

Foraging Behavior and Resource Partitioning by Diving Birds During Winter in Areas of Strong Tidal Currents

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Abstract.—We investigated the distribution and behavior of 21 species of diving birds wintering in tidally active nearshore ocean off southern Vancouver Island, British Columbia, Canada. Using vessel surveys in one site and land-based observations at a second site, we found significant differences in the use of tidally affected water types among and within three foraging guilds (piscivores, plankton feeders and benthic invertebrate predators) and five families (Gaviidae, Podicipedidae, Phalacrocoracidae, Anatidae, Alcidae). The only abundant plankton feeder, Ancient Murrelets (*Synthliboramphus antiquus*), foraged more frequently than other birds in areas of deeper water (>10 m) with fast tidal flow and turbulence. Their abundance and diving activity were significantly higher at maximum tide flow than at slack tides. Piscivores used both slack water and moderate currents in a wide range of depths but, apart from alcids and Pelagic Cormorants (*Phalacrocorax pelagicus*), avoided areas of high current and turbulence. Pigeon Guillemots (*Cepphus columba*) had higher abundance at tide phases with maximum current, and within a channel with strong tidal flow they showed repetitive upstream flights interspersed with downstream diving bouts. Fish-eating mergansers and most diving ducks taking benthic invertebrates foraged in relatively shallow (<10 m) and slack water, and avoided turbulence. Six species representing all three guilds showed changes in the use of depth categories as tides changed between slack and maximum current, and four species changed their behavior in different depth categories. Although there was considerable overlap in foraging niches, the differences in distribution and behavior of guilds, families, and species of diving birds indicate a degree of resource partitioning within tidally-driven water categories during winter. Received 25 January 2002, accepted 15 April 2002.

Key words.—Foraging behavior, diving birds, tidal currents, resource partitioning, Vancouver Island, alcids.

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Millions of waterbirds, including loons, cormorants, grebes, waterfowl and alcids, overwinter in the ice-free, sheltered waters of Alaska, British Columbia, and Washington. There is considerable literature on their numbers, distribution and, for some taxa, foraging behavior (e.g., Vermeer and Butler 1989; Vermeer *et al.* 1992; Vermeer and Morgan 1997). Relatively little is known about the use by wintering birds of marine habitats created by variation in depths and tidal currents in these complex nearshore areas. We investigated aspects of resource partitioning, marine habitat use, and the effects of tidal currents in a community of diving seabirds wintering off Victoria, southern Vancouver Island, British Columbia, Canada.

Prey availability, and hence feeding success of seabirds, is determined by both abundance and accessibility of prey. In nearshore waters these processes are strongly affected by tidal effects. Tidal mixing can enhance prey abundance through increased primary production and local nutrient enrichment

(Pingree *et al.* 1974; LeBlond 1989). Accessibility of mobile prey to seabirds is often strongly dependent on tidal upwelling bringing prey to the surface (Vermeer *et al.* 1987a; Hunt *et al.* 1998), convergent tidal fronts concentrating prey (Kinder *et al.* 1983; Brown and Gaskin 1988; Day and Byrd 1989; Schneider *et al.* 1990; Hunt 1997; Hunt *et al.* 1998), and accumulation of prey in back-eddies (Hamner and Hauri 1977; Alldredge and Hamner 1980; Braune and Gaskin 1982). Strong currents and turbulent water might also inhibit foraging by some diving birds.

We investigated responses to tidal currents and water depth in a variety of diving bird species which use several food types and trophic levels, including plankton feeders (murrelets, small grebes), piscivores (loons, cormorants, mergansers, murrelets, guillemots) and benthic feeders (scoters and similar ducks). Within trophic guilds, there might be additional resource partitioning based on the selection of prey types and fine-scale foraging areas (Hunt *et al.* 1998). Foraging

behavior, social aggregations, habitat use and resource partitioning of non-breeding seabirds are poorly known, but are obviously important in affecting the distribution and evolution of seabirds. In the breeding season, proximity to colonies and dietary requirements of young may restrict the choice of foraging areas, whereas in winter, foraging areas might more accurately portray characteristics chosen by adult birds (Croll 1990).

Significant associations of seabirds and prey can usually be found at coarse scales (100s of km), but are less obvious at smaller scales (Safina and Burger 1985; Schneider and Piatt 1986; McClatchie *et al.* 1989; Cairns and Schneider 1990). Our study focused on the distribution and behavior of diving birds at fine spatial scales (tens to hundreds of meters). At this scale there are likely strong interactions between birds and prey, but these are difficult to document due to their patchy and short-lived nature (Hunt and Schneider 1983).

Our specific objectives were to document the number of diving birds of each species within tidally-generated water types at various stages of the tidal cycle; determine if any species showed preferences for feeding within water types or depth categories; compare the numbers of birds present and proportions feeding with current speeds; and establish predictable associations, avoidance or disregard of diving birds with fine scale hydrodynamic features of current channels.

METHODS

Water Types and Depth Categories

Our study was confined to nearshore waters, here defined as protected coastal waters, including bays and inlets, generally shallow (usually <20 m) and within 1-2 km of shore (Kessel 1979). Tidal flow through narrow channels and over shallow ridges creates a variety of hydrodynamic forces that result in water types that can be recognized at the ocean surface (Thomson 1981).

Back-eddies form in the wake of an obstacle (e.g., headland, or island), where downstream water, cut off from the main current, loses laminar flow around the side of the obstacle, and creates a counter-current. Suspended materials, including zooplankton (Allredge and Hamner 1980), accumulate in back-eddies, probably because the counter-current is much slower than the main flow. Upwelling zones may form in areas where rapid changes in bathymetry or vortices force water to the surface. Upwelling is often indicated by the pres-

ence of "boils", which appear as dome-shaped zones of smooth water at the water surface. Upwelling aggregates plankton and other prey for birds by bringing them to the surface in boils or concentrating them at depth (Braune and Gaskin 1982; Vermeer *et al.* 1987a; Coyle *et al.* 1992; Hunt *et al.* 1998). Tidal convergences are downwelling zones that occur at the junction of two tidally driven flows, or where water recirculated in a back-eddy converges with the main flow (eddyline). Convergences are often marked by the accumulation of debris (tidelines). Tide rips are areas of rapid flow, typically with standing waves, that form from the interaction between ocean wave trains and currents. If current flow is strong enough, it will stop the propagation of opposing wave trains, causing the waves to pile up (Thomson 1981).

We recognized the following water types resulting from the interactions of currents and bathymetry. Slack water (S), defined as having no obvious currents, included all water at times of slack tide, but was restricted to sheltered areas between islands or within kelp beds at times of maximum tidal flow. We did not make surveys when strong winds would have produced surface currents. Eddies (E) included back-eddies and eddy-lines. Main flow (M) consisted of smooth flowing current. Turbulent water (T) marked areas of most rapid tidal flow and was apparent by either standing waves associated with tide rips or boils associated with upwelling. Three depth ranges were recorded, by comparing bird locations with nautical charts, taking into account the tide level: shallow (<5 m), intermediate (5-10 m) and deep (>10 m).

Study Area

Off the southeast of Vancouver Island, strong currents develop where water flowing between the Strait of Juan de Fuca and the Strait of Georgia is constricted through the adjoining Haro Strait (Canadian Hydrographic Charts). Sea life in the inter- and sub-tidal zones in this complex marine area is enormously richer than the surrounding regions of unconstricted water (LeBlond 1989). Currents are particularly strong (9-11 km h⁻¹) in passages with shallow and uneven bathymetry near Discovery, Chatham and Trial islands, and in Baynes Channel (Fig. 1) in our study area. These strong currents create many areas with strong vertical mixing, and a range of water types, including areas of slack water sheltered by islands and headlands. Strong tide rips and standing waves up to 1.5 m high develop in Baynes Channel and on the east side of Discovery Island, especially with high winds. Areas of slower, smooth flowing water are common, particularly on the northeast side of Discovery and Chatham Islands. Boils develop during both ebb and flood tides near Strongtide Island in Baynes Channel. Strong eddies also occur near Strongtide Island and in Rudlin Bay. A consistent convergence zone (marked by a tideline) forms at the mouth of Rudlin Bay, where the back-eddy converges with the main flow. During ebb currents a convergence also occurs at the confluence of Plumper Passage and Juan de Fuca Strait.

Our second study area covered Enterprise Channel, between Vancouver Island and Trial Island (Fig. 1). Currents flowing through this channel were approximately half the speed of those at Baynes Channel (maximum 5.4 km h⁻¹; Canadian Hydrographic Charts), but several water types were evident. These included: tide rips in the shallow central channel, where the water depth de-

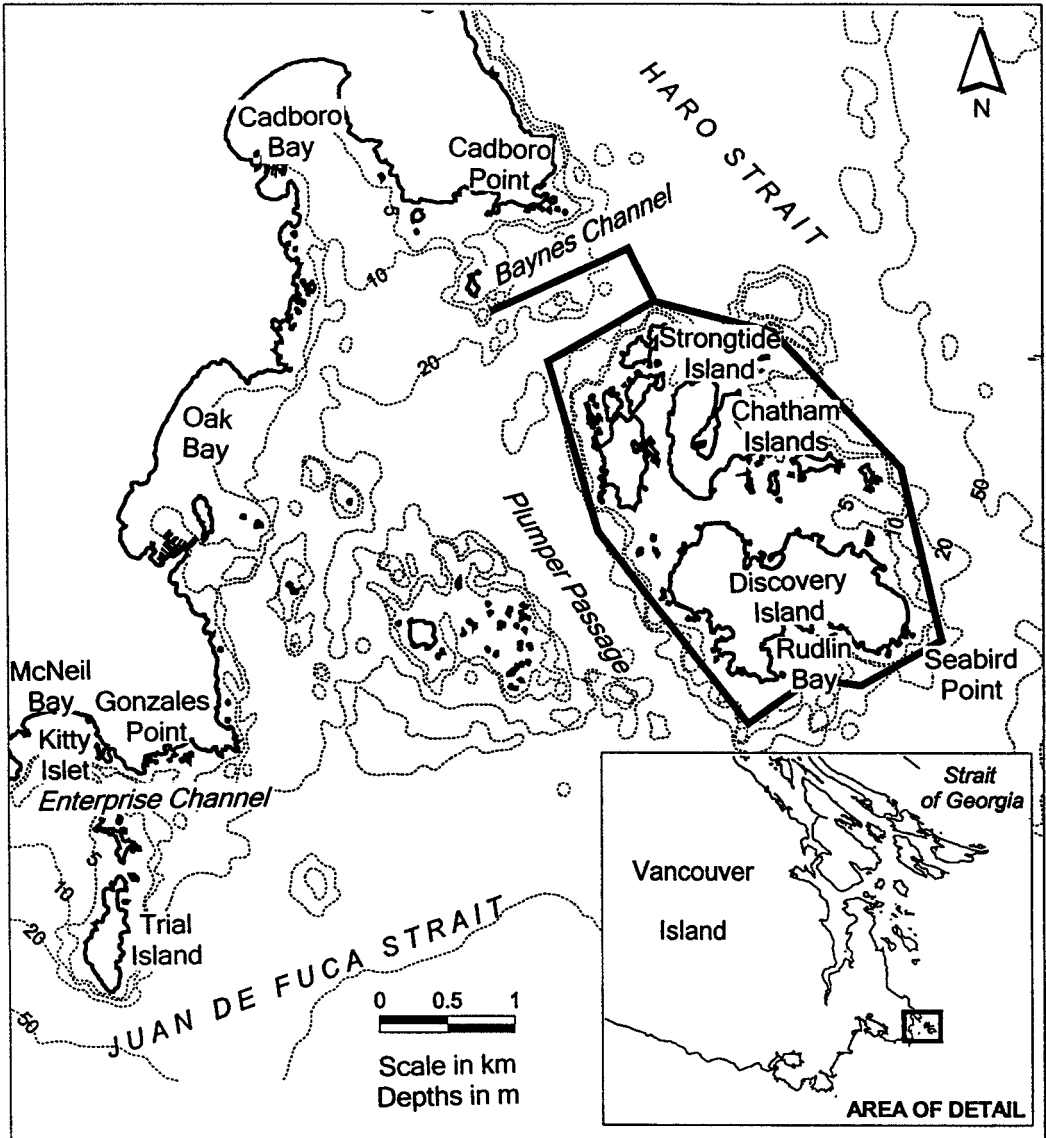


Figure 1. Map of the study area off Victoria, Vancouver Island, British Columbia, showing the boat transect route in Baynes Channel and around Chatham and Discovery Island (thick black line) and the point from which land-based observations were made (Kitty Islet). Depth contour lines are at 5, 10, 20, and 50 m.

creases to one m at very low tides; sheltered areas of slack water; a large eddy, and associated eddyline/convergence zone forming in McNeil Bay during ebb tides; smooth main flow through this bay in flood tides; and, swift flowing eddies near Trial Island.

Vessel-based Transects

Vessel-based strip transect surveys were conducted along a fixed route, through Baynes Channel and approximately 200 m offshore around Discovery and Chatham Islands, to measure distributions and habitat use of birds (Fig. 1). Ten vessel surveys were completed along the transect route between November 1998 and February 1999 using an 8 m boat (observer eye height

two m). To accentuate tidal effects, we surveyed at maximum flood ($N = 4$ surveys), maximum ebb ($N = 2$), and at slack tides ($N = 4$), starting 45 min before the peak of each tide phase in order to complete the survey within the selected phase. All surveys were conducted at similar tide heights (2.2.5 m above standard low tide), to eliminate confounding effects of changes in water depth. Tide charts and a current atlas (Canadian Hydrographic Service Pacific Region 1987; Dunkley 1998, 1999; Fisheries and Oceans Canada 1999) were used to determine the time of each tidal stage, and the current speed at maximum flow and at slack tide. To control for visibility, surveys were conducted only when wind speeds were less than 28.5 km h^{-1} and wind waves were less than 0.6 m.

Table 1. Results of tests comparing the habitat and depth used by each species with those used by other species in the same guild, or in the same family. Foraging guilds included piscivores (PI), plankton feeders (PL) and benthic-foraging ducks (BE). Separate tests were done for data from vessel surveys (V) and scan surveys (S).

| Family/group | Species | Foraging guild | No. of birds counted | | | | | | Habitat based on current | | | | | | Habitat based water depth | | | | | | | | |
|--------------|------------------------|----------------|--------------------------|-----|---------------------------|------|--------------------------|------|---------------------------|------|--------------------------|------|---------------------------|------|---------------------------|------|---------------------------|------|--------------------------|------|---------------------------|------|----|
| | | | V | | S | | V | | S | | V | | S | | V | | S | | V | | S | | |
| | | | Compared with same guild | | Compared with same family | | Compared with same guild | | Compared with same family | | Compared with same guild | | Compared with same family | | Compared with same guild | | Compared with same family | | Compared with same guild | | Compared with same family | | |
| Loons | Common Loon | PI | 12 | 9 | — | — | — | — | — | — | — | — | — | — | — | n.s. | — | — | n.s. | — | n.s. | >5 | |
| | Pacific Loon | PI | 35 | 42 | n.s. | n.s. | n.s. | n.s. | — | — | — | — | — | — | — | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | >5 | |
| | All loons | PI | 47 | 51 | n.s. | n.s. | — | — | — | — | — | — | — | — | — | n.s. | n.s. | — | — | — | — | >5 | |
| Cormorants | Brandt's Cormorant | PI | 72 | 23 | n.s. | n.s. | * | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | >5 | |
| | Pelagic Cormorant | PI | 109 | 34 | *** | *** | * | * | * | * | * | * | * | * | * | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | >5 | |
| | All cormorants | PI | 184 | 63 | *** | *** | * | — | — | — | — | — | — | — | * | n.s. | n.s. | — | — | — | — | >5 | |
| Grebes | Red-necked Grebe | PI | 47 | 101 | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | >5 | |
| | All grebes | PI | 92 | 101 | n.s. | n.s. | n.s. | n.s. | — | — | — | — | — | — | * | n.s. | n.s. | — | — | — | — | >5 | |
| Diving ducks | Bufflehead | BE | 48 | 0 | — | — | — | n.s. | — | — | n.s. | — | — | — | — | — | — | — | — | — | — | 0-5 | |
| | Harlequin Duck | BE | 163 | 73 | — | — | — | *** | *** | *** | *** | *** | *** | *** | — | — | — | — | — | — | — | 0-10 | |
| | Long-tailed Duck | BE | 33 | 20 | — | — | — | * | * | * | * | * | * | * | — | — | — | — | — | — | — | >5 | |
| | Surf Scoter | BE | 294 | 493 | — | — | — | *** | *** | *** | *** | *** | *** | *** | — | — | — | — | — | — | — | 0-10 | |
| | White-winged Scoter | BE | 317 | 19 | — | — | — | ** | ** | ** | ** | ** | ** | ** | — | — | — | — | — | — | — | 0-10 | |
| Mergansers | Hooded Merganser | PI | 4 | 28 | — | *** | — | *** | — | n.s. | — | — | — | — | — | *** | n.s. | n.s. | n.s. | n.s. | n.s. | 0-5 | |
| | Red-breasted Merganser | PI | 26 | 7 | *** | ** | *** | ** | n.s. | — | — | — | — | — | *** | — | n.s. | n.s. | — | — | — | 0-10 | |
| | All mergansers | PI | 34 | 39 | *** | *** | *** | *** | — | — | — | — | — | — | *** | *** | — | — | — | — | — | 0-10 | |
| Alcids | Common Murre | PI | 21 | 0 | n.s. | — | n.s. | — | n.s. | — | n.s. | — | — | — | — | — | — | — | * | * | — | >10 | |
| | Marbled Murrelet | PI | 46 | 0 | n.s. | — | n.s. | — | * | — | — | — | — | — | n.s. | — | n.s. | n.s. | n.s. | n.s. | n.s. | >5 | |
| | Pigeon Guillemot | PI | 120 | 94 | ** | *** | *** | *** | *** | * | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | n.s. | n.s. | >5 |
| | All piscivorous alcids | PI | 191 | 97 | ** | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | >5 |
| | Ancient Murrelet | PL | 337 | 18 | — | — | — | *** | — | — | — | — | — | — | — | — | — | — | — | n.s. | n.s. | >10 | |

Notes: Chi-squared tests with Yates' correction: *P < 0.05; **P < 0.01; ***P < 0.001; ****P < 0.0001; n.s. = not significant; — = no comparison possible.

The number and species of birds within 150 m on either side of the vessel were continuously recorded using a tape recorder. Bird activities were coded as diving, surface swimming, head dipping, resting, preening and flying. The position of each bird was described by water type and depth range. For analysis of distribution in current channels we used counts of birds which were foraging, including those diving, surface swimming, and head-dipping, but excluding those resting, preening or flying.

Land-based Observations

Land-based scan surveys were conducted at Enterprise Channel from an observation point on Kitty Islet (Fig. 1). It was impossible to overlap the areas used by each method; Enterprise Channel was too shallow and small for boat surveys and Discovery and Chatham Islands could not be regularly visited for land-based observations.

A total of 17 one-hour land-based surveys were conducted using a 10-45 power zoom spotting scope, between November 1998 and February 1999. Behavioral patterns were determined using the instantaneous scan technique (Martin and Bateson 1986), with scans at 15-min intervals, conducted in the hour surrounding three tidal stages: maximum flood (N = 4 hours), maximum ebb (N = 7), and slack water (N = 6). Surveys of maximum ebb, maximum flood, and slack water tidal stages were spread across morning, mid-day, and afternoon to avoid possible diurnal effects on activity patterns. Within each scan, birds of each species were counted and their activities, water types and depth ranges were recorded using the same categories as in vessel surveys. Surveys were conducted only when winds were less than 28.5 km h⁻¹ and waves less than 0.6 m.

Data Analysis

It was not possible to compare the number of birds in each habitat with the relative availability (spatial area) of each habitat, because the availability changed with each phase of the tide and it was impossible to draw accurate boundaries between habitats. Consequently we noted the water type and depth in which each bird or flock was seen, and focussed our analysis on general descriptions of the use of each water type and depth, as well as comparisons among and within guilds and families. If the distribution of birds across water types and depths was random, species, guilds and families should inhabit these areas at similar frequencies.

Non-parametric Mann-Whitney tests were used to compare densities and behavior of birds in each survey area with increasing tidal currents (slack water vs. maximum ebb or flood flow). The use of water types and depths was tested using a hierarchical analysis and treating the counts of birds from vessel and scan surveys separately. First, comparisons were made among guilds (piscivores, plankton feeders and benthic foragers; species classified in Table 1). We assigned species to foraging guilds based on a review of available dietary information for the eastern North Pacific (Munro and Clemens 1931; van Tets 1959; Robertson 1974; Vermeer and Levings 1977; Vermeer 1981, 1983; Johnsgard 1987, 1993; Vermeer *et al.* 1987b; Vermeer and Ydenberg 1989; Scott 1990; Ewins 1993; Gaston *et al.* 1993; Burkett 1995; Byrkjedal *et al.* 1997; Gaston and Jones 1998). Second, each species and family was compared to the sum

of all other species within the same guild, to detect possible specializations within the guild. Third, each species was compared to the sum of all other species in the same family to test for variations within families. This last test was possible only for piscivores, because all the benthic foragers were in the same family (Anseriformes), and Ancient Murrelet (*Synthliboramphus antiquus*) was the only plankton feeder with sufficient data for testing. Chi-squared goodness of fit test was used in each test, and the Yates' correction was applied (Zar 1996: 464), to account for small samples in some tests, and to reduce the chance of getting spurious significant results in repeated tests. Statistical tests were made using SPSS 10.0.

Bubble plots were used to portray combined effects of water current and depth. The area of each bubble represents the proportion of birds in each species or guild counted in each habitat type. Data from both vessel and scan surveys were combined in these plots, to simplify the presentation of data, and because we found few differences in habitat use between these two samples. Sample sizes used in the plots differed slightly from the total bird counts (Table 1) because repeated scan surveys involved variable numbers of birds, and birds resting, preening or flying were excluded in the plots. Double-crested Cormorant (*Phalacrocorax auritus*), Horned Grebe (*Podiceps auritus*), Western Grebe (*Aechmophorus occidentalis*), Common Merganser (*Mergus merganser*), and Rhinoceros Auklet (*Cerorhinca monocerata*) were counted too seldom for separate species analysis, but their counts were included in their family and guild totals.

RESULTS

Changes in Distribution and Behavior with Tide Cycles

The numbers of birds and proportions in each activity in scan counts showed no evidence of diurnal variation. The vessel-based observations were too sparse for similar comparisons but showed no obvious diurnal effects. Diurnal variations were therefore not considered in the analyses.

In the vessel surveys, we compared bird densities between four surveys made at slack tide and the combined data from five surveys in flood or ebb tides. Significant differences occurred for Ancient Murrelets (slack: 9.27 ± 4.60 (SD) birds km⁻², N = 4; flood/ebb: 32.60 ± 18.27, N = 5; Mann-Whitney test, Z = 1.96, P < 0.05) and Pigeon Guillemots (*Cephus columba*) (slack: 4.20 ± 2.07 birds km⁻²; flood/ebb: 11.53 ± 4.73; Z = 1.98, P < 0.05), but not for any of the other 14 species with sufficient data for testing (P > 0.05). The eight most common species in the vessel surveys (Table 1) provided sufficient data to

test changes in behavior with changing tides. The proportion of Ancient Murrelets diving was significantly higher during flood/ebb tides ($83.2\% \pm 7.8\%$ [S.D.], $N = 5$) than during slack tides ($55.0\% \pm 18.8\%$, $N = 4$; Mann-Whitney test, $Z = 2.21$, $P < 0.03$), but no other species showed significant differences in activities with changing tides. Small samples limit the power of these tests and subtle differences in behavior might have been overlooked.

At Enterprise Channel, where current speeds were half those at Baynes Channel, scan surveys showed no significant differences in bird numbers between slack and ebb/flood tides for any species (Mann-Whitney tests, n.s.). Ancient Murrelets were rarely seen in these surveys. There was a significant positive correlation between counts of Pigeon Guillemots and current speed (Pearson $r_{15} = 0.50$, $P < 0.05$), but not for any other species. Analysis of flight patterns showed that Pigeon Guillemots repeatedly flew to the upstream end of the channel, and then drifted through the channel while diving. Of the 19 Pigeon Guillemots recorded in flight, flights were always upstream at maximum current (twelve flew east at ebb, seven flew west at flood, and no birds were recorded flying at slack tides). No other birds showed any tidal effects in flight activity. The proportions of birds diving did not change significantly between slack and flood/ebb tides for any species in the scan data (Mann-Whitney tests, n.s.).

Six species showed significant changes in water depth between slack water and maximum tidal flow (Fig. 2). With increased current, the use of deep water was higher for Ancient Murrelets, but lower for White-winged Scoters (*Melanitta fusca*) seen in vessel surveys. Harlequin Ducks (*Histrionicus histrionicus*) moved from shallow to intermediate depths with increasing current (vessel data). At Enterprise Channel, Pacific Loons (*Gavia pacifica*) and Red-necked Grebes (*Podiceps griseus*) increased their use of intermediate depths with higher tide flow, while Surf Scoters (*Melanitta perspicillata*) increased their use of intermediate and deep water. No other species showed significant differences in depth use with changing current.



Figure 2. Percentage of birds counted in deep (>10 m), intermediate (5-10 m) and shallow (<5 m) areas, for species where there was a significant difference (Chi-squared tests, $P < 0.05$) between maximum tide flow (M) and slack water (S). The differences for Harlequin Ducks, White-winged Scoters and Ancient Murrelets were recorded in vessel surveys, whereas those for Pacific Loon, Red-necked Grebe, and Surf Scoters were in scan surveys.

Four species showed significant changes in behavior at particular depths between slack water and maximum current speed (Fig. 3). With increased current speed, the proportion of Pelagic Cormorants (*Phalacrocorax pelagicus*) and Ancient Murrelets recorded diving in deep water increased significantly (vessel surveys). Harlequin Ducks in the shallow areas increased their diving activity with stronger currents (scan data). Surf Scoters showed a slight decrease in diving activity and more time surface-swimming with increased current in deep-water conditions, but an increase in diving with increased current in shallower conditions.

Distribution of Birds Relative to Current Zones and Water Depth

Variations among trophic guilds.—Significant differences were found among the three trophic guilds (piscivores, plankton

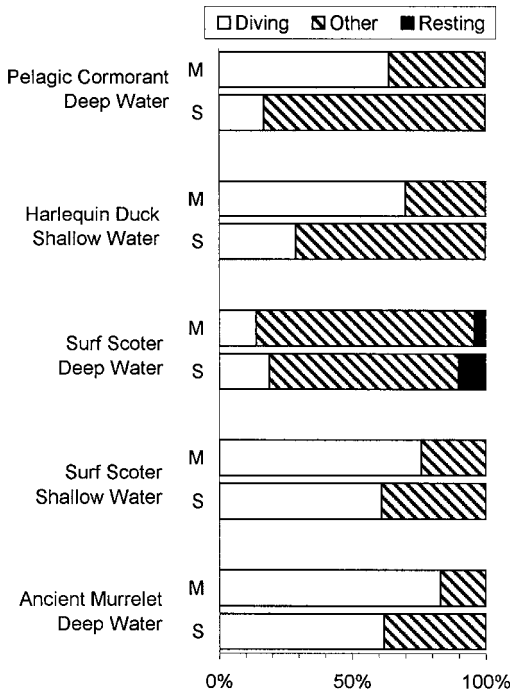


Figure 3. Percentage of birds counted in depth categories where the frequency of birds engaging in each activity was significantly different (Chi-squared tests, $P < 0.05$) between maximum tide flow (M) and slack water (S). The differences for Ancient Murrelets and Pelagic Cormorants were recorded in vessel surveys, whereas those for Harlequin Ducks and Surf Scoters were recorded in scan surveys. Note that Surf Scoters showed significant differences in behavior in both shallow and deep water.

feeders, and benthic-feeding ducks) in their use of water types (vessel surveys: $\chi^2_6 = 318$, $P < 0.001$; scan surveys: $\chi^2_6 = 55.9$, $P < 0.001$) and water depth (vessel surveys: $\chi^2_4 = 320$, $P < 0.001$; scan surveys: $\chi^2_4 = 335$, $P < 0.001$). Data from vessel and scan surveys were pooled in bubble plots because the trends were the same (Fig. 4). Piscivores predominantly used water more than five m deep in slack and main-flow areas. Plankton feeders (virtually all Ancient Murrelets with a few Hooded Mergansers *Lophodytes cucullatus*) likewise foraged mainly in water more than five m deep, but used main-flow and turbulent water more, and slack water less, than the other guilds. Benthic-feeding ducks were mainly in slack water less than ten m deep.

Variations within trophic guilds.—Piscivores included all loons, cormorants, grebes (ex-

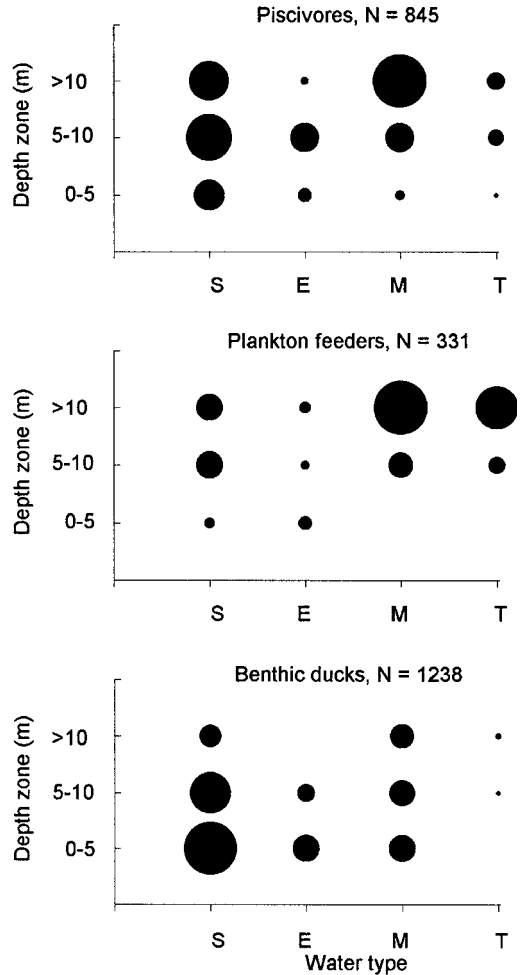


Figure 4. Distribution of birds within the three major foraging guilds relative to water type and depth off Victoria in winter. Water types, ranked in increasing current strength, included slack water (S), eddies (E), main flow (M) and turbulence (T). The area of the bubbles represents the relative proportion of the birds in each combination of water type and depth. The sample size shows the total count of each guild. Data from the vessel surveys and scan surveys were combined.

cept for the uncommon Horned Grebe), mergansers, and all alcids except Ancient Murrelets. Within this guild, significant differences in the use of habitat zones and water depth were found for many species (Table 1, Figs. 5 and 7). The general pattern among loons, cormorants and Red-necked Grebes was that most birds foraged in slack and main-flow water, mainly in water more than five m deep. Pelagic Cormorants used turbulent water more than other piscivorous species. Mergan-

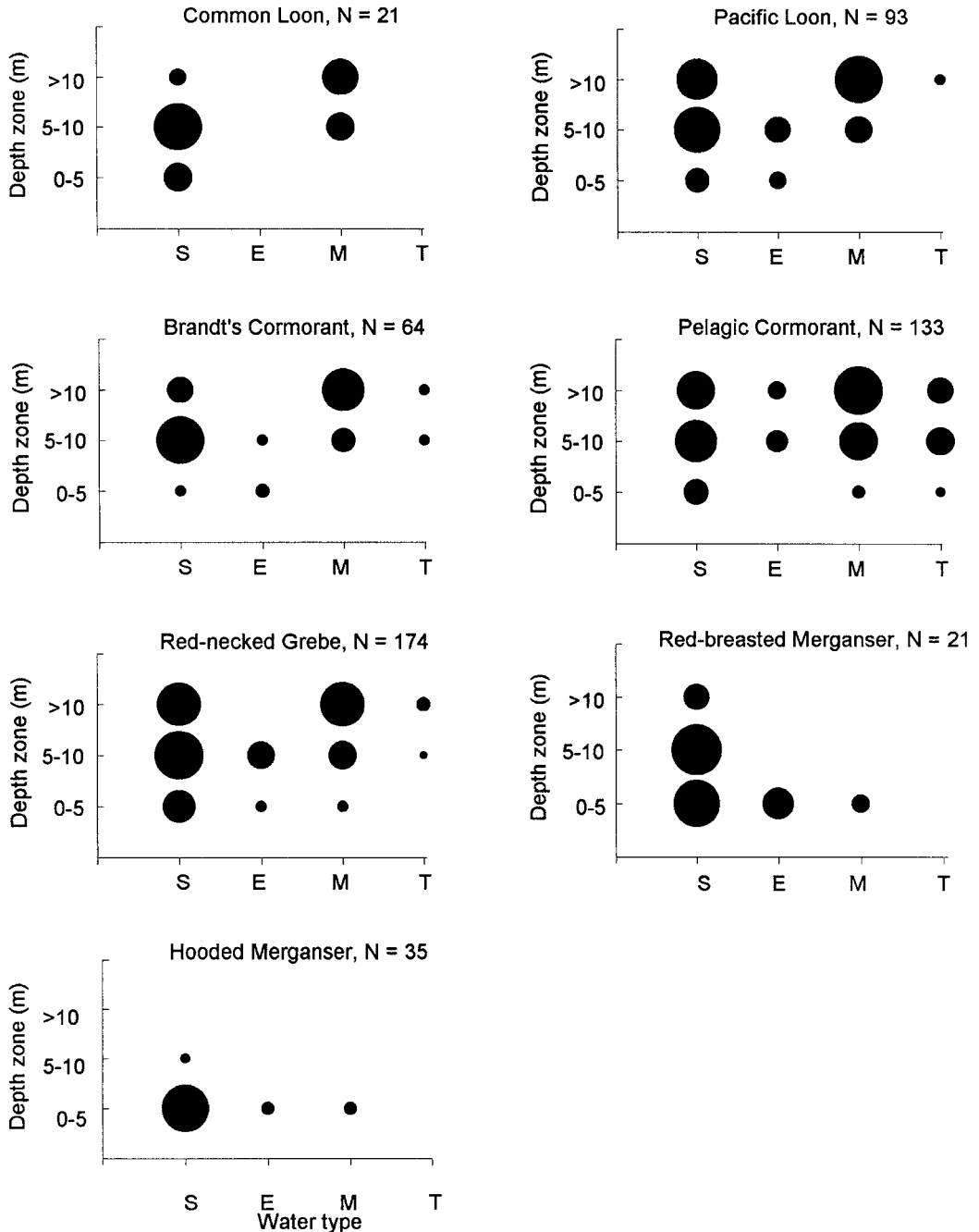


Figure 5. Distribution of loons, cormorants, grebes and mergansers relative to water type and depth off Victoria in winter. Symbols, water types and bubble format as in Figure 4. The sample size shows the total count of each species in both vessel and scan surveys; only species with counts of ten or more birds were plotted.

ers differed from other piscivores by remaining largely in slack water less than ten m deep. The piscivorous alcids (Common Murre *Uria aalge*, Marbled Murrelet *Brachyramphus marmoratus* and Pigeon Guillemot), all avoided

water less than five m deep, and used slack water somewhat less than other piscivores. Many Pigeon Guillemots also used eddies.

Ancient Murrelets were the only plankton feeders with sufficient data for analysis

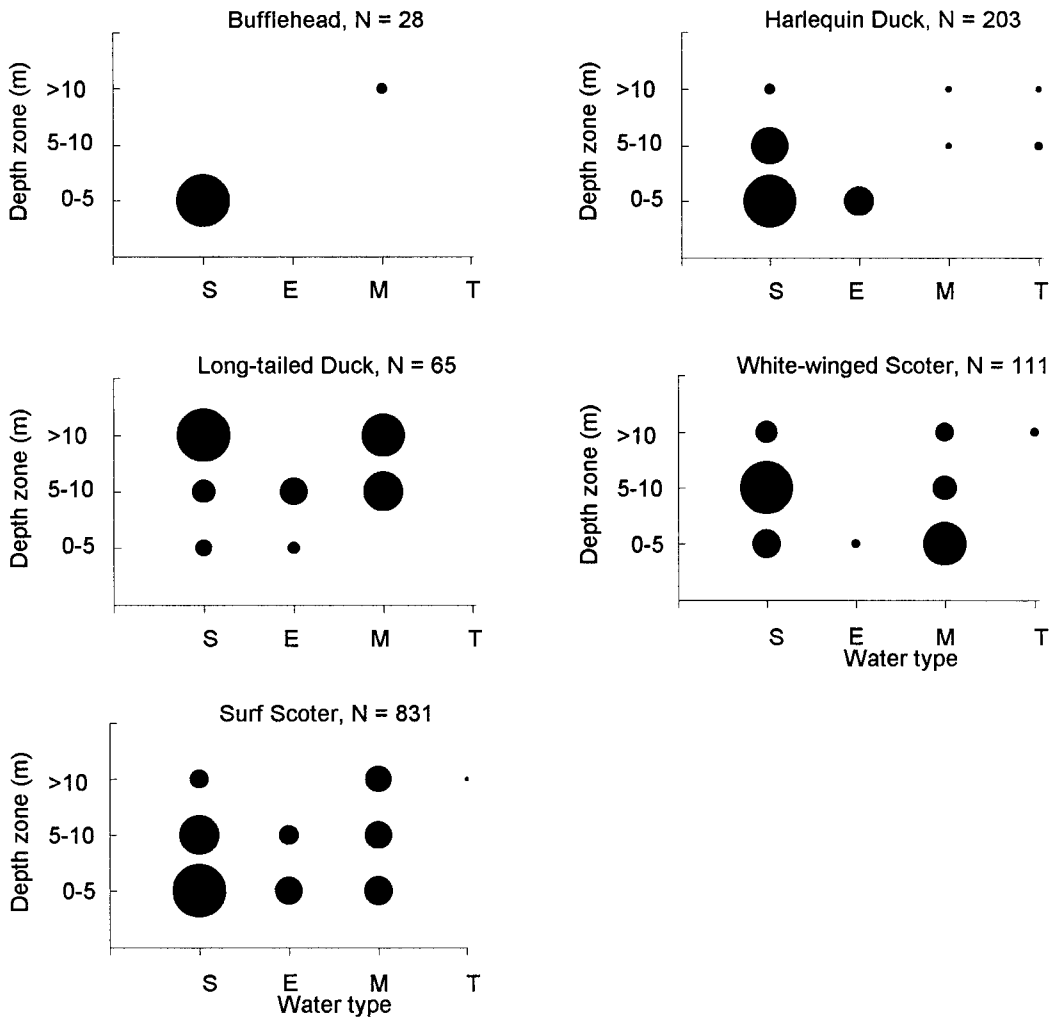


Figure 6. Distribution of benthic-feeding ducks (excluding mergansers) relative to water type and depth off Victoria in winter. Symbols, water types and bubble format as in Figure 4. The sample size shows the total count of each species in both vessel and scan surveys; only species with counts of ten or more birds were plotted.

(Fig. 7), and so comparisons within this guild were not possible. Benthic-feeding ducks, especially Buffleheads (*Bucephala albeola*) and Harlequin Ducks, generally avoided water more than ten m deep and turbulent water (Fig. 6). Long-tailed Ducks (*Clangula hyemalis*) used deep water more than other ducks, and along with the two scoter species, they also ventured into stronger currents than Buffleheads and Harlequin Ducks.

Variations within families.—No significant differences in habitat and depth use were found among the loon species or among mergansers (Table 1, Fig. 5). Brandt's Cormo-

rants (*Phalacrocorax penicillatus*) and Pelagic Cormorants (*P. pelagicus*) differed in their use of current zones, but not water depth. Comparisons among grebe species were not possible because of inadequate counts of all except Red-necked Grebes. Significant differences among alcid species were predominantly in their use of current zones, and only Common Murres differed from other alcids in their depth distribution, being found exclusively in water more than ten m deep (Table 1, Fig. 7). Significant differences among benthic feeding ducks were described above since the entire guild was in the same family.

DISCUSSION

Variations among trophic guilds.—This study appears to be the first to investigate the responses to tidal currents of diving bird species wintering within an area of strong nearshore currents. The primary purposes were to discern if and how diving bird species, including those unlikely to use currents in feeding, responded to tidal currents, and to seek evidence of resource partitioning among and within the foraging guilds. The tidal effects (boils, convergent fronts, etc.) around Discovery and Trial Islands may not have concentrated prey over sufficiently prolonged periods to attract persistent large flocks of seabirds, as are sometimes seen at tidally affected areas nearby (Vermeer *et al.* 1987a). Nevertheless, tidal currents affected the fine-scale distribution and behavior of the majority of diving birds in our study areas.

We had expected that the responses of diving birds to tidal currents would be linked to the relative sensitivity of their prey types to these currents. Plankton feeders, piscivores and benthic foragers were expected to show decreasing affinities to strong tidal currents. Many studies have documented tidally generated concentrations of zooplankton (Braune and Gaskin 1982; Vermeer *et al.* 1987a; Brown and Gaskin 1988; Day and Byrd 1989; Cairns and Schneider 1990; Schneider *et al.* 1990; Coyle *et al.* 1992; Hunt 1996; Hunt 1997; Hunt *et al.* 1998), but few have reported tidally forced aggregations of small fish (Pingree *et al.* 1974; Alldredge and Hamner 1980; Hoffman *et al.* 1981). Off southern Vancouver Island, the only abundant plankton feeder, the Ancient Murrelet, foraged in areas with the highest current velocity. In general piscivores commonly used areas of strong current, and benthic foragers were distinct in their frequent use of areas with little or no current, but not all piscivores and benthic foragers followed these patterns.

Plankton feeders.—The Ancient Murrelet was the only diving bird to consistently select strong tidal currents at all scales of analysis. Over the entire Discovery Island survey site, they had higher densities and a higher proportion of the birds were diving with increas-

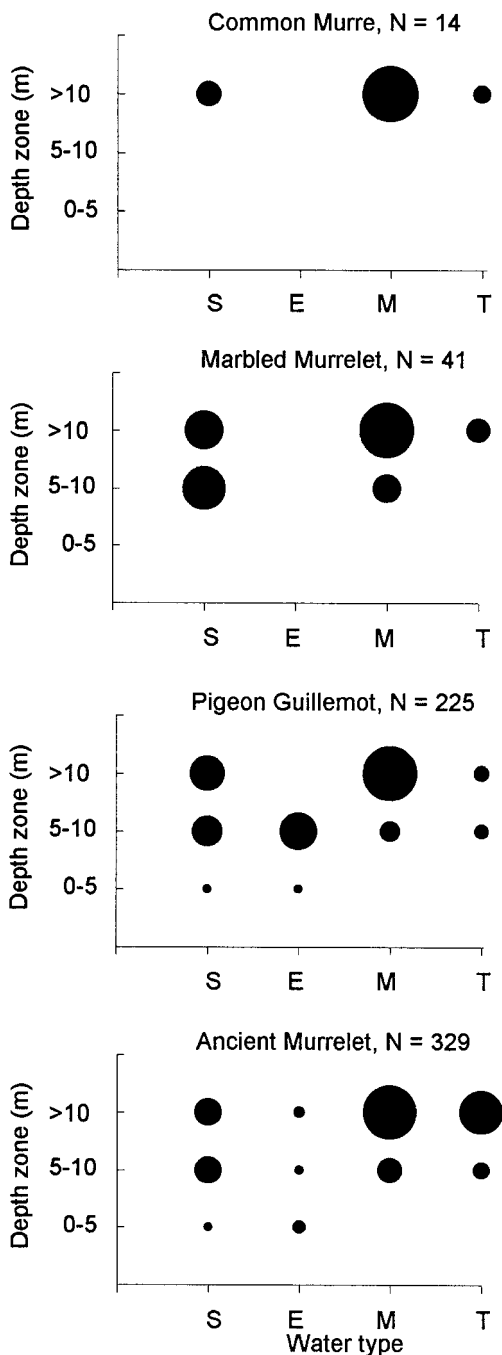


Figure 7. Distribution of alcids relative to water type and depth off Victoria in winter. Symbols, water types and bubble format as in Figure 4. The sample size shows the total count of each species in both vessel and scan surveys; only species with counts of ten or more birds were plotted.

ing current velocity. Within current channels, Ancient Murrelets predictably associated with

deeper water where the current was strongest. They were not necessarily associated with specific current features known to upwell or concentrate prey, but foraged in many water types with accelerated current, and may simply have selected well mixed water. Gaston *et al.* (1993) found that Ancient Murrelets wintering near Discovery Island fed almost exclusively on euphausiids, their abundance increased significantly with tidal amplitude, and they often fed in tide rips. Elsewhere in British Columbia, Sealy (1975) found that Ancient Murrelets fed mainly on euphausiids and immature fish, and he speculated that deep-dwelling euphausiids were made available to these birds by strong upwellings.

Similar patterns have been recorded in several studies of planktivorous auklets. In the Aleutian Islands, Least (*Aethia pusilla*), Crested (*Aethia cristatella*), and Parakeet (*Cyclorhynchus psittacula*) Auklets timed their foraging in a constricted pass to coincide with the presence of strong tidal currents (Hunt *et al.* 1998). Strong tidal currents were the dominant factor affecting the distribution and abundance of prey for Whiskered Auklets (*Aethia pygmaea*) (Byrd and Gibson 1980; Day and Byrd 1989). Haney (1991) showed that small-bodied planktivorous alcids (especially Least Auklets) in the Anadyr Strait relied on mixing of water to bring zooplankton, usually at depth during the day, to the surface. In several other areas, upwelling boils and convergence zones were important foraging areas for other planktivorous seabirds, including surface-feeders (Braune and Gaskin 1982; Vermeer *et al.* 1987a; Brown and Gaskin 1988; Hunt *et al.* 1998).

Piscivores.—Pigeon Guillemots, which in our area fed primarily on epibenthic fish (Drent 1965, Koelink 1972), were the only species in our study area, apart from Ancient Murrelets, with significantly higher abundance at times of maximum tidal flow. Their distribution within tidal channels also indicated selection of water types formed by currents. Their repetitive flight patterns at Enterprise Channel suggested that they sometimes used currents as a feeding "conveyor-belt"; they may have improved their foraging success, either by moving with the

current and sampling a new benthic site with each dive, or by keeping in contact with more pelagic prey which were being swept along by the current. The repetitive upstream flights showed that guillemots were trying to remain within Enterprise Channel, rather than continuously drifting downstream. Guillemots also commonly fed at a convergence zone bordering a large eddy in McNeil Bay. Further research into the availability of prey types and their use by guillemots in this area might help explain the benefits of hydrodynamic forces.

The overall abundance and diving activity of Pelagic Cormorants near Discovery Island did not increase significantly with tidal amplitude, but within current channels they fed significantly more than expected in turbulent water, especially in boils. At Enterprise Channel, where hydrodynamic forces were weaker, Pelagic Cormorants were still abundant, but foraged in different water types. At coarse-scales Pelagic Cormorants did not change their distribution to inhabit areas of strong hydrodynamic forces, but responded to fine-scale hydrodynamic forces creating favorable foraging conditions.

Benthic foragers.—Diving ducks feeding on benthic organisms were most common in shallow water with little or no current. Benthic-feeding diving ducks generally forage most efficiently in shallow water if prey density is adequate, even though species might be capable of much deeper dives (Ydenberg 1988; Guillemette *et al.* 1993). Tidal flow would not change the distribution or density of sessile organisms during the tidal cycle, but strong currents might hinder the birds feeding on them. Ducks might therefore avoid foraging when and where tidal currents are strong.

The exception among the diving ducks was the Long-tailed Duck, which was usually seen in water more than 10 m deep and often in strong but not turbulent currents. This species is among the most proficient divers in the Anatidae, capable of reaching depths of 60 m and making prolonged dives often exceeding one minute (Nilsson 1972; Cramp and Simmons 1977). These abilities, in part due to their use of wings for underwater propulsion

(Snell 1985), might allow Long-tailed Ducks to exploit benthic organisms not regularly taken by other birds. They are often found in more exposed, deeper water than other diving ducks (Pehrsson 1984). In our study area, the scoter species showed lesser tendencies to forage in deeper areas with stronger currents than did the Long-tailed Duck.

The availability of prey to seabirds, presumably here affected by tidal currents, is often more important than their presence (Croxall and Prince 1980). In the Strait of Georgia, patchy spatial distributions and seasonal and yearly fluctuations in the abundance of fish prey favor opportunistic feeding by seabirds (Hay *et al.* 1989). Opportunistic selection of foraging area did not, however, result in similar distributions among the species in our study area. We found significant differences in the use of water types and depth categories among species at all levels of comparison (guild, family, and species). These results are consistent with the separation of foraging zones as a common means of resource partitioning in marine birds (Ashmole and Ashmole 1967; Croxall and Prince 1980; Weimerskirch *et al.* 1988; Hunt *et al.* 1998).

The coupling between biological and physical processes is key in interpretations of patterns in seabird biology (Hunt 1997). Further research on the interactions between seabirds, prey organisms and their fluid environment will contribute to understanding the birds' coexistence and resource partitioning during the non-breeding season, and help identify critical areas of important habitat that may require protection.

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