

# Behaviour of Harlequin Ducks and three species of scoters wintering in the Queen Charlotte Islands, British Columbia

R. Ian Goudie<sup>1</sup>

Pacific Wildlife Research Centre, Canadian Wildlife Service, 5421 Robertson Road, Delta, BC, Canada V4K 3N2

## Abstract

Diving behaviour and activity budgets were determined for Harlequin Ducks *Histrionicus histrionicus* and three species of scoters (*Melanitta* spp.) wintering in the Queen Charlotte Islands, British Columbia. Harlequin Ducks had the most diverse behavioural repertoires. Based on over 100 hours of behavioural sampling, the four species of sea ducks spent in excess of 60% of daylight hours in feeding activities. There was a general pattern of increased feeding from fall to winter, when daylight was shorter and inclement weather more frequent (ranging from an average of 52% of daylight hours in October to 71% in February). Harlequin Ducks did not spend significantly more time feeding than the larger scoters. Relatively mild climatic conditions, availability of energy-rich foods, and extensive shallow-water habitat may account for the lack of body size effect. Linear regression models indicated no significant relationship with environmental variables, whereas tidal regimes accounted for significant variation in proportion of time spent feeding in Black Scoters *M. nigra* and especially Harlequin Ducks. Harlequin Ducks decreased feeding activity with rising tides and increasing amplitudes, whereas Black Scoters increased feeding with increasing tidal amplitude.

Harlequin Ducks and White-winged Scoters *M. fusca* exhibited the highest dive to pause ratios, although the difference from the Surf *M. perspicillata* and Black scoters was not marked. The analyses for sequence effects indicated that Harlequin Ducks and White-winged Scoters might defer full physiological recovery between dives during a diving sequence. Some possible explanations might include optimizing foraging during suitable tidal regimes, limited daylight hours during feeding in winter, optimal foraging of mobile prey items (e.g., crabs), and synchronized flock vigilance to minimize predation.

## Résumé

On a établi le comportement de plongée et l'emploi du temps des Arlequins plongeurs (*Histrionicus histrionicus*) et de trois espèces de macreuses (*Melanitta* spp.) hivernant dans les îles de la Reine-Charlotte, en Colombie-Britannique.

Les Arlequins plongeurs présentaient le répertoire comportemental le plus diversifié. Selon un échantillonnage de plus d'une centaine d'heures, les quatre espèces de canards de mer consacraient plus de 60 p. 100 des heures de clarté des activités d'alimentation. On a observé un accroissement général de ces activités de l'automne à l'hiver, au moment où les heures de clarté étaient plus courtes et le temps, moins clément (allant d'une moyenne de 52 p. 100 des heures de clarté en octobre à 71 p. 100 en février). Les Arlequins plongeurs n'ont pas passé beaucoup plus de temps à se nourrir que les macreuses de plus grande taille. Des conditions climatiques relativement douces, la disponibilité d'aliments riches en énergie et un vaste habitat de petits fonds peuvent expliquer l'absence d'effets reliés à la taille du corps. Des modèles de régression linéaire n'ont indiqué aucune relation significative avec les variables environnementales, tandis que les régimes de marée étaient liés à une importante variation de la proportion de temps consacré aux activités alimentaires chez les Macreuses noires (*M. nigra*), en particulier chez les Arlequins plongeurs. Ces derniers diminuaient leurs activités alimentaires avec la montée des marées et l'accroissement des amplitudes, tandis que les Macreuses noires se nourrissaient davantage avec l'accroissement des amplitudes.

Les Arlequins plongeurs et les Macreuses à ailes blanches (*M. fusca*) présentaient la plus forte proportion de plongeurs par rapport aux pauses, bien que la différence avec les Macreuses noires et à front blanc (*M. perspicillata*) n'ait pas été marquée. Les analyses des effets de séquence ont indiqué que la récupération physiologique complète des Arlequins plongeurs et des Macreuses à ailes blanches ayant lieu habituellement entre les plongeurs pourrait être reportée durant une séquence de plongeon. Les explications possibles à cela peuvent inclure l'optimisation de la récolte durant les périodes de marée favorables, le nombre limité d'heures de clarté propices à l'alimentation en hiver, la récolte optimale de proies mobiles (p. ex. les crabes) et la surveillance synchronisée des volées pour réduire au minimum la prédation.

<sup>1</sup> Current address: Harlequin Conservation Society, Eastern Office, 17 Waterford Bridge Road, St. John's, NF, Canada A1E 1C5.

## 1.0 Introduction

In northern marine biomes, feeding activity and diets may be significantly influenced by body size. For example, Goudie and Ankney (1986) demonstrated that smaller species of sea ducks spent proportionately more time feeding and had diets that yielded a higher energy per unit mass of food. Smaller species adjusted activities less in relation to deteriorating environmental conditions. The ratio of pause length to the preceding dive length has been suggested to indicate diving efficiency (e.g., Dewar 1924; Nilsson 1970). Diving behaviour may set upper limits to habitat use by species of sea ducks, as the pause time to recover from dives increases exponentially beyond a certain threshold of water depth. For example, Nilsson (1970) suggested that this may explain the more northerly midwinter distribution of male Common Goldeneye *Bucephala clangula* compared with the smaller females in coastal Sweden.

Specific habitat use by sea ducks has been poorly documented. For the four species in this study, epibenthic foods are pried from the substrate using the chisel-shaped bills with strong down-curved terminal nails in water depths generally less than 10 m (Bellrose 1976). Harlequin Ducks use rocky shorelines, whereas scoters may use sandy through boulder-cobble to bedrock substrates (Stott and Olson 1973; Bellrose 1976; Hirsch 1980; Goudie and Ankney 1988).

Sea ducks spend some, or all, portions of the annual life cycle on marine habitats. Little is known of the ecology and demography of sea ducks in the north Pacific, where many populations are declining (Goudie et al. 1994). Relatively large populations of sea ducks occur in winter in the Queen Charlotte Islands (hereafter called Haida Gwaii), and especially large aggregations occur during migration and the annual feather moult (Savard 1988; Campbell et al. 1990). Large concentrations of sea ducks in coastal British Columbia, notably scoters (*Melanitta* spp.), are probably related to the mild environmental conditions, high productivity of nearshore waters, the general lack of hunting interest, and abundance of refuge areas.

This study focused on aspects of the ecology of four species of sea ducks — namely, White-winged Scoter *M. fusca*, Surf Scoter *M. perspicillata*, Black Scoter *M. nigra*, and Harlequin Duck *Histrionicus histrionicus* — in Haida Gwaii in winter. Data collection was focused in the area of Skidegate Inlet but also included the eastern shore of Graham Island north to Tlell and the area of McIntyre Bay around Yakan Point and Tow Hill (Fig. 1). Specific objectives were 1) to determine the time-activity budgets and 2) to compare diving behaviour among the four species.

## 2.0 Methods

### 2.1 Activity budgets

Observations of flocks of sea ducks were balanced across species and three time periods: namely, dawn–11:00, 11:00–14:00, and 14:00–dusk. Each sampling unit consisted of a 30-minute watch of a “species” flock with scans every 60 seconds, during which individuals were allocated to the behaviours outlined in Table 1. After each 30-minute watch, a different flock or species was selected. Observations for each watch were summed and the totals converted to proportions.

Figure 1  
Map of study area

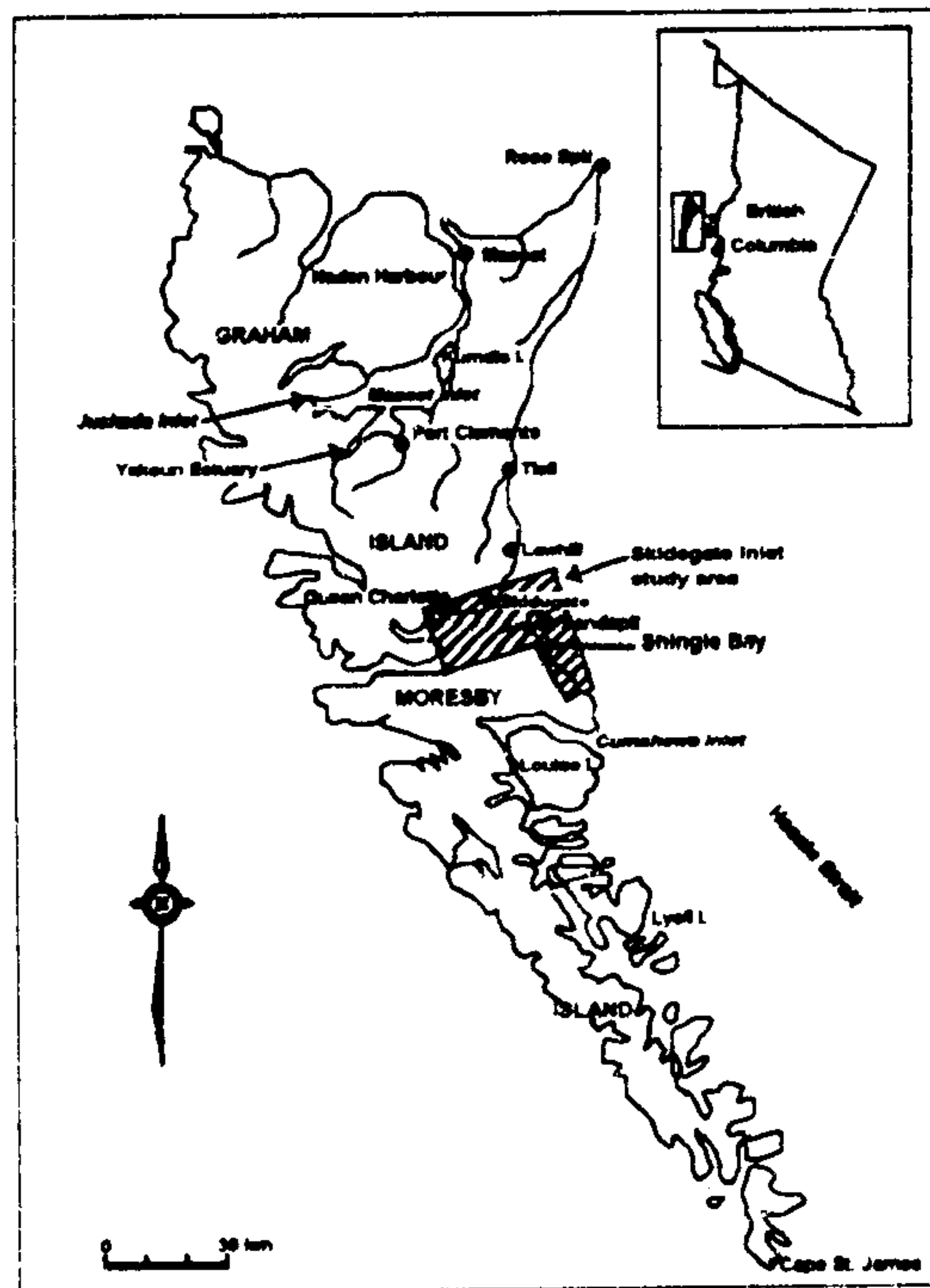


Table 1  
Behaviours recorded and categories used in this study

Category	Behaviours recorded
Feeding bout	Peer Dip Dive Pause Submerge
Resting bout	Rest Preen Haul out
Locomotion	Swim Fly
Social	Agonistic Courtship

### 2.2 Diving behaviour

Data on sequential dives and pauses were collected using a digital stopwatch. Individuals engaged in feeding bouts were observed, and an attempt was made to record a maximum of 10 sequential dives and pauses. Afterwards, a different individual of the same or different species was selected. Sea ducks generally alternate feeding periods (10–20 minutes) with resting periods of similar duration, during which they process captured prey through the muscular gizzard (see Ydenberg and Guillemette 1991).

## 2.3 Data analyses

Behavioural watches (30 minutes) were summed and converted to proportions that were transformed to arcsine square roots (after Zar 1974) for parametric statistical testing (mainly linear regression). Proportions of time spent feeding or resting were regressed on sea state, tidal amplitude (to nearest 0.1 m), tide cycle, time of day, month, wind speed (km/hour), wind direction, ambient temperature, dewpoint, air pressure (kPa), precipitation, and cloud cover (%). Only independent variables that contributed significantly to the model were retained. The following transformations were applied to independent variables: temperature as degrees Kelvin; wind direction sine (east-west components) and cosine (north-south components).

Dummy variables were created for wind influence (light/no winds, onshore winds, crosswinds, lee winds) and time of day (morning, midday, and afternoon). Precipitation was entered as a rank variable (0 = none, 1 = patchy fog, 2 = solid fog, 3 = mist/light rain, 4 = heavy rain, 5 = light snow, 6 = heavy snow). Sea state was entered as an estimate of wave height to nearest 0.1 m. Tidal cycle was entered as a categorical dummy variable (low slack, rising, high slack, ebbing). Month of observations was entered as an ordinal variable (October = 1 to February = 5).

Differences in proportions of time spent feeding, resting, or in social behaviour were tested using the non-parametric Kruskal-Wallis test. For significant findings, the significant interactions were ascertained using Mann-Whitney U tests.

For diving behaviour, the data collected per feeding bout (usually 5–10 sequential dives) were grouped and the mean values used in order to meet the assumptions of independent data. The length of pause (seconds) was regressed on the length of dive. Interspecific comparisons were made using the dive to pause ratio of the independent mean values calculated above. Differences among species were tested using analysis of variance (ANOVA) and multiple range tests. The relationships between the residuals of the dive-pause regression to dive length and sequence number were analyzed to assess if there was an influence of sequence on the relationship of pause to dive.

## 3.0 Results

### 3.1 Activity budgets

#### 3.1.1 Overall time budgets

In total, 209 watches of 30-minute duration were achieved, for an effective sample of 104.5 hours divided among the four species of sea ducks. Behavioural repertoires were most diverse in the Harlequin Duck (Fig. 2), notably because of the additional foraging strategies of peering and dipping. Dipping was used inshore to obtain food at receding tide lines or amongst floating algae (especially *Fucus* spp.) and was similar to the foraging techniques of dabbling ducks (tribe Anatini). Peering may have been of value in locating suitable substrates or prey items and was similar to techniques used by the mergansers (*Mergus* spp.). Only Harlequin Ducks hauled out of water during resting bouts (Fig. 3), a behaviour that permits the resightings of coloured alphanumeric tarsal bands for studies of demography and philopatry (see Robertson et al., this volume).

#### 3.1.2 Time budgeted to foraging

Overall, the four species in this study budgeted a similar proportion of time to feeding ( $P > 0.50$ ), averaging from 61% to 68% of the daylight hours. There was a general pattern for feeding to increase through the winter period, ranging from an average of about 52% of daylight hours in October to 71% of daylight hours in February, when weather was most inclement (Fig. 4). There was no relationship of body size to proportion of time spent feeding ( $P > 0.90$ ).

The general patterns of foraging indicated some apparent interspecific differences. For example, Harlequin Ducks increased the proportion of daylight budgeted to feeding from October to January but subsequently decreased it in February, whereas White-winged Scoters increased proportion of time feeding in each subsequent month and Surf Scoters maintained similar proportions of time feeding in January and February. Black Scoters decreased feeding in January but increased proportion of time budgeted to feeding in February (Fig. 4).

#### 3.1.3 Time budgeted to courtship and agonistic behaviour

Courtship and agonistic behaviours were relatively uncommon (1–2% of budget) and appeared most frequently in Harlequin Ducks and Surf Scoters. Their low levels are consistent with the high flock synchrony and long-term pair bonds observed in sea ducks (Robertson et al. 1998).

#### 3.1.4 Environmental influences on foraging

The stepwise multiple regression models suggested that proportion of time spent feeding was not significantly influenced by ambient temperature, dewpoint, air pressure, wind speed, or wind direction ( $P > 0.10$ ). Tide cycles and amplitude strongly influenced feeding activities for two species. Harlequin Ducks decreased feeding with rising tides ( $P = 0.024$ ) and increased feeding with decreasing tidal amplitude ( $P < 0.0001$ ) ( $F_{2,66} = 11.45$ ,  $P < 0.0001$ ,  $R^2 = 0.249$ ), in the following relationship:

$$\% \text{ of time feeding} = 1.403 - 0.097 \text{ amplitude} - 0.177 \text{ rising tides}$$

Black Scoters increased feeding with higher tidal amplitude ( $P = 0.25$ ) and increased feeding with rising tides ( $P = 0.014$ ) ( $F_{2,45} = 3.39$ ,  $P < 0.05$ ,  $R^2 = 0.131$ ) according to the following relationship:

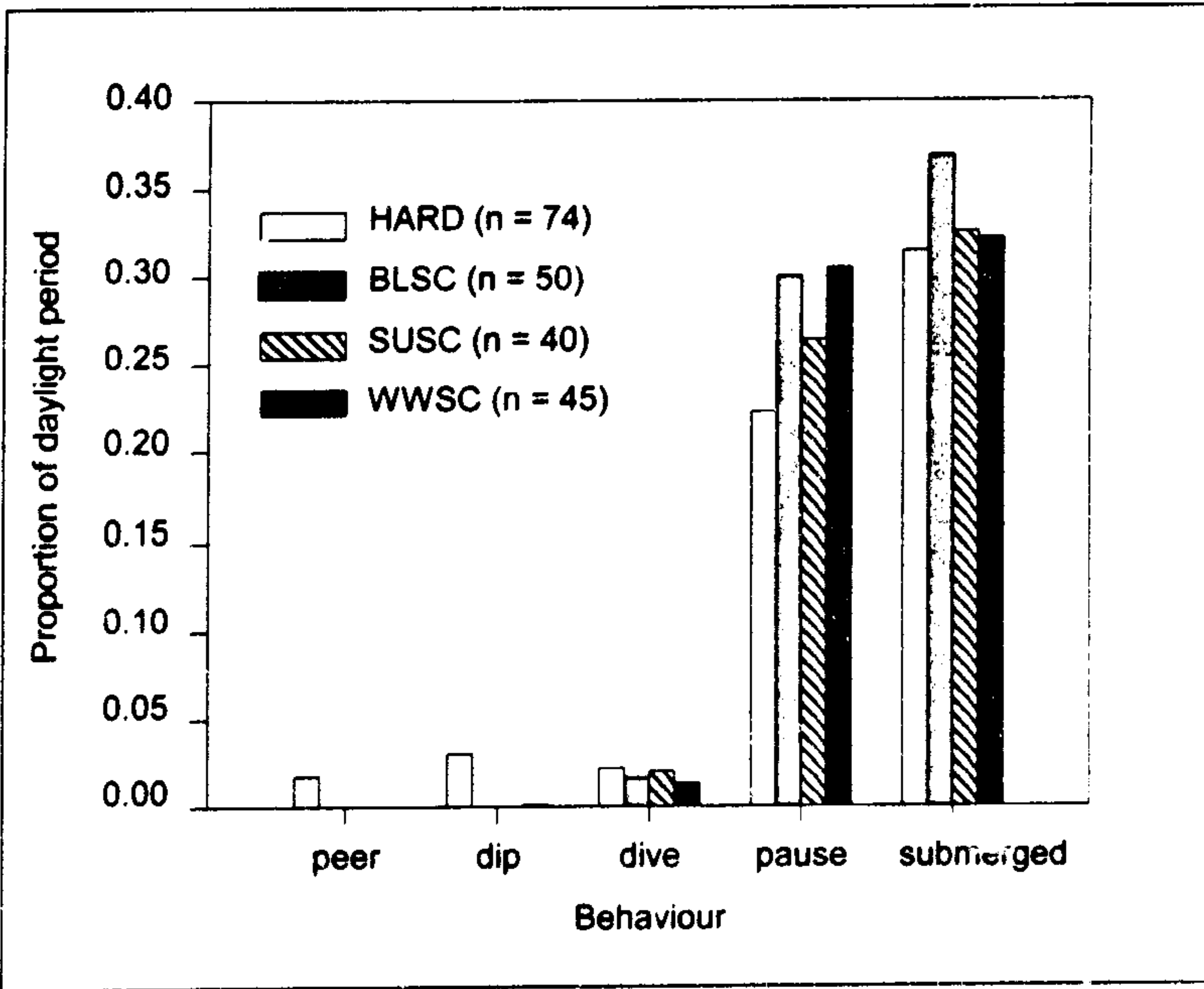
$$\% \text{ of time feeding} = 0.701 + 0.034 \text{ amplitude} + 0.222 \text{ rising tides}$$

The pattern of increased feeding with increasing tidal amplitude ( $P = 0.136$ ), rising tides ( $P = 0.031$ ), and ebbing tides ( $P = 0.019$ ) was somewhat evident in White-winged Scoters, although the overall model was not significant ( $F_{3,39} = 2.329$ ,  $R^2 = 0.152$ ,  $P = 0.089$ ). There was no apparent relationship of feeding behaviours of Surf Scoters to tidal cycle and amplitude ( $P > 0.50$ ).

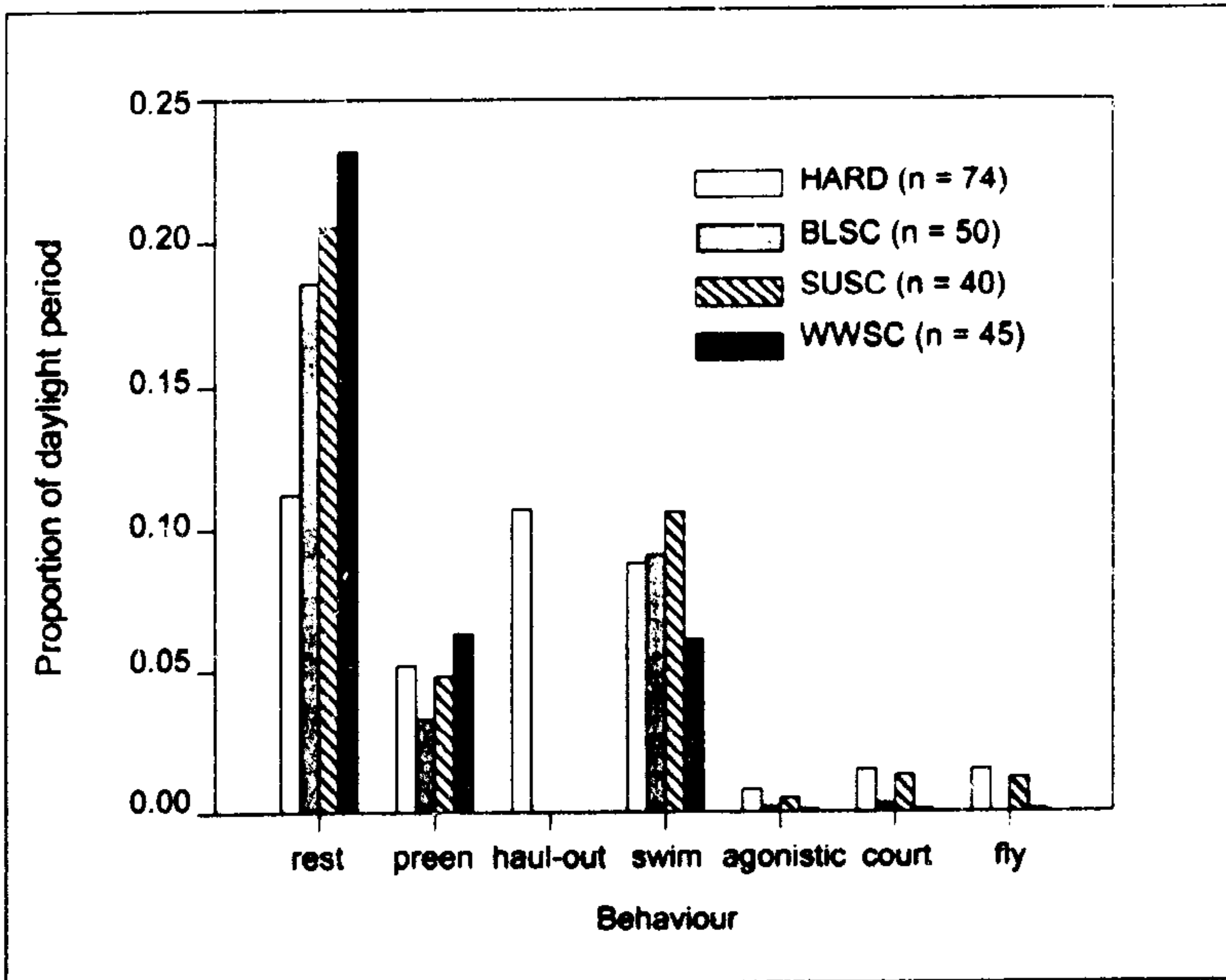
### 3.2 Diving behaviour

Average lengths of dives and pauses were highest in the larger species (Table 2). The ratio of the length of the dive to the subsequent pause was highest for the Harlequin Duck and White-winged Scoter and lower for the other two

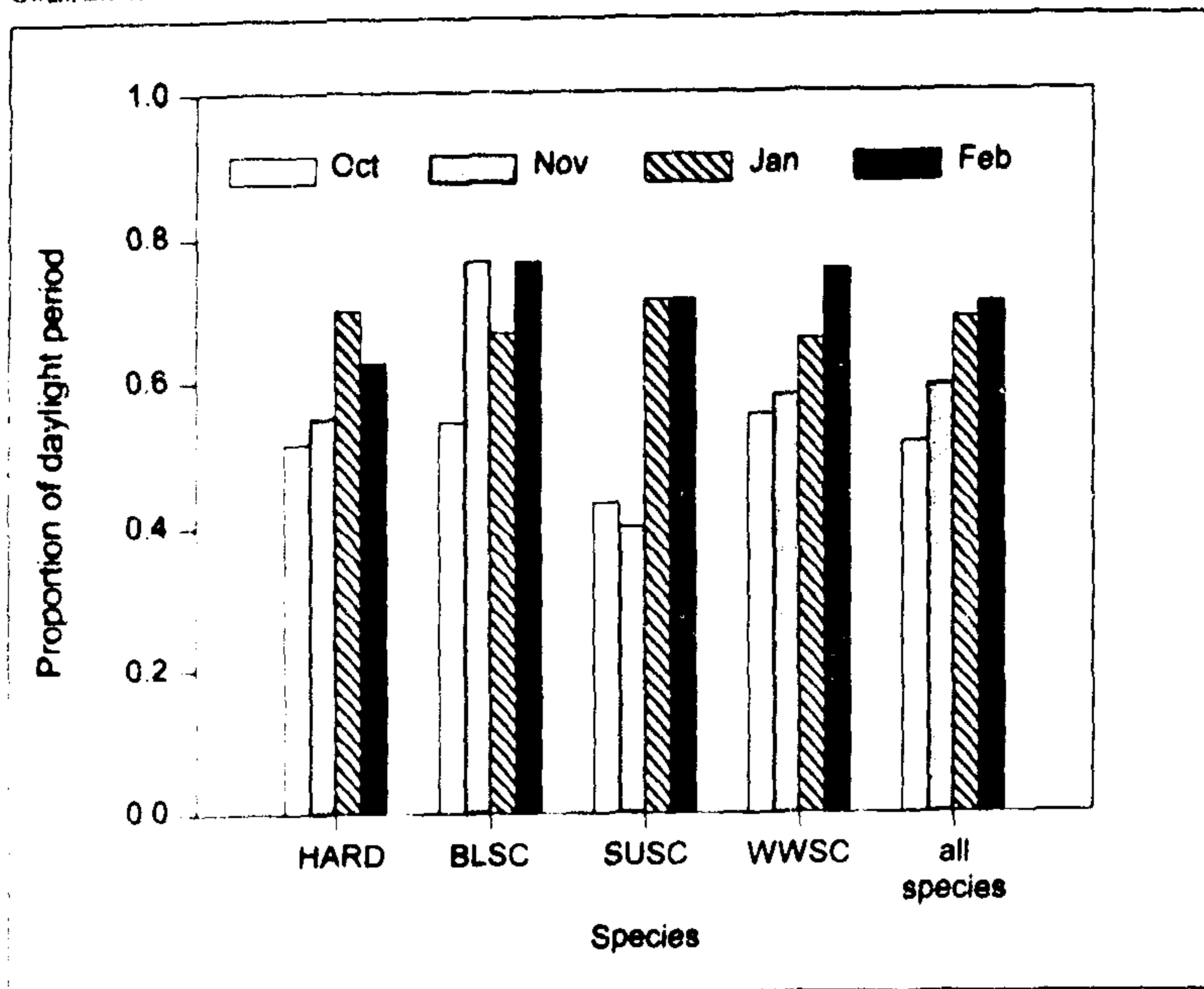
**Figure 2**  
Time spent in various feeding behaviours by four species of sea ducks wintering in Haida Gwaii, British Columbia



**Figure 3**  
Time spent in nonfeeding behaviours by four species of sea ducks wintering in Haida Gwaii, British Columbia



**Figure 4**  
Proportion of daylight hours spent foraging over the winter season by four species of sea ducks wintering in Haida Gwaii, British Columbia



**Table 2**  
Mean lengths of dive and pause for sea ducks wintering in Haida Gwaii, British Columbia

Species	n	Mean dive length $\pm$ SD (s)	Mean pause length $\pm$ SD (s)	Dive:pause ratio
Harlequin Duck	368	21.7 $\pm$ 7.4	12.0 $\pm$ 6.3	1.81
Black Scoter	162	23.3 $\pm$ 8.0	17.7 $\pm$ 9.5	1.32
Surf Scoter	96	34.9 $\pm$ 16.7	23.3 $\pm$ 19.7	1.49
White-winged Scoter	196	31.7 $\pm$ 8.0	17.8 $\pm$ 8.6	1.78

\* Ratios are based on all data (i.e., not segregated by cycles).

species of scoters. In general, Black Scoters and Surf Scoters displayed much higher variance than Harlequin Ducks and White-winged Scoters (Table 2).

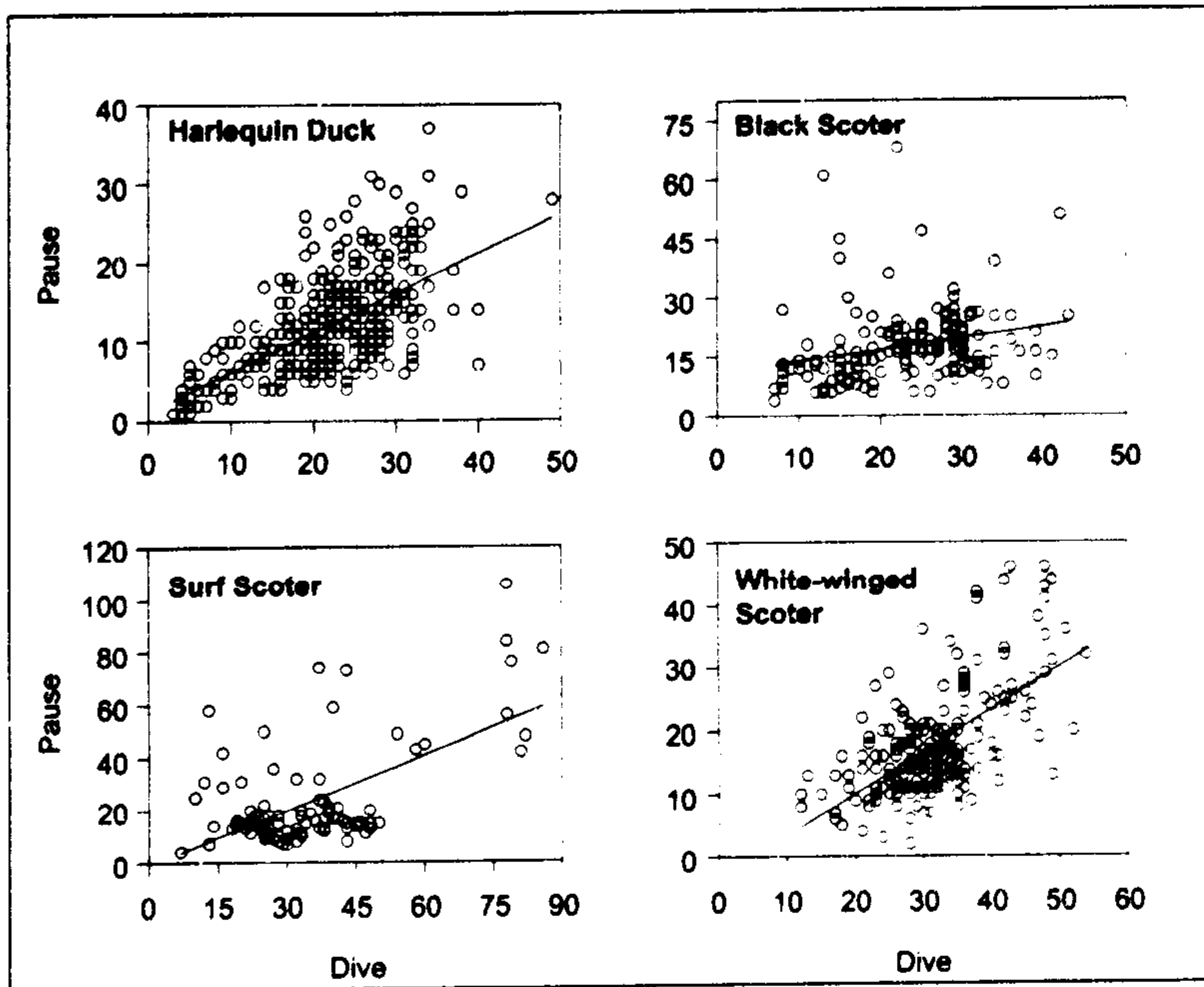
There were also considerable differences in the relationship of pause to the preceding dive for the three species of scoters. White-winged Scoters demonstrated proportionately longer pause times (steeper slope) than Surf Scoters, which generally paused longer than Black Scoters (Fig. 5).

In analyzing the relationship of pause to preceding dives, it was apparent that use of all sequential data may have violated the assumptions of parametric statistics (independence of samples), as data and residuals were strongly truncated. Use of average values for each collected series in a bout (cycle) resulted in somewhat higher values for the dive-pause relationship (Table 3). However, using these mean values considerably increased the power of the regression coefficient; for example, for Harlequin Ducks and White-winged Scoters,  $R^2$  was increased from 0.35 and 0.38 to 0.55 and 0.74, respectively. However, there was still

evidence of truncation in the data when using mean values per cycle, as indicated by the increasing variance in pause length with increasing dive length seen in Harlequin Ducks (Fig. 6). This suggested that some individuals may have incurred a physiological debt, as proportionately longer pauses may be necessary for longer dives, and that the length of the pause may be influenced by the sequence number within the feeding bout.

The relationship of the length of pause to the length of the preceding dive was affected by dive sequence. In Harlequin Ducks and White-winged Scoters, there was a positive relationship between the residuals of the dive-pause regression with dive length and sequence number — i.e., the length of pauses accelerated as sequence increased (Table 4). This suggested that Harlequin Ducks and White-winged Scoters may defer complete physiological recovery when into a feeding cycle.

**Figure 5**  
Relationship between dive and subsequent pause (in seconds) in four species of sea ducks wintering in Haida Gwaii, British Columbia



**Table 3**  
Mean lengths of dive and pause for each bout of sea ducks wintering in Haida Gwaii, British Columbia

Species	n (bouts)	Mean dive length $\pm$ SD (s)	Mean pause length $\pm$ SD (s)	Dive:pause ratio <sup>a</sup>	CV
Harlequin Duck	45	22.7 $\pm$ 6.8	12.9 $\pm$ 5.3	1.90 $\pm$ 0.59	0.31
Black Scoter	25	26.2 $\pm$ 7.2	18.6 $\pm$ 1.4	1.72 $\pm$ 0.94	0.54
Surf Scoter	14	33.4 $\pm$ 18.3	25.3 $\pm$ 18.4	1.69 $\pm$ 0.89	0.53
White-winged Scoter	24	33.2 $\pm$ 7.6	19.8 $\pm$ 7.8	1.78 $\pm$ 0.36	0.20

<sup>a</sup> Ratios are based on mean value per dive cycle.

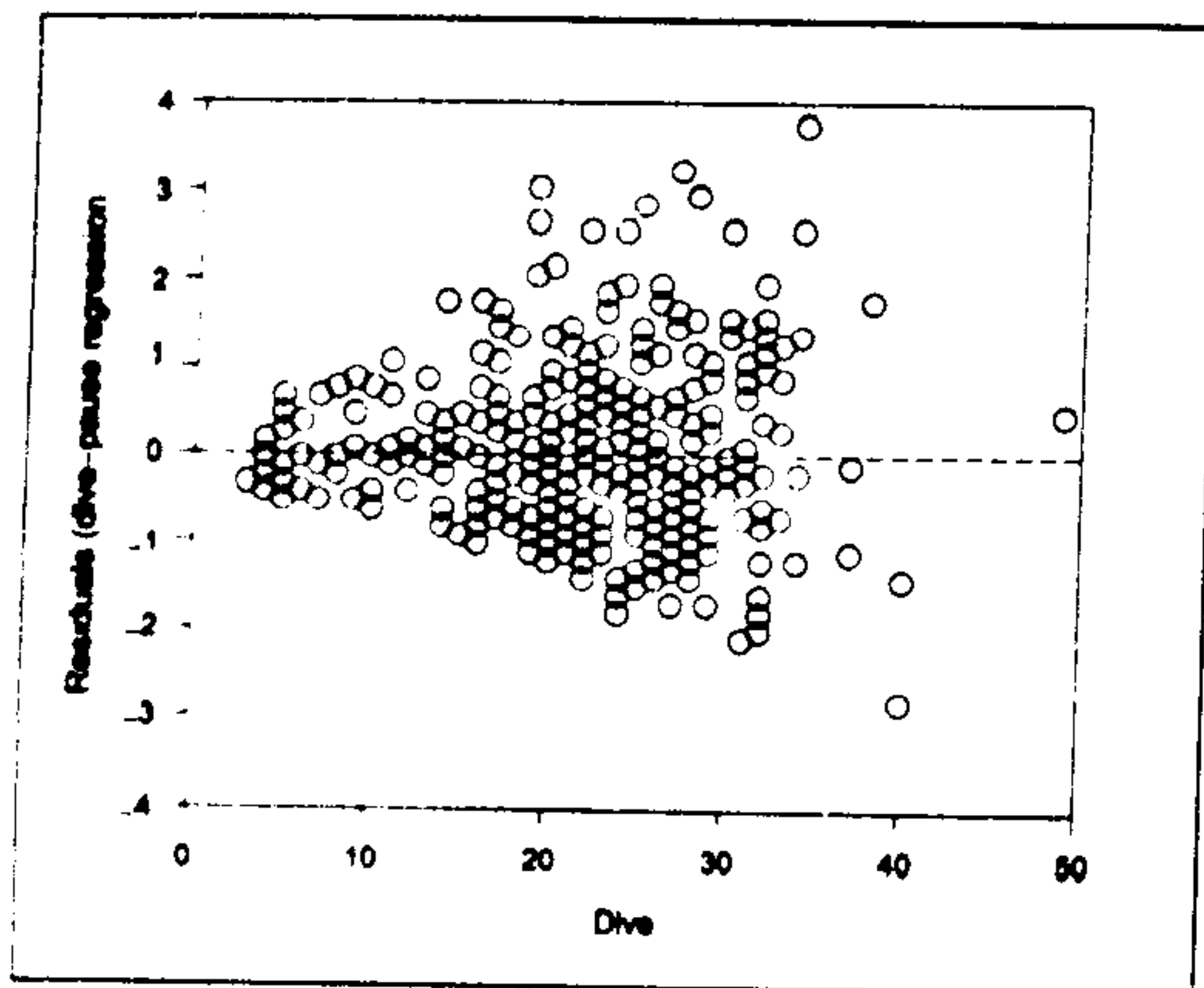
#### 4.0 Discussion

##### 4.1 Activity budgets

In Haida Gwaii, the four species of sea ducks in this study foraged for similar durations during the winter, averaging about 65% of daylight hours. This contrasts sharply with studies in the northwest Atlantic, where smaller species such as Harlequin Duck spent longer periods of daylight seeking food. Goudie and Ankney (1986) proposed that thermodynamic implications of small body size might require smaller species to forage more and select higher-quality foods because of the allometric relationship of body size to metabolic rates and heat loss. For this study, the differences in body size were less pronounced for the scoter species — i.e., White-winged Scoter: females (f) = 1200 g, males (m) = 1500 g; Surf Scoter: f = 900 g, m = 1000 g; Black Scoter: f = 800 g, m = 1100 g; Harlequin Duck: f = 558 g, m = 687 g (from Dunning 1993).

There are two proposed explanations for the lack of a demonstrated body size effect in this study in Haida Gwaii: climate and water depth. The winters in Haida Gwaii are mild, and ambient temperatures only rarely drop below freezing. Therefore, much feeding activity occurs in the range of thermoneutrality, where allometric implications of metabolic rate and body size would not be expected to manifest (Calder 1974). In this study, Harlequin Ducks foraged mostly in very shallow waters and even spent considerable periods dipping for food amongst algae along the shoreline or along receding tide lines. Scoters foraged entirely by diving in deeper waters, and this was especially the case for the Surf Scoter, which foraged at the greatest distance from shore. Hence, Harlequin Ducks were likely feeding more intensely but in shallower water, and this reduced the proportion of the day required for foraging activities — i.e., less transit time to substrates. Goudie and Ankney (1986) suggested this explanation to account for the high proportion of daylight spent in feeding by the

**Figure 6**  
Relationship between dive length (in seconds) and standardized residuals from a regression of dive length on pause length in Harlequin Ducks wintering at Haida Gwaii, British Columbia



**Table 4**  
Relationship of the standardized residuals of the regression of dive to pause on dive length and sequence number within dive cycles for Harlequin Ducks and White-winged Scoters wintering in Haida Gwaii

Species	Linear regression	R <sup>2</sup>	Probability
Harlequin Duck	Residuals = 0.12 + 0.011 Dive + 0.037 Sequence	0.05	F <sub>2,104</sub> = 9.61 P < 0.0001
White-winged Scoter	Residuals = -0.353 + 0.002 Dive + 0.05 Sequence	0.042	F <sub>2,101</sub> = 4.22 P < 0.02

deep-diving Oldsquaw *Clangula hyemalis* at Cape St. Mary's, Newfoundland.

The strong relationship of Harlequin Ducks to tidal regimes in Haida Gwaii demonstrated the close tracking of the shallow-water zone by this species. At Cape St. Mary's, Harlequin Ducks fed closer to shore in more shallow waters than other sea ducks (Goudie and Ankney 1986). A weak pattern of increased feeding with rising tides in Black Scoters and White-winged Scoters might be explained by inundation, enabling individuals to access intertidal molluscs, which are important prey for these species (Vermeer and Bourne 1984).

Foraging might be expected to increase in these diurnal feeders in winter, when daylight is short and weather conditions worsen. This appears to be the general case for the study area, as feeding time ranged from roughly 50% of daylight hours in fall up to 70% or more in January–February. During winter, water temperatures are cooler, environmental conditions deteriorate, and prey items often yield minimum energy per unit consumed. These findings are consistent with a hypothesis that winter conditions might impose greater demographic constraints on sea duck populations than conditions at other times of the year.

#### 4.2 Diving behaviour

The relationship of the length of the dive to the length of the pause has been interpreted to infer diving ability (Dewar 1924; Nilsson 1970). In Haida Gwaii, major

interspecific differences were not evident in the species studied, although the highest ratio was evident for the Harlequin Duck, closely followed by the White-winged Scoter. The dramatic values reported for Harlequin Ducks by some authors were not evidenced here (e.g., 4:1 in Pool 1962).

For sea ducks, a complete dive cycle comprises underwater time, during which prey are captured, and surface time between successive dives. Surface time is used for recovery from the physiological effects of diving — i.e., oxygen depletion and lactic acid buildup in muscle tissue (anaerobic metabolism) — and food handling (Ydenberg 1988). Mean dive length is a general indication of mean water depth in which individuals are feeding. Hence, the lowest average dive length recorded (21.7 seconds) suggests that Harlequin Ducks are feeding in shallower waters than the inshore Black Scoters (23.3 seconds), White-winged Scoters (31.7 seconds), and the more subtidal Surf Scoters (34.9 seconds). These dive lengths may also provide some indication of foraging strategy. For example, the White-winged Scoters frequently fed inshore in the same range as Black Scoters but displayed higher bottom times and often emerged some distance from the site of submergence, in contrast to the other three species.

The role of sequence in dive cycle has been little investigated in sea ducks. Some waterbird species, such as Western Grebes *Aechmophorus occidentalis*, may defer aerobic metabolism between dives in an effort to maximize catch success on schooling fish prey (Ydenberg and Forbes 1988). Ydenberg and Guillemette (1991) demonstrated that, at least at a low level, Common Eiders *Somateria mollissima* may accumulate physiological debt — i.e., use anaerobic metabolism during dive cycles. Examination of the relationship of pause to preceding dives in Harlequin Ducks and White-winged Scoters in Haida Gwaii suggested that individuals may defer complete physiological recovery during dives early in each cycle or bout, as relatively longer pauses were taken for the same dive length later in the cycle. Explanations for this phenomenon may include the maximization of foraging during optimal tidal cycles, optimal foraging once mobile prey are located (e.g., small crabs by Harlequin Ducks), or synchronized flock vigilance, to minimize predation rates or to maximize food intake during limited daylight. Sea ducks are thought to forage during feeding bouts until the gullet is full, after which individuals enter a resting bout, during which food is processed through the muscular gizzard (see Goudie and Ankney 1986; Ydenberg and Guillemette 1991). The surface time during the resting bout (usually 20–30 minutes) would provide plenty of time for physiological recovery due to oxygen depletion during diving and thereby optimize catch per unit effort during diving cycles.

#### Acknowledgments

The development of this study was encouraged by Rick McKelvey of the Pacific Wildlife Research Centre. My stay while in the Skidegate Inlet area was made especially comfortable by Bonny Wasleski (Seaport Bed and Breakfast). Further thanks go to Stuart H. Jackson for field assistance. Margo Hearne provided the location of some potential sea duck sites near Masset.

## Literature cited

- Bellrose, F.C. 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, Pennsylvania. 544 pp.
- Calder III, W.A. 1974. The consequences of body size for avian energetics. Pages 86-151 in R.A. Paynter (ed.), Avian energetics. Nuttall Ornithological Club 15, Cambridge, Massachusetts.
- Campbell, R.W.; Dawe, N.K.; McTaggart-Cowan, I.; Cooper, J.M.; Kaiser, G.W.; McNall, M.C.E. 1990. The birds of British Columbia. Vol. 1. Nonpasserines: Introduction, loons through waterfowl. Royal British Columbia Museum/Canadian Wildlife Service, Victoria. 514 pp.
- Dewar, J.M. 1924. The bird as a diver. H.F. and G. Witherby, London.
- Dunning, J.B. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, Florida.
- Goudie, R.I.; Ankney, C.D. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology 67:1475-1482.
- Goudie, R.I.; Ankney, C.D. 1988. Patterns of habitat use by sea ducks wintering in southeast Newfoundland. Ornis Scand. 19:249-256.
- Goudie, R.I.; Brault, S.; Conant, B.; Kondratyev, A.V.; Petersen, M.R.; Vermeer, K. 1994. The status of sea ducks in the North Pacific Rim: toward their conservation and management. Trans. North Am. Wildl. Nat. Resour. Conf. 59:27-49.
- Hirsch, K.V. 1980. Winter ecology of sea ducks in the inland marine waters of Washington. MSc thesis, University of Washington, Seattle. 92 pp.
- Nilsson, L. 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. Oikos 21:145-154.
- Pool, W. 1962. Feeding habits of the Harlequin Duck. Wildfowl Trust Annu. Rep. 13:126-129.
- Robertson, G.J.; Cooke, F.; Goudie, R.I.; Boyd, W.S. 1998. The timing of pair formation in Harlequin Ducks. Condor 100:551-555.
- Savard, J.-P. L. 1988. A summary of current knowledge on the distribution and abundance of moulting sea ducks in the coastal waters of British Columbia. Can. Wildl. Serv. Tech. Rep. Ser. No. 45, Pacific and Yukon Region, Delta. 82 pp.
- Stott, R.S.; Olson, D.P. 1973. Food-habitat relationships of sea ducks on the New Hampshire coastline. Ecology 54:996-1007.
- Vermeer, K.; Bourne, N. 1984. The White-winged Scoter diet in British Columbia waters: resource partitioning with other scoters. Pages 30-38 in D.N. Nettleship, G.A. Sanger, and P.F. Springer (eds.), Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.
- Ydenberg, R.C. 1988. Foraging by diving birds. Proc. Int. Ornithol. Congr. 19:1832-1842.
- Ydenberg, R.C.; Forbes, L.S. 1988. Diving and foraging in the Western Grebe. Ornis Scand. 19:129-133.
- Ydenberg, R.C.; Guillemette, M. 1991. Diving and foraging in the Common Eider. Ornis Scand. 22:349-352.
- Zar, J.H. 1974. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, New Jersey.