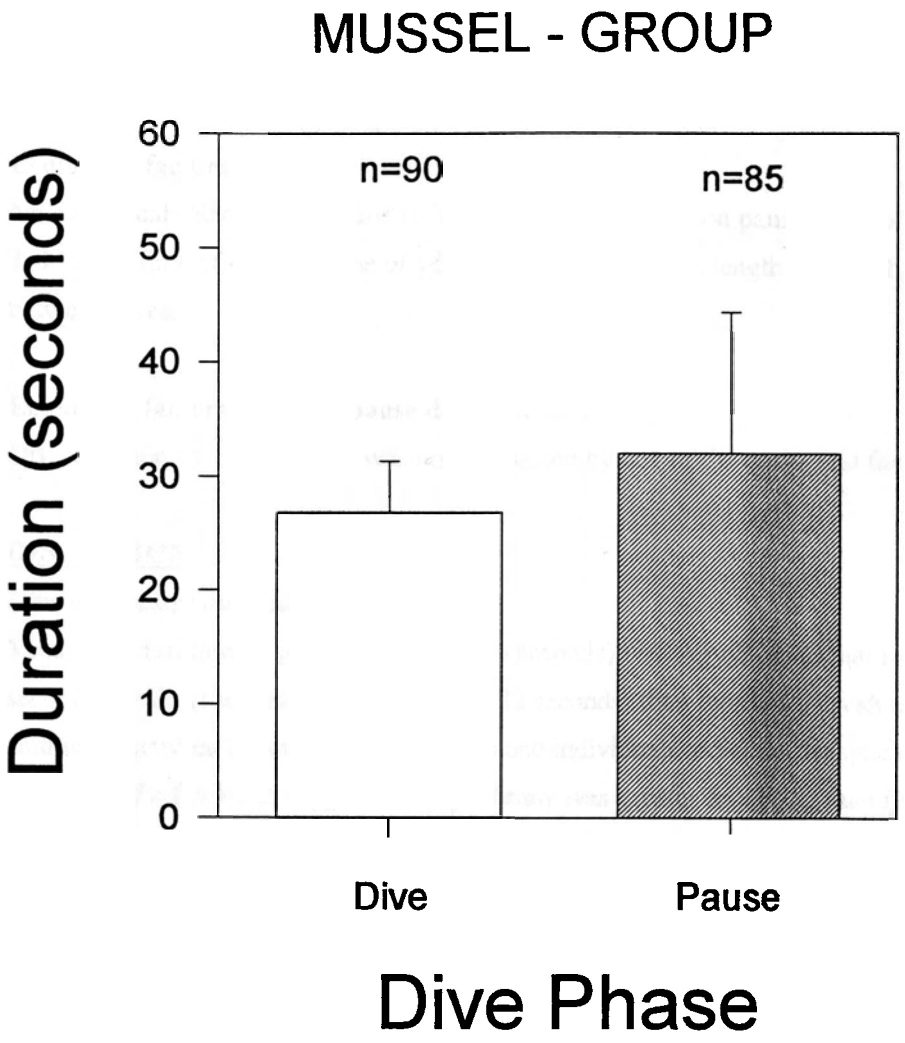
Relationship between dive and pause duration

Reactive vs. anticipatory breathing

For all dives by flocks, I compared two regression equations which differed in whether I used dive preceding or following the pause. Using the following dive increased the explanatory power of the equation slightly from 4% to 15%. This was not a large increase in explanatory power and is not a strong indication that eiders are anticipatory breathers. Hence, I used previous dive duration in subsequent analyses.

The overall relationship between dive and subsequent pause was positive and linear for group dives for mussels. The regression equation is Pause = 18.27 +0.52 (Dive) ($r^2 = 0.037$, $n = 307$, $P < 0.001$). Although longer pauses followed longer dives, a quadratic term added to the equation was not significant ($P = 0.33$),

Figure IV-1. Mean dive duration (± 1 s.d.) of each phase (dive and pause) of dive cycles by groups of Common Eiders feeding on mussels. Sample size (number of feed bouts for which mean durations were obtained) is at top of bars.


MUSSEL - GROUP
n=90
n=85
Duration (seconds)
0
10
20
30
40
50
60
Dive
Pause
Dive Phase

indicating there was no acceleration in pause duration over the range of dives observed. The stepwise multiple regression model confirmed this significant relationship between dive and pause; dive duration explained 17% of the total variation observed in group pause duration after other factors are considered (Table IV-1). Pause duration increased with dive duration (Fig. IV-2).

Ecological factors affecting pause duration

No ecological factors were found to have significant effects on pause duration (Table IV-1) by eider flocks. Tide level, time of day and time of year did not influence the length of time that eider groups paused between dives.

Ecological factors affecting pause duration

Dive duration by eider groups was not influenced by any of the ecological factors tested (Table IV-2).

DISCUSSION

Dive and pause duration

Mean dive duration by groups of eiders (26 seconds) was very close to that recorded for individuals (27 seconds) while group pauses were longer (32 seconds) than those of individuals (26 seconds). The general similarity between mean values for groups and individuals indicates the synchrony of activity among members of a flock but suggests that synchrony was greater for diving than for surfacing. Schenkeveld and Ydenberg (1985) found that Surf Scoters also exhibited greater synchrony when diving. Beauchamp (1992) demonstrated that diving synchrony increased with flock size in Surf Scoters and Common Goldeneyes and suggested that the reduction in interbird distance in large flocks required even tighter cohesion to avoid crashing among flockmates and loss of prey. This argument would apply to smaller flocks too.

The analysis of group data did not indicate that eiders were anticipatory breathers when feeding on mussels. The 11% increase in explanatory power of the dive/pause regression equation that resulted from using the following dive instead of the preceding dive was not large enough [illegible] confirm that eiders were loading oxygen for an upcoming dive. Previous dive duration accounted for more of the variation in pause duration for groups of eiders (17%) than for individuals (9%) but it still was still quite low and suggested other factors influenced pause duration.

Ecological factors affecting pause duration, and comparison with individual dives

However, none of the ecological variables tested had an effect on pause duration by groups. Tide level had a highly significant effect on the pause duration of individual eiders and I expected a similar result in the multiple regression analysis for groups, especially considering the greater sample size. It is possible that the loss of synchrony that evidently occurred while birds were underwater, and which led to a longer pause

Table IV-1. Results of stepwise multiple regression model for pause duration by groups of Common Eiders feeding on mussels (n=88).

Variable	r^2	*P*
dive duration	0.174	0.0001
distance from shore (depth)	<0.01	NS
year [a]	---	---
sex [b]	---	---
julian date	<0.01	NS
tide level	<0.03	NS
time of day	<0.06	NS
flock size	<0.04	NS
gull [c]	---	---
predation	<0.03	NS
number of dives in sequence	<0.02	NS

[a] Group dives only recorded for flocks in 1996
[b] All birds in flock observed as one unit
[c] Gulls did not attend flocks feeding on mussels

Figure IV-2. Relationship between dive and pause duration of Common Eider groups feeding on mussels.

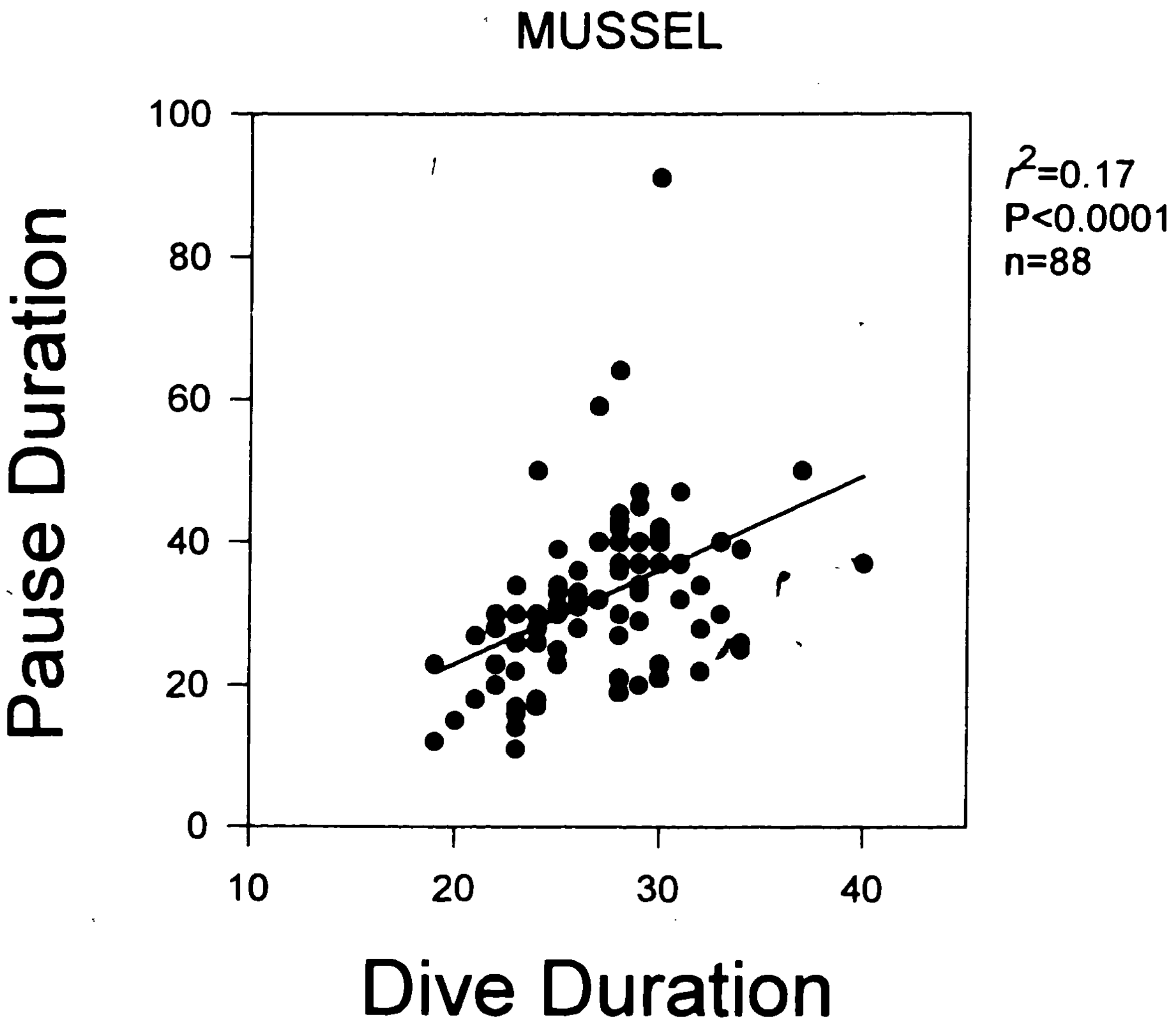

MUSSEL
r^2=0.17
P<0.0001
n=88
Pause Duration
100
80
60
40
20
0
10
20
30
40
Dive Duration

Table IV-2. Results of stepwise multiple regression models for dive duration by groups of Common Eiders feeding on mussels (n=93).

Variable	r^2	P
distance from shore (depth)	<0.03	NS
year [a]	---	---
sex	<0.01	NS
julian date	<0.01	NS
tide level	<0.01	NS
time of day	<0.01	NS
flock size	<0.01	NS
gull [b]	---	---
predation	<0.01	NS
number of dives in sequence	<0.01	NS

[a] Dive cycles for mussels only recorded in 1996
[b] Gulls only attended flocks feeding on urchins

duration recorded for groups, masked any adjustments in pause duration which may have been made by groups in response to the ecological varaibles measured. If so, it points to the importance of monitoring individuals within synchronously diving groups in order to resolve patterns in diving behaviour. Radiotelemetry would be a valuable, albeit expensive, tool for tracking individuals in large, synchronous groups. Visual observation of focal individuals is obviously limited in some ways (e.g., obtaining information on complete series of dives) but offers several advantages, including identification of prey type, flock size, presence or absence of predators and/or kleptoparasites, and knowledge of atypical activities such as the extension of a pause duration for courting or the abrupt panicked end to a feed bout.

Time of season also had a significant effect on pause duration of individuals but not of groups. Although I started recording data on groups in mid-January, the majority of observations occurred in March and April when I began observing large groups of > 1000 birds feeding on mussels at Cat's Cove and Redland Point. Although I cannot be sure these groups were present at these sites early in the season, it is likely they moved inshore to feed once safer, offshore sites had become depleted (R.I. Goudie, pers. comm.). Guillemette et al. (1996) documented substantial removal of mussels from reefs by wintering Common Eiders in the Gulf of St. Lawrence and concluded that prey depletion affected the eiders' distribution and movement among mussel reefs. Whether similar movements occurred at Cape St. Mary's or not, the apparent bias in my sample towards the end of the winter may have made it difficult to find seasonal effects on pause duration.

Benefits of social foraging and synchronous diving

Flocking behaviour may confer several advantages to individuals within a group, including a decreased risk of predation to an individual (Hamilton 1971) through several mechanisms. Predators may be more easily detected through increased vigilance simply because, as group size increases, there are more eyes scanning the environment for predators (Pulliam 1973; Lima 1995). Individual vigilance has been shown to decline with group size in many avian species (Poysa 1994; Lima 1995) and lead to inceased foraging rates (Elgar 1986; Metcalfe 1989; Carrascal and Moreno 1992). Bustnes (1993) demonstrated that Common Eider females accompanied crèches in the brood-rearing season to exploit the increased vigilance of brood-caring females. Flocking behaviour by Common Eiders during the brood-rearing period is well-known and is often explained in terms of reduction of predation to ducklings (Gorman and Milne 1972; Munro and Bedard 1977). Females that did not care for young but which foraged in or near crèches spent significantly more time feeding than lone females or females feeding in flocks.

Flocking may also decrease the probability of predation of an individual through confusion of the predator or diluted predation risk to individuals of large flock size. White-headed Ducks *Oxyura leucocephala* foraged alone at night but congregated with others in large rafts during preening and resting periods (Fox *et* *al.* 1994). Although larger groups were more likely to be subject to frequent and prolonged attacks by predatory gulls *Larus* spp., synchronous diving of the ducks confused gulls which were usually only successful once an individual was separated from the group and exhausted by repeated attacks. Since ducks grouped more tightly *after* gulls attacked and dived to escape, Fox *et al.* (1994) concluded that rafting did not appear to be related to predator detection or deterrance, but that individuals benefited from the confusion effect of synchronous diving by the group and by the dilution effect. In the Gulf of St. Lawrence, avian predators of Common Eiders were common and flocking was suggested to be, in part, a predator evasion tactic (Guillemette et al. 1993). On several occasions, I observed eiders at Cape St. Mary's fly out from an inshore feeding site when a falcon or eagle flew by. Birds sometimes pattered across the surface of the water for a short distance before taking to flight but this appeared to be the result of difficulty in becoming airborne rather than a deliberate attempt to confuse a predator. More commonly, the sudden appearance of a seal led to a panicked response. Sometimes, a group of eiders that had been submerged burst out of the water and propelled themselves forward and away over the water surface by beating their wings, simultaneously massing together. When this happened, I usually saw a seal surface quietly in the location where the eiders had been feeding. If a seal appeared near a flock sitting on the surface, the birds would adopt an alert posture, group together very tightly, and swim quickly away Seals did appear to attack birds on a couple of occasions, although I could not be sure of the outcome, and local hunters reported seeing seals attacking duck decoys. Presumably, detection and evasion of underwater predators is also enhanced by flocking behaviour. Ainley (1972) described Adelie Penguins *Pygoscelis adeliae* as highly social in all seasons, feeding, travelling, and bathing in flocks (Ainley 1972). Flocking in penguins may increase efficiency of prey location and capture (Williams 1995) and may also be a response to the presence of the Adelie Penguin's major predator, Leopard Seals *Hydrurga leptonyx*. Adelie Penguins hesitated to enter the water alone, dove into the water as a group, and porpoised in unison through the zone where seals often hunted to bathe 50 m beyond the surf (Ainley 1972). Individuals bunched more tightly together in the presence of a human or seal and spaced out again when the threat passed.

Just as flocking may swamp predators, it may swamp kleptoparasites. A bird surfacing with prey would be less likely to be singled out by a kleptoparasite if it surfaced simultaneously with many individuals rather than surfacing alone or with just a few other birds. Similarly, a bird would have to dive and retrieve prey at the same time as flockmates in order to ensure it was ready to surface with them. This was presumed to be the mechanism driving synchronous diving in Surf Scoters which exhibited greater synchrony when attended by kleptoparasitic Glaucous-winged Gulls *Larus glaucescens* (Schenkeveld and Ydenberg 1985). Foraging synchrony similarly benefited Common Eiders handling urchins in the presence of gulls at Cape St. Mary's. Eiders did not appear to adjust prey selection criteria in the presence of gulls, i.e., dive or handling duration did not change when gulls were nearby, but it is possible eiders minimized the risk of of kleptoparasitism by choosing urchins similar in size to those being eaten by flockmates. Assuming handling duration increases with increasing urchin size, an eider with an atypically large urchin might still be handling it after flockmates had swallowed their urchins, and, thus, become targeted by a kleptoparasite. Because I have no measure of consistency in handling times among flockmates in the presence/absence of gulls, I cannot conclude eiders chose urchins close in size to those being chosen by flockmates, but it seems plausible.

Although Ingolfsson (1969) documented Herring Gulls *Larus argentatus* and Greater Black-backed Gulls *L. hyperboreus* stealing prey (most likely mussels) from Common Eiders, gulls did not attend eiders feeding on mussels at Cape. St. Mary's since eiders swallowed mussels underwater. The maintenance of synchrony among eiders not at risk from kleptoparasitic gulls, i.e., when feeding on mussels, suggests that there are other benefits of flocking. Beauchamp (1992) found no effect of gull presence on synchrony in Surf Scoters or Common Goldeneyes. In this study, kleptoparasitism was relatively infrequent, but synchrony was still quite high. Beauchamp (1992) suggested that ducks maintained synchrony to avoid collision between individuals and subsequent loss of prey when a flock was feeding over a mussel bed. Collisions among eiders feeding on mussels at Cape St. Mary's could cause injury but would be unlikely to lead to loss of prey since eiders swallowed mussels underwater.

Information-sharing among individuals in a group is another benefit of flocking. For example, an experimental study of Red-winged Blackbirds showed that naïve flock members discovered new food sources and used them more quickly by following experienced birds (Avery 1994). For birds such as Common Eiders feeding on patchy prey, associating with others offers the same advantage. Guillemette et al. (1993) found that 95% of Common Eiders wintering in the Gulf of St. Lawrence congregated in flocks of > 300 birds. The authors suggested that information exchange was responsible for flocking behaviour in a site where wind and currents could carry eiders away from a localized food source, the mussel beds. The only birds feeding in small flocks of less than 30 individuals (Guillemette *et al.* 1992) were underweight and were feeding mainly on crabs which were difficult to find but which offered very high energy return once captured. Eiders in small flocks were dispersed and diving activities were poorly synchronized (Guillemette 1994). Synchrony among members searching for rare and unevenly distributed prey such as crabs may actually be a disadvantage since it would probably curtail search time by some individuals.

While information-sharing benefits group members in finding food (Ward and Zahavi 1973), it also means food has to be shared once found. In some birds, increased population density is associated with increased interference competition. For example, in oystercatchers *Haematopus palliatus*, increased population size led to increased aggression (Vines 1980), decreased ingestion rates and increased dispersion rates (Ens and Goss-Custard 1984). Increased flock size in White-winged Crossbills *Loxia leucoptera* corresponded with increased agonistic encounters and decreased feeding rates by subordinate age-sex classes (Benkman

1997). However, feeding flocks of Common Eiders in winter can be as large as 17,000 birds (Bourget *et al.* 1986) and aggression is rarely observed (Campbell 1978, Goudie and Ankney 1988). Guillemette *et al.* (1993) noted that eiders increasingly crowded onto mussel reefs as population size increased, rather than dispersing and using more reefs, indicating that the benefits of flocking matched or outweighed any possible costs. At Cape St. Mary's, eiders sometimes occurred in mixed flocks with Black Scoters *Melanitta nigra* which foraged almost exclusively on mussels (Goudie and Ankney 1986) yet there was no conclusive evidence of interference competition between the two species (Goudie and Ankney 1988).

I witnessed only one incident of attempted kleptoparasitism of eiders by conspecifics, in which an immature male followed an adult female in possession of an urchin. Since I found no mention of intraspecific kleptoparasitism in other accounts of eider foraging ecology (Nilsson 1970; Player 1971; Campbell 1978; Goudie and Ankney 1988; Guillemette *et al.* 1992), I assume it is rare and, therefore, not a cost of flocking in eiders.

CONCLUSIONS

In summary, the variety of contexts in which flocking behaviour by Common Eiders is evident, including brood-rearing (Gormon and Milne 1972; Munro and Bedard 1977), moulting (Palmer 1976; Madge and Burn 1988; Frimer 1995) and wintering (Bourget *et al.* 1986; Goudie and Ankney 1988; Guillemette *et al.* 1993), suggests that flocking may have several functions. It is likely an antipredator behaviour which decreases predation risk to an individual through increased vigilance and the dilution effect. Synchrony while diving is obviously important to maintaining cohesion, since birds which stay underwater too long or dive later than the others may lose contact with the flock. Several times, I observed a few individuals become isolated from the flock as a result of prolonging dives. The rest of the flock flew off while the "stragglers" were still underwater. Upon surfacing and finding themselves in a flock of only two or three birds, the remaining individuals appeared alarmed, quit foraging, and quickly moved offshore. Flocking and synchrony in dive cycles would swamp kleptoparasitic gulls when eiders fed on urchins. Synchrony among eiders feeding on mussels is more likely an information-sharing mechanism which allows eiders to maintain position over a food patch (mussel bed), especially when currents and strong winds contribute to drift.

Whatever the benefits of group foraging, maintaining contact with flockmates above and below the surface must require eiders to occasionally curtail or extend dive and pause duration. Thus, coordination of activites may explain some of the variation remaining in pause duration after consideration of physyiological and ecological factors.

Chapter V
Synthesis

SUMMARY

I studied diving and foraging behaviour of wintering Common Eiders at Cape St. Mary's Ecological Reserve in southeastern Newfoundland. My main objective was to investigate adjustments in diving patterns in relation to ecological conditions. I first tested the assumption that eiders are "reactive" breathers. i.e., the amount of time an eider spends at the surface between dives is related to the duration of the dive it has just completed rather than the expected duration of an upcoming dive ("anticipatory" breathing). There was a positive, linear relationship between pause and previous dive duration, regardless of prey type. Substituting the following dive for previous dive in this regression equation did not improve the explanatory power of this relationship and I, therefore, concluded that eiders were reactive breathers and did not optimize surface breathing time, as predicted by Kramer's optimal breathing model. Common Eiders at Cape St. Mary's rarely exceeded an estimated aerobic dive limit of 83 seconds and typically spent more time at the surface between dives than necessary to replenish oxygen stores. Thus, it appears eiders did not regularly incur physiological debt nor postpone recovery, as suggested by Ydenberg and Guillemette (1991) for Common Eiders in the Gulf of St. Lawrence. The relatively short duration of dives suggested that eiders were not maximizing bottom foraging time. Dive and pause durations varied according to prey type, with dives and pauses being longer when eiders fed on urchins than when they fed on mussels. There were no sex or age differences in diving performance, either because body size differences between cohorts were not sufficient to affect diving ability, eiders were not diving near their physiological limits, or because all individuals in a flock were coordinating diving activity.

The results of multiple regression models incorporating ecological factors showed that, as predicted, eiders adjusted foraging effort in response to several ecological conditions. Changes observed as the winter progressed, including shorter durations between dives for mussels, longer resting bouts after mussel feed bouts, longer urchin dive durations and shorter urchin handling times, were consistent with possible prey depletion of invertebrate populations. When feeding on mussels at low and falling tides, eiders spent less time on the surface between dives and fed for longer durations, presumably to take maximum advantage of lower water depths and, hence, decreased travel time to the bottom. Dive and pause duration were unrelated to the number of dives performed in a series, time of day or to disturbance effects such as risk of kleptoparasitism or hunting. However, eiders fed for shorter durations at sites where predation by hunters was possible. Dive duration and ecological factors explained only 35% and 43% of the observed variation in urchin and mussel pause duration, respectively.

While untested variables such as weather conditions may have accounted for some of the remaining unexplained variation, it is likely that a substantial proportion of that variation was due to social behaviour, i.e., coordination of individual Common Eiders with their flockmates. Eiders fed and rested together in large groups and synchronized diving and pausing activity while feeding. Flocking in eiders may provide one or more benefits to individuals, including increased detection of predators, decreased risk of predation and kleptoparasitism through the dilution effect, and information exchange regarding the location of patchy prey, especially mussels, at a site where wind and currents cause drift of eiders away from the food patch. Synchrony in diving and surfacing is necessary to maintain cohesion within the group and some individuals must inevitably adjust dive and pause duration to keep in contact with flockmates. Social interactions should, therefore, be considered along with physiological and ecological factors when investigating diving patterns of social foragers such as Common Eiders.

FUTURE DIRECTIONS

This type of study would be complemented by a laboratory component in which the aerobic dive limit of Common Eiders was determined through analysis of blood lactate after dives of various durations. An ADL determined through physiological measurements would unequivocally resolve the question of whether eiders were incurring oxygen debt after prolonged dives. It would also be a useful benchmark for other studies of diving birds as the only species for which such a measurement is presently available is the Weddell Seal. Similarly, laboratory experiments with freely-diving eiders could provide information on the time necessary for eiders to replenish oxygen stores at the surface. Data on blood gas tensions during surface intervals and/or data on ventilation rates between dives would address this issue.

The use of time-depth recorders (TDR's) and radiotransmitters would provide valuable information that is difficult or impossible to get from visual observations of unmarked individuals. Diving performance could be continuously montitored over a period of weeks, with TDR's recording depth, dive and pause durations, and the time at which dives occur. Ascent and descent rates and transit and bottom times could also be estimated from these types of data. Of course, capture of Common Eiders (in order to deploy and retreive monitoring equipment) at this site may well be impossible due to the topography, rough seas and the general wariness of eiders of all human activity. However, it could be more easily accomplished with flightless males during the moulting season or nesting females during the breeding season. Female Common Eiders feed intensively during this time in order to lay down fat reserves before a month-long incubation fast, and a study of their diving and foraging activity during this period would be especially interesting.

Visual observation of marked individuals should not be overlooked, however, since it can provide information not available from the above equipment, including presence/absence of predators and kleptoparasites, location, weather conditions, flock size, or the occurrence of an event such as the abrupt ending of a dive or foraging bout as a result of a scare. It would also allow observation of several individuals simultaneously and provide valuable insight on individual variation between flockmates. This would allow a test of the idea that a negative correlation may exist between dive and pause duration, i.e., that an individual which surfaced later than its flockmates would have a relatively short pause because it would submerge again quickly in order to remain with the group. Such data would elucidate the influence of social factors on dive and pause duration.

Ingestion of cold invertebrates and water by eiders may lead to body cooling. Body temperature could be monitored in a laboratory setting to confirm whether temperature does indeed fall during a feed bout and, if so, whether rewarming occurs between dives or during rest bouts. One could quantify the possible costs and benefits of such body cooling, including extension of ADL as a result of lower metabolic rate and, therefore, lower rate of oxygen consumption while diving, and the cost of rewarming.

In conjunction with the above, digestive constraints could be investigated in the lab. For example, the efficiency of digestion and/or warming of a meal may vary according to prey type or size, or meal size.

MANAGEMENT IMPLICATIONS

The changes observed in foraging activity of eiders throughout the winter strongly suggest seasonal depletion of urchin and mussel populations in and around the Cape St. Mary's Ecological Reserve. Because food is limited, offshore feeding sites such as the rocks known as the Bull, Cow and Calf should be included within the reserve in order to ensure that eiders have access to these significant feeding sites. Encompassing this site and banning boat activity within the reserve are important to conservation of eiders in this area. It is common for hunters to use speedboats to flush ducks out of the reserve, in which hunting is prohibited, and drive them towards the Bull, Cow and Calf, where hunting is legal. In the winter of 1996, locals reported that over 400 eiders were shot in this manner - an estimate that is probably lower than the true number and which does not include crippling losses.

In addition to exposing the ducks to hunting by forcing them into unprotected waters, boat disturbance causes birds to leave areas where they commonly feed and usually not return for several days, in contrast to interruptions in feeding caused by naturally occurring events such as the appearance of a seal, after which ducks resume feeding within minutes. When forced into offshore waters, ducks may have to dive deeper to obtain food or concentrate in larger than normal numbers at limited shoal feeding sites. Either situation may lead to a decreased energy intake for individual ducks. The birds are also unable to gain shelter from harsh weather if confined to offshore sites. If the situation is prolonged or repeated, it could lead to weight loss which may result in decreased winter survival and/or decreased breeding success for underweight birds.

Similarly, ducks may be flushed out of feeding areas by the presence of people on the cliffs above. The tendency of eiders to decrease feed bout durations at sites where people have access to the water emphasizes the birds' sensitivity to disturbance. Cape St. Mary's Ecological Reserve has become increasingly popular as a tourist destination and winter activity is also being promoted by the Parks and Natural Areas Division. The vulnerability of eiders to disturbance should be kept in mind, however, and inexperienced groups should be accompanied by a guide, in the same way that tourists must be escorted by guides onto island seabird colonies under the Division's jurisdiction.

Sea urchin and kelp harvesting and mussel aquaculture are growing industries in Newfoundland and may pose problems for eiders in several ways. Obviously, removal of sea urchins and of kelp, which provides habitat for mussels, would put even greater pressure on an eider population already declining in numbers and experiencing seasonal declines in prey abundance. Therefore, these activities should be prohibited within the reserve. Commercial growers of mussels often experience trouble with eiders feeding on artificially created mussel beds and attempt to resolve the situation by shooting the birds. If such aquaculture operations are established in the Placentia/St. Mary's Bays, the staff of Cape St. Mary's Ecological Reserve could have an important role to play in educating mussel farm operators and the general public about the futility of coping with the problem in this way and the threat that such action poses to the local eider population.

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