

**DISTRIBUTION AND FORAGING BEHAVIOUR  
OF WINTERING WESTERN GREBES**

by

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## ABSTRACT

The Western Grebe, *Aechmophorus occidentalis*, is a species which breeds mainly in the prairie regions of Canada and the United States and winters on the Pacific Coast. Little is known of its distribution and behaviour during this period on coastal marine waters. I studied the seasonal distribution, the diurnal distribution, and the foraging behaviour of Western Grebes off southern Vancouver Island. I found that Western Grebes arrive in Saanich Inlet in late August and remain until mid May. Excluding migratory transients, coastal populations reach peak numbers in mid winter. Seasonal changes in flock numbers appear to be the result of both transitional migrants as well as birds that disperse to adjacent foraging areas.

This research is the first to show that wintering Western Grebes are nocturnal predators. Roosting flocks disperse at dusk to take advantage of vertically migrating prey that is available in surface waters at night. In daytime Western Grebes form large roosting flocks as an anti-predator defense while resting. While nocturnal foraging is not an unusual strategy among birds, it is most unusual for a bird that specializes on pelagic fish as prey. How can birds find such cryptic elusive prey in darkness? I suggest that Western Grebes may use ambient marine bioluminescence to locate and capture prey. This mechanism of prey capture has not previously been suggested for birds and may explain how grebes can take advantage of the increased abundance of fish in the surface waters at night.

## DEDICATION

...

Clouds must be clouds always, even if  
they've not decided what to be at all,  
and trees trees, stones stones, unnoticed,  
the magic power of anything is gone.

...

(Purdy 1972)

## ACKNOWLEDGMENTS

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## GENERAL INTRODUCTION

The Western Grebe, *Aechmophorus occidentalis*, is a diving bird whose range extends from southwestern Canada through western United States to Baja California and the Mexican Plateau (Fig. 1) (Storer and Nuechterlein 1992). It breeds on inland lakes and marshes and winters in coastal waters of western North America and on some large interior lakes (Storer and Nuechterlein 1992, Campbell *et al.* 1990). Five other grebes, of the Family *Podicipedidae*, inhabit western North America; the Clark's Grebe (*Aechmophorus clarkii*), the Red-necked Grebe (*Podiceps grisegena*) the Horned Grebe (*Podiceps auritus*), the Eared Grebe (*Podiceps nigricollis*) and the Pied-billed Grebe (*Podilymbus podiceps*).



**Figure 1.** Wintering and breeding range of the Western Grebe in North America.

Although hundreds of thousands of Western Grebes winter in coastal marine waters (Burger 1997), they are "Red Listed" as an endangered species in British Columbia (B.C. Conservation Data Centre 1997). The concern for this grebe is because of disturbance to breeding habitats and not to disturbance on the wintering grounds. In 1996 fewer than 200 pairs of Western Grebes nested in British Columbia (Burger 1997). Breeding birds are disturbed by recreational boaters, and habitat is lost to industrialization, urbanization, and livestock encroachment (Burger 1997).

Are wintering grebes safe from similar threats? Although wintering populations in British Columbia are much larger than breeding populations, they are threatened by oil spills, gill nets, aquaculture, and chemical pollution (Burger 1997). Since flocks can include several thousand grebes, it is possible that a single incident to a wintering flock could affect an entire breeding population.

While there have been several studies of Western Grebes on the breeding grounds, little information has been collected on the wintering grounds. Birds from Canada winter on coastal waters from British Columbia to northern Mexico (Eichhorst 1992). Breeding colonies may either remain together within larger flocks on the wintering grounds or disperse among grebes from other breeding locations.

We know little of the diet of wintering grebes. Most studies of foraging behaviour are from the breeding grounds (Lawrence 1950, Forbes 1985, Ratti 1985, Forbes and Sealy 1988, Ydenberg and Forbes 1988, Ydenberg and Clark 1989). The few behavioural observations of wintering Western Grebes are observations of mate feeding (James 1989), a study of winter foods of grebes (Phillips and Carter 1957), and two studies of contaminant accumulation in grebes (Vermeer *et al.* 1993, Henny *et al.* 1990). Several additional studies provide few behavioral observations, but contribute necropsy data for evidence of winter prey selection (Wetmore 1924, Munro 1941, Lawrence 1950, Chatwin 1956, Herman 1973, Robertson 1973, Vermeer and Ydenberg 1989).

It is difficult to make appropriate management decisions and to protect grebes without better information on their seasonal requirements. With increasing human presence on coastal marine waters, we need to know the distribution, habitat use, and food requirements of wintering grebes. We cannot directly apply research from the breeding grounds to birds wintering in the marine waters since breeding birds often select different prey and have different behavioral and energetic goals and constraints.

This study originates from an interest by the Canadian Wildlife Service in the biology of Western Grebes. It provides information that will assist managers making decisions that affect wintering grebes and the preservation of provincial breeding populations. This thesis discusses the seasonal distribution, diurnal distribution and flocking, and the foraging behaviour of Western Grebes wintering in Saanich Inlet off southern Vancouver Island. There are 3 chapters preceded by a general introduction and followed by a synthesis. Chapter 1 discusses seasonal distribution, Chapter 2 discusses diurnal distribution and flocking behaviour, and Chapter 3 discusses nocturnal foraging.

## **CHAPTER 1 - SEASONAL DISTRIBUTION**

### *INTRODUCTION*

Many waterbirds undertake seasonal migrations between inland breeding sites and coastal marine wintering areas. This general pattern is seen for many of the species, such as goldeneyes, buffleheads, wigeons, mergansers, scoters, loons, and grebes, that winter off the coast of British Columbia. The annual departure from the breeding areas in the fall is due to a colder climate in the inland areas and the freezing of most inland lakes and ponds. Coastal marine waters seldom freeze and offer continued foraging opportunities for birds in the aquatic environment.

The timing of seasonal movements of waterbirds depends on several life history factors specific to the species in question and often varies with sex and age. If males do not share in the feeding and maintenance of young, they may leave the breeding grounds early. The young of the season may be the last to leave the breeding grounds as they build up reserves before migrating. An additional complication to the timing of seasonal movements of birds is whether or not the species performs a moult migration.

Moult migration is the seasonal movement of birds to special moulting sites where they remain until simultaneous moult is completed and they are again able to fly. Several factors are important to the timing of moult in birds (Holmgren and Hedenstrom 1995) but moult migrations usually occur after breeding and before the migration to wintering grounds (Salomonsen 1968). Female birds often perform their moult on the breeding grounds while attending their young, hence moult migrations may involve only post-breeding males or nonbreeding birds.

Some species of grebes are known to perform a moult migration (Storer and Jehl 1985, Jehl 1990), however, there is little direct evidence of moult migration or the specific timing of the moult in Western Grebes. Storer and Nuechterlein (1985) suggest

that adult Western Grebes simultaneously moult their flight feathers in the fall from July to October. They base their estimate on 22 grebe specimens from Mono Lake and Topaz Lake (California) showing moult (14 male and 8 female), as well as analysis of the feather wear pattern in an additional 13 specimens. Sibley (1970), however, reports that 35 grebes killed in an oil spill in coastal waters of California were wing moulting in January and early February. Since wing moulting strategy may vary with both age and sex, the discrepancy in timing between these samples may be explained by these factors; Sibley's (1970) data, however, lacked this information. There is no direct evidence of a moult migration in Western Grebes since specimens examined by Storer and Nuechterlein (1985) were taken from lakes where many grebes both breed and overwinter (Herman 1973). The Great Crested Grebe performs a moult migration to Lake IJsselmeer in the Netherlands where both males and females moult flight feathers in August to the first half of October (Storer and Jehl 1985, Piersma 1988). It is likely that Western Grebes perform moult migrations, but we know little of the timing of this behaviour or the location of the moulting sites.

Banding returns indicate that Western Grebes from Manitoba winter anywhere along coastal North America from British Columbia to southern California (Eichhorst 1992, Storer and Nuechterlein 1992). Seasonal counts from several sites in British Columbia as well as naturalists' observations indicate local increases in grebe numbers as migrating birds pass through (Campbell *et al.* 1990, Cannings *et al.* 1987), but without marked birds and recovery data it is difficult to determine the origin and destination of the flocks.

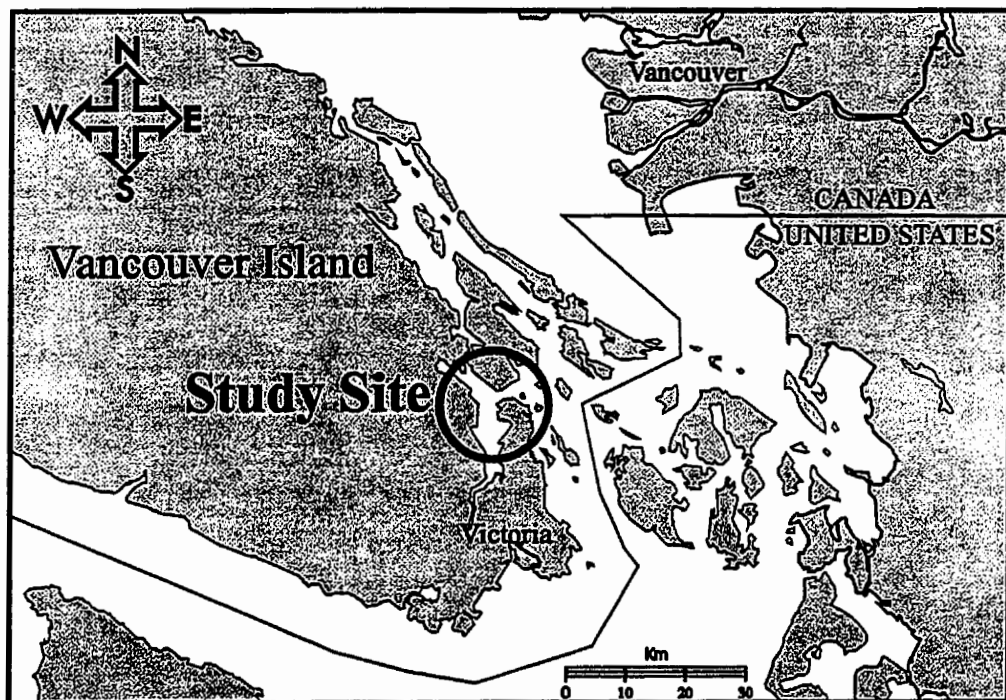
As part of a larger study on the wintering behaviour of Western Grebes, I determined the seasonal occurrence and distribution of grebes and recorded the numbers of grebes in flocks off southern Vancouver Island. By examining the seasonal distribution of grebes I discuss reasons why Western Grebe flocks appear when they do,

how grebes disperse while on the wintering grounds, and why certain sites are more consistently used than others.

## ***METHODS***

### *Study site:*

Wintering Western Grebes were observed in the waters off southern Vancouver Island, British Columbia (Fig. 2) from August 1994 to May 1995 and from August 1995 to May 1996. The study site was located in Saanich Inlet and surrounding waters. Observations were conducted from a 6 meter (m) boat.



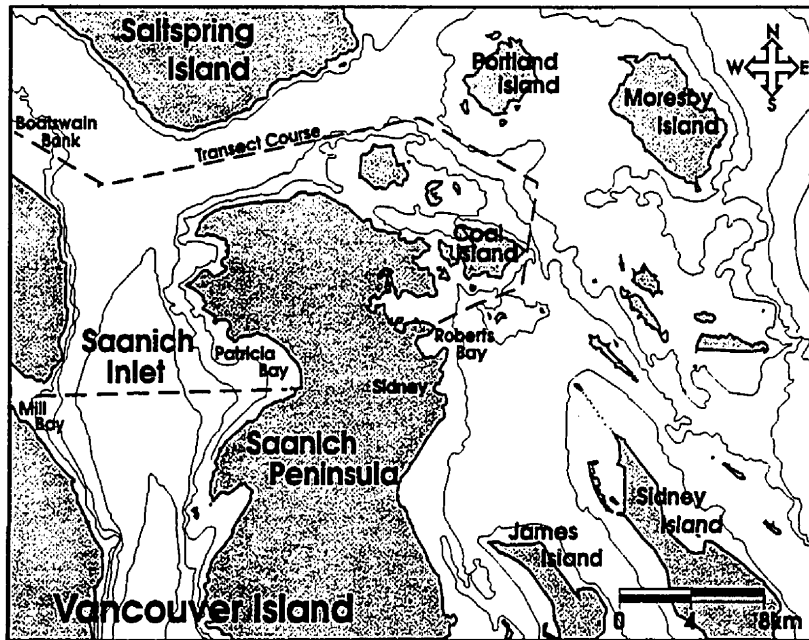
**Figure 2.** Map showing the location of the study site on Vancouver Island, British Columbia.



*Seasonal distribution surveys:*

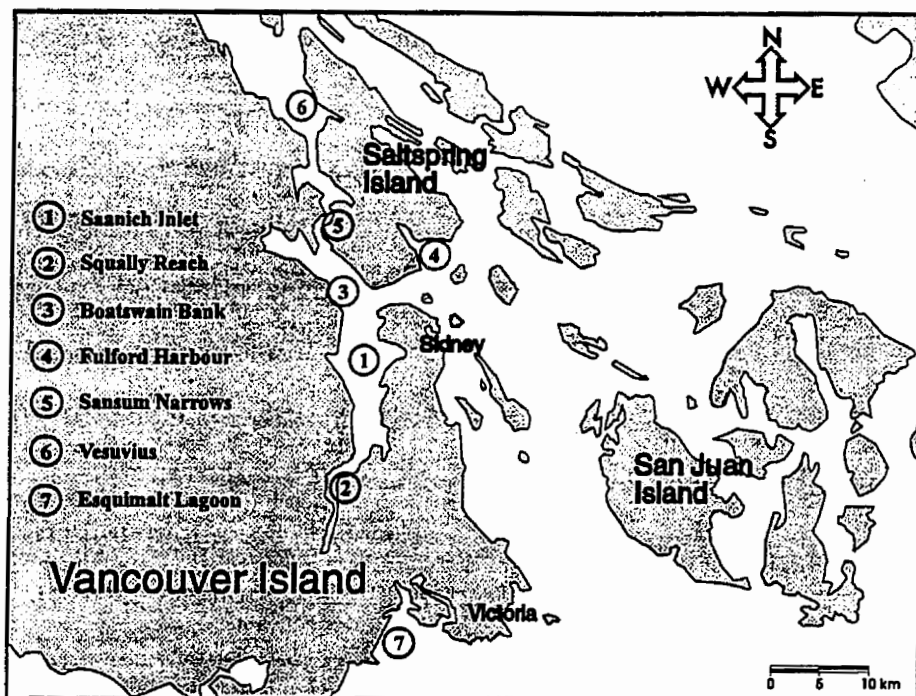
Marine surveys were designed to detect the fall arrival and spring departure and seasonal distribution of Western Grebes over a large area encompassing the waters to the east, north and west of the Saanich Peninsula on Vancouver Island. The surveys were conducted at weekly intervals from July 24, 1994 to October 22, 1995. In that period I completed 57 surveys. The survey route consisted of two line transect segments, one 20.2 kilometers (km) long (Robert's Bay to Boatswain Bank) and the other 6.6 km long (Mill Bay to Patricia Bay) (Fig. 3). Observations were taken from a 6 metre (m) open boat traveling at constant speed of approximately 13 km/hr. I recorded all birds within 150 m of each side of the boat. Usually a single observer identified all birds encountered. Birds were recorded as flying or on the water. Data included time of observation, species, behaviour, and group size. I calculated mean group size and Typical Group Size (TGS) of fish-eating marine birds throughout the yearly cycle.

Typical Group Size (Jarman 1974) is a measure of grouping behaviour that emphasizes the preferences of the members of the species rather than from an observers' point of view. Consider a marine transect where four separate groups of grebes are encountered, three groups of 2 each and one group of 20 birds. From an observers point of view, 75% of groups encountered contain 2 birds; however, from the bird's point of view 77% (20 of 26 birds encountered) of grebes prefer to be in a group of 20 birds.



**Figure 3.** Map showing location of seasonal distribution surveys off southern Vancouver Island.

I regularly censused the marine waters around southern Vancouver Island within a radius of approximately 30 km from the Saanich Inlet site, and circumnavigated Saltspring Island to locate adjacent roosting flocks (Fig. 4). In the wintering seasons of 1994-1995 and 1995-1996 I censused the seasonal changes in the numbers of Western Grebes in flocks adjacent to the study site in Saanich Inlet. These flocks were located at Esquimalt Lagoon, Squally Reach, Boatswain Bank, Sansum Narrows, Fulford Harbour, and Vesuvius (Fig. 4). The Esquimalt Lagoon site was censused using a spotting scope from shore once a month in both wintering seasons of 1994/95 and 1995/96. The remaining flocks were censused by boat once a month in both wintering seasons.



**Figure 4.** Roost flock locations off southern Vancouver Island.

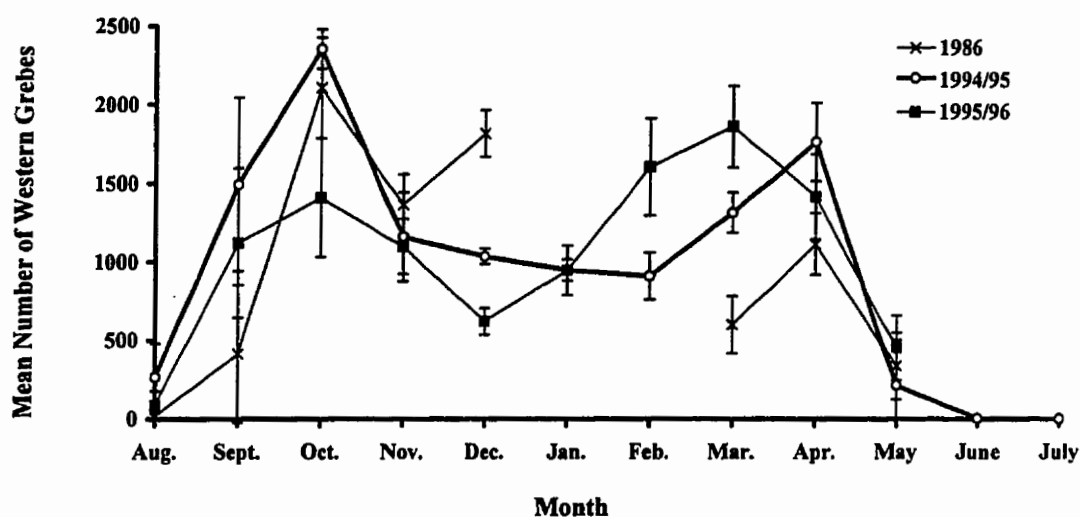
*Analysis:*

All observations have been adjusted to Pacific Standard Time. Sun rise and sunset times were calculated at Patricia Bay, Saanich Inlet, Lat. 48° 39' N , Long. 123° 30' W. Field observations of sunrise and sunset differ because of surrounding hills. Day observation times are expressed in deciles (tenths) of daylight hours to allow for seasonal differences in sunrise and sunset times, and daylengths. Sunrise is the start of the 1st decile and sunset is the end of the 10th decile of daylight hours. Night observations are expressed in deciles of nighttime hours where the start of the 1st decile is sunset and the end of the 10th decile is sunrise.

## RESULTS

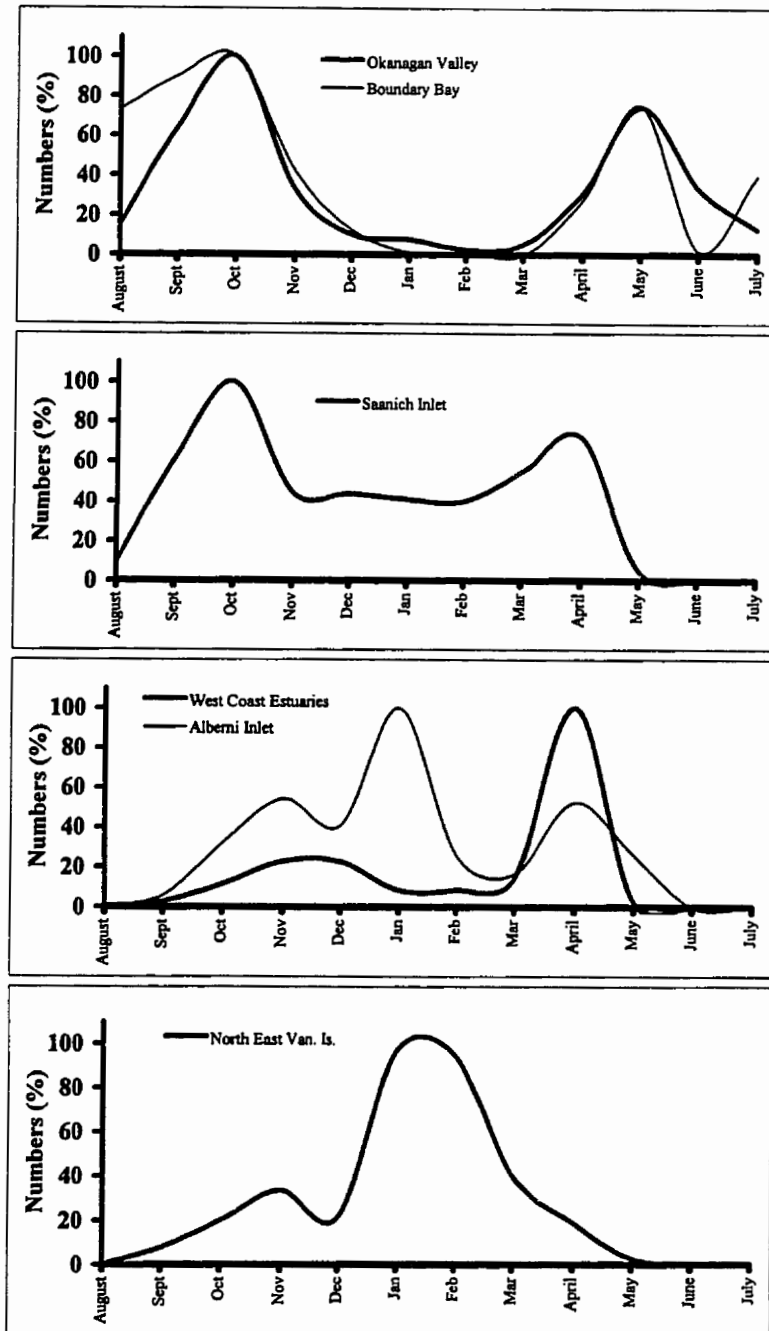
### *Seasonal distribution surveys:*

The number of Western Grebes in the Saanich Inlet flock was recorded on weekly marine bird surveys in the 1994/95 wintering season and in monthly observations in 1995/96 (Fig.3). Data collected by Morgan (1989) in 1986 are plotted for comparison. Seasonal changes in the number of Western Grebes in Saanich Inlet are summarized in Figure 5.



**Figure 5.** Mean monthly number of Western Grebes in the Saanich Inlet flock based on weekly surveys. Error bars are standard deviation of the mean. Data for 1986 are from Morgan (1989).

Figure 6 shows comparative changes and seasonal occurrences of Western Grebes at 6 sites in British Columbia. Since I was interested primarily in the seasonal pattern, I plotted the numbers at each site as a percent of the maximum number that was observed at that site, so that different sites could be examined using the same y axis.

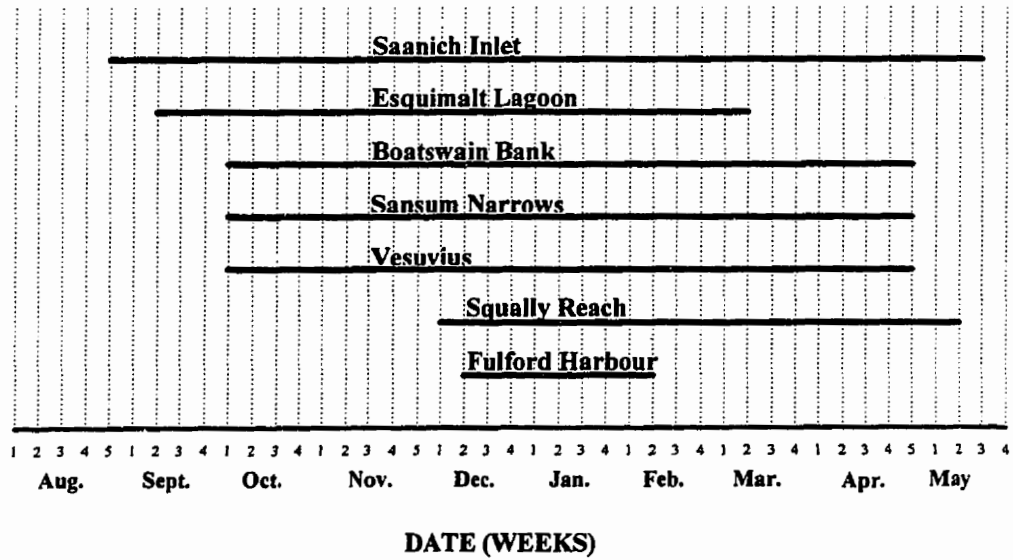


**Figure 6.** Changes in numbers of Western Grebes at 6 sites in British Columbia. Numbers of grebes are scaled to per cent of maximum observed at each site. Okanagan data from Cannings *et al.* (1987), Boundary Bay data from Fred Cooke (unpublished data), Saanich Inlet (this study), Northeast coast Vancouver Island data from Campbell *et al.* (1990), Alberni Inlet data from Vermeer and Morgan (1992), and West Coast Estuaries data from Vermeer *et al.* (1992).

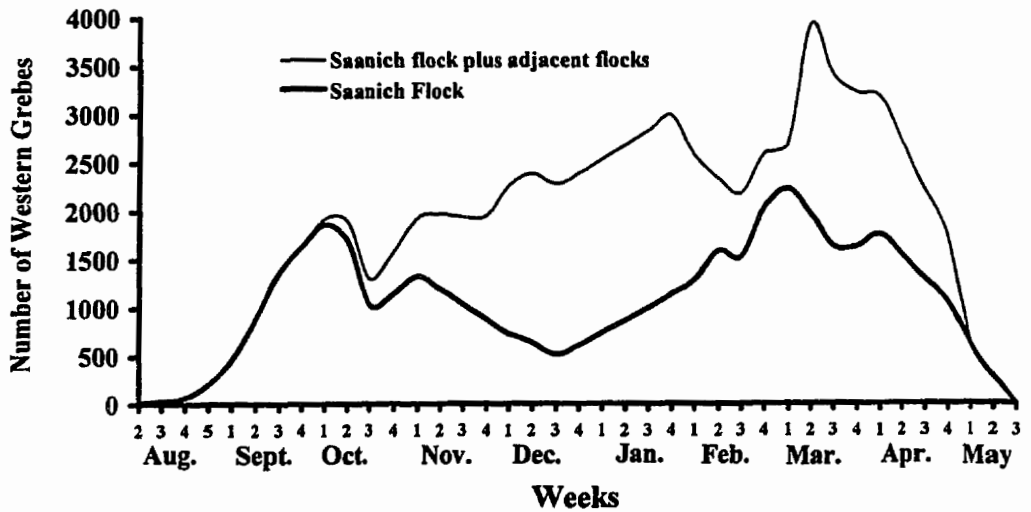
Figure 7 shows comparative arrival times, departure times, and duration of roosting flocks off southern Vancouver Island. To investigate dispersal of birds to adjacent flocks, I compared seasonal changes in numbers of grebes in Saanich Inlet to the numbers of birds in Saanich Inlet plus adjacent flocks (Fig. 8).

I developed three scenarios to model changes in numbers of birds censused at winter roosting flocks (Fig. 9).

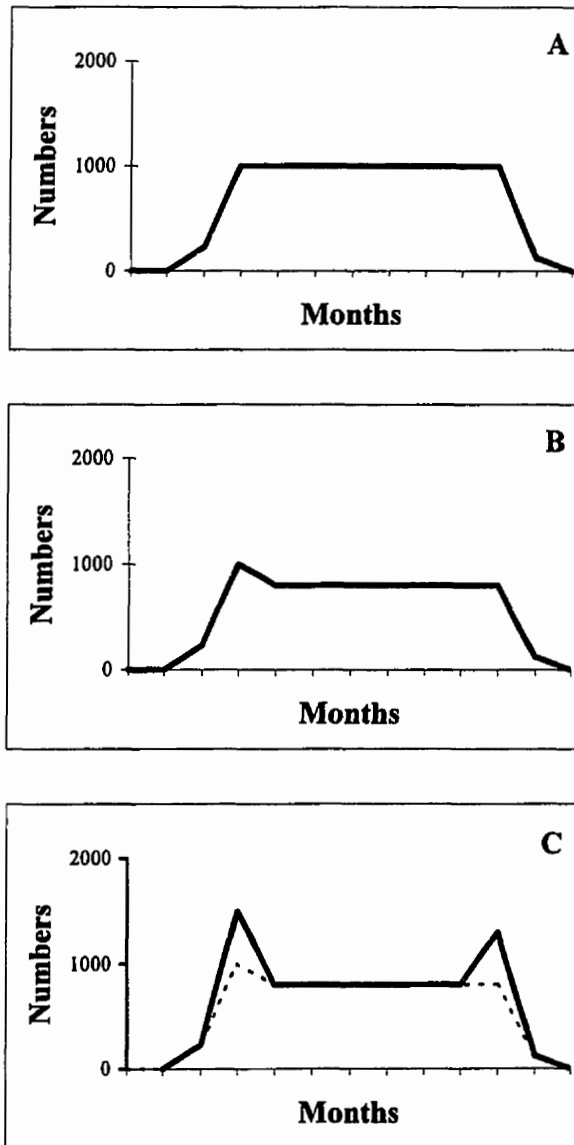
In April 1995 I observed grebes performing synchronous take-off sequences in preparation for spring migration. Large groups of grebes started rushing along the surface in a take-off run, others joined in until most of the flock of more than 1000 birds were involved. After short flights along the water, the flock settled down.



**Figure 7.** Comparative arrival times, departure times, and duration of roosting flocks off southern Vancouver Island.



**Figure 8.** Changes in numbers of grebes in the Saanich Inlet flock compared to changes in the total number of grebes in Saanich Inlet plus adjacent flocks.



**Figure 9.** Three scenarios to model changes in numbers of birds censused at a coastal wintering location. A) Birds migrate directly to a specific wintering site with no further migration or dispersal into areas outside of the census. B) Birds migrate to the wintering site and then some birds disperse into adjacent areas (not censused). There is no migration through the site. C) Birds migrate into the site and then some disperse outside of the censused area, plus a further 500 birds that migrate through and are counted in the spring and fall.



The mean group size of other fish eating birds encountered on marine bird surveys was significantly different from Western Grebes (kruskal-wallis test statistic = 255.879, df = 9,  $p = 0.000$ )(Table 1).

**Table 1.** Mean group size with standard deviation (SD) and Typical Group Size (TGS) of fish-eating birds encountered on marine weekly transects from July 1994 to October 1995. Data from April and May and September and October were excluded to avoid group sizes influenced by migratory behaviour. FIGU=Pigeon Guillemot, COLO=Common Loon, RNGR=Red-necked Grebe, MAMU=Marbled Murrelet, PECO=Pelagic Cormorant, RBME=Red-breasted Merganser, RHAU=Rhinoceros Auklet, COMU=Common Murre, PALO=Pacific Loon, WEGR=Western Grebe.

<b>SPECIES</b>	<b>TGS</b>	<b>MEAN GROUP SIZE</b>	<b>SD</b>	<b>RANGE</b>	<b>n (groups)</b>	<b>N (birds)</b>
<b>FIGU</b>	2.1	1.5	0.95	1-9	386	584
<b>COLO</b>	2.5	1.5	1.26	1-12	162	236
<b>RNGR</b>	2.7	1.6	1.34	1-20	393	629
<b>MAMU</b>	4.2	2.2	2.08	1-29	750	1671
<b>PECO</b>	5.8	2.4	2.85	1-20	460	1110
<b>RBME</b>	8.2	3.3	4.05	1-25	64	211
<b>RHAU</b>	9.3	2.7	4.31	1-25	38	104
<b>COMU</b>	19	3.3	7.42	1-32	17	56
<b>PALO</b>	51.5	5.6	16.06	1-130	138	769
<b>WEGR</b>	954	140.9	339.96	1-1413	131	18456

## *DISCUSSION*

This discussion of seasonal distribution of Western Grebes draws data from several other sources in the literature as well as contributions from other researchers. By compiling these data I hope to provide some insights into the possible causes of seasonal variations of numbers at the study site. There are, however, few census data that encompass the annual cycle and in some cases comparisons must be made of data collected in different years. Seasonal numbers of grebes counted at Saanich Inlet and Boundary Bay are both recent and concurrent data and will offer the best comparisons. Additionally, it is possible that major aggregations of Western Grebes are not accounted for in the literature or in our data since systematic aerial surveys have not been done.

If we compare the census data for the Saanich Inlet flock with historical data we can see evidence that, although numbers may fluctuate from year to year, the pattern of seasonal distribution has changed little from 1986 to 1996 (Fig. 5). In our two years of observations, Western Grebes arrive first in Saanich Inlet in late August and then appear off Esquimalt Lagoon, Boatswain Bank, Sansum Narrows, Vesuvius Bay, Squally Reach, and then Fulford Harbour (Fig. 7).

The census data from six sites in British Columbia (Fig. 6) show several patterns of seasonal distribution. The most eastward site is the Okanagan Valley which is likely on the migration route from the intensive breeding areas in Manitoba (Eichhorst 1992). Traveling east to west, the first site on coastal British Columbia is Boundary Bay, then Saanich Inlet on the east coast of Vancouver Island, Alberni Inlet, and finally the West Coast Estuaries. North of Saanich Inlet, and also on the east coast of Vancouver Island, I have included data from the Northeast Vancouver Island. If we examine these data some consistent patterns emerge in both fall and spring migrations (Fig. 6).

In the fall there are two general patterns of peak abundance. In the Okanagan Valley, Boundary Bay, and Saanich Inlet, peak numbers occur in October, while in

Alberni Inlet, West Coast Estuaries, and Northeast Vancouver Island, there are minor peaks in November (Fig. 6). Since few Western Grebes breed or winter in the Okanagan Valley, and since this site is the most eastward of our census locations and closest to breeding sites, data showing seasonal peaks in grebe numbers can be used to establish migration chronology (Cannings *et al.* 1987) (Fig 6). The synchronous occurrence of peak numbers in the Okanagan Valley, Boundary Bay, and Saanich Inlet suggests that these sites may be specific stopover locations for birds arriving at the coast. The numbers at Boundary Bay, however, begin to increase in late June while numbers in the Okanagan and Saanich Inlet do not begin to increase until August. Boundary Bay may be the destination of an early moult migration, but it is difficult to determine if the other sites are moulting sites as well or temporary stopover points of grebes traveling to more distant wintering sites.

Although we don't know the duration of wing moult for Western Grebes, the Great Crested Grebe completes a wing moult in 17 days (Piersma 1987, 1988) and Eared Grebes complete a wing moult in 35 days (Storer and Jehl 1985). If we assume that Western Grebes complete their wing moult in approximately 21 days, we would expect that plots of numbers at moulting sites would show a broad peak in numbers during the moulting period. This trend, however, would be masked if arrival times differed for moulting flocks, if nonmoulting birds stopped briefly at the site as well, and if census data were averaged over a long period of time. Because numbers in Boundary Bay begin to increase early in the summer, it may be a moulting site for males and nonbreeding birds. We would require more intensive census data, and observations of moulting status and marked birds, to confirm this speculation.

The second pattern of fall distribution is the minor peak in numbers recorded at Alberni Inlet, West Coast Estuaries, and Northeast Vancouver Island in November. This pattern would be expected if birds traveling to these areas stopped over at more eastward sites before traveling on to these locations.

In the spring we see another pattern of seasonal distribution, as birds again pass through these areas to return to the breeding grounds. There is, however, a noticeable difference in timing between sites on the mainland and sites on Vancouver Island. Both Boundary Bay and the Okanagan Valley show peak numbers in May while the Alberni Inlet, West Coast Estuaries and Saanich Inlet show peaks in April (Fig.6). The numbers at Northeast Vancouver Island show a pattern different from the others with peak abundance in January and birds leaving the area well before spring migration.

In the fall, peak occurrences at Saanich Inlet were synchronized with those in Boundary Bay and the Okanagan Valley. In the spring, however, the pattern at Saanich Inlet is more similar to that in the Alberni Inlet and West Coast Estuaries. The later occurrence of peak abundances in Boundary Bay and the Okanagan Valley may be consistent with birds leaving the more westerly sites and stopping over before continuing to the breeding grounds. I lack sufficient data to determine the specific cause of the differing seasonal patterns at these sites. It is also possible that the birds leaving the westerly sites in April may fly directly to the breeding grounds and that birds leaving Boundary Bay and the Okanagan Valley in May are from a different population.

Without marked birds it is difficult to determine the cause of changing numbers of grebes in Saanich Inlet over the wintering period, but by comparing the numbers of local flocks, I can offer some probable solutions. Census data from the Okanagan Valley, Boundary Bay, and Saanich Inlet all show similar increases in numbers in the fall (Fig. 6). Western Grebes from interior breeding sites may briefly stopover at these sites to moult and then continue their migration. This may be why numbers at Boundary Bay and Saanich Inlet are greatest in the Fall and decline in mid winter. Another reason may be that, as numbers increase, and perhaps due to intraspecific competition for food, birds disperse over local waters and form other flocks. Data from Saanich Inlet

and adjacent flocks suggest the possibility of this kind of dispersal since smaller adjacent flocks do not appear until after numbers peak in Saanich Inlet (Fig. 5, Fig. 7 ).

How can we tell if the appearance of adjacent flocks is due to new birds migrating into the area or to birds dispersing from Saanich Inlet? If we construct a simple model of seasonal population changes in a wintering flock we may be able to generate the pattern we see in Saanich Inlet. Consider three scenarios of monthly flock counts in a single flock through a wintering period (Fig. 9): A) Birds migrate directly to a specific wintering site; numbers steadily rise in the flock until all wintering birds arrive and then remain at that amount until spring migration to the breeding grounds. I assume no further migration or dispersal into areas outside of the census. B) Birds migrate to the wintering site and when numbers peak in the flock, some birds disperse into adjacent areas (not censused); there is no migration through the site. C) Birds migrate into the site and then some disperse outside of the censused area, plus a further 500 birds migrate through and are counted in the spring and fall.

The predicted pattern of population change for a site which experiences both migratory peaks and dispersal (C, Fig. 9) appears very similar to what I see at Saanich Inlet and Boundary Bay (Fig. 6). It is likely that the migration and dispersal patterns are more complicated than these simple scenarios since if I plot the Saanich Inlet data together with the numbers of adjacent flocks I do not get a simple flat plot with migration peaks (Fig. 8).

It is difficult to say why migrating flocks of grebes would choose specific sites such as Saanich Inlet and Boundary Bay as migration stop over points. If these areas are used as moulting sites, then grebes would likely choose sites somewhat free from predators, that offer some protection from storms, and that offer a consistent food supply. To properly test these predictions, I would require more complete data on several more roosting sites. Both these sites offer protection from prevailing storms and both sites have habitat known to be important to juvenile prey fish. Saanich Inlet has

been described a rearing ground for juvenile fish because it has an unusually dense population of vertically migrating euphausiids and copepods (Barraclough and Herlinveaux 1961). Boundary Bay has extensive areas of eelgrass beds (*Zostera* spp.) which provide prey fish habitat (Hutchinson *et al.* 1989). The continued use of Saanich Inlet since 1986 (Fig. 5) suggests that a consistent food supply has been available for wintering grebes.

## CHAPTER 2 - DIURNAL DISTRIBUTION AND FLOCKING

### INTRODUCTION

The distribution of wintering birds is likely a result of several factors affecting their survival during the wintering period. These factors may include the distribution of food, safety from predators, shelter from adverse weather, and social contact. The flocking pattern of wintering Western Grebes is unusual when compared to other sympatric fish eating diving birds. Unlike Red-necked Grebes (*Podiceps grisegena*), Pacific Loons (*Gavia arctica*), Common Loons (*Gavia immer*), Pelagic Cormorants (*Phalacrocorax pelagicus*), Red-breasted Mergansers (*Mergus serrator*), Common Murres (*Uria aalge*), Pigeon Guillemots (*Cepphus columba*), Marbled Murrelets (*Brachyramphus marmoratus*), and Rhinoceros Auklets (*Cerorhinca monocerata*), Western Grebes often associate in flocks of a hundred to several thousand birds (Table 1). Other fish-eating birds may associate in large flocks during migration, but after dispersing on the wintering grounds they seldom consistently form large flocks.

The Ideal Free Distribution (IFD) (Fretwell and Lucas 1970) predicts that competitors for a resource will distribute themselves among resource patches so that they all experience equal energetic gains. The model assumes that 1) all competitors are of equal competitive ability, 2) the habitat contains resources patches that vary in fitness value, 3) competitors can move freely and without cost between patches, and 4) the fitness value in a patch declines with the number of competitors in the patch. Although the ideal free distribution predicts how animals distribute themselves while foraging, it does not address the distribution of animals outside of the foraging period.

Refuging, according to Hamilton and Watt (1970), is the rhythmical dispersal of animals from, and their return to, a fixed point in space. Hamilton *et al.* (1967) studied the winter roosting and foraging behaviour of starlings, but other animals that refuge

are the social insects, bats, seals and sea lions, colonial birds, as well as primitive humans (Hamilton 1966, Hamilton and Watt 1970). Refuging theory states that animals will roost in a central location (core) within the area of resource gain and disperse from this location to forage. The area surrounding the core is an undefended foraging patch in which individuals experience intraspecific competition for resources. The theory assumes that individuals experience a reduction in intraspecific competition as they travel farther from the core roost site. In this way, foragers may tradeoff the energetic cost of additional travel for a reduction in competition for resources. A limit to the dispersal area or arena occurs when an individual's travel costs exceed the benefits of returning to the core roost site. Refuging theory has the benefit that it predicts the behaviour of the animal outside of the foraging period while the Ideal Free Distribution theory better describes the distribution of individuals while foraging.

It is common in natural systems to find that animal movements coincide with the spatial distribution and temporal availability of food. A characteristic feature of refuging systems is the rhythmic dispersal of animals from a central roosting site. Starlings (*Sturnus vulgaris*) for example, disperse from roosts when sufficient daylight is available to forage (Hamilton and Gilbert 1969). In marine systems animals may time their dispersal to coincide with tides that expose foraging grounds. Nocturnal foraging may occur when low tides are at night. The vertical migration of marine invertebrates creates a rhythmic system of varying abundance where food, for surface dwelling predators, is more readily available at night. Invertebrates flee to deeper waters during the day where darkness helps them escape predation (Gliwicz 1986, Ohman 1990, Bollens 1996). It is not uncommon for birds to have daily dispersal patterns that synchronize foraging bouts to nocturnal abundance of prey (Martin 1990a, McNeil *et al.* 1993, in press).

Flocking patterns are likely a consensus of many factors that affect the fitness of wintering birds. In addition to those mentioned above, birds benefit from sharing the



cost of vigilance while resting in flocks and from social contact if mate selection begins in winter. By examining the distribution and flocking of wintering grebes and by making predictions based on Hamilton's refuging theory, the Ideal Free Distribution, and Optimal Foraging Theory, I hope to further understand grebe behaviour in light of factors affecting their winter survival. The questions I address are: 1) Why do Western Grebes form flocks? 2) Why and when do grebes disperse to forage? 3) Are grebes solitary or group foragers? and 4) Why are flock locations consistent from year to year? Habitat ecologists may be interested in how grebe flocking and dispersal patterns are connected to prey numbers and distribution. Can observations of grebe flocking and dispersal patterns help us evaluate and predict prey and habitat quality?

## *METHODS*

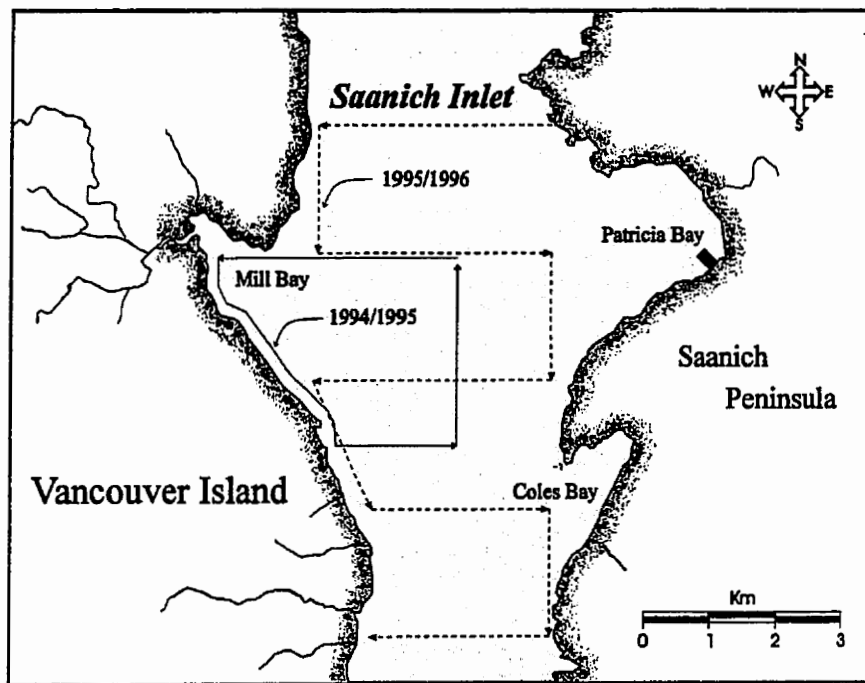
### *Study site:*

Wintering Western Grebes were observed in the waters off southern Vancouver Island, British Columbia (Fig. 2) from August to May in 1994-95 and in 1995-96. The study site was located in Saanich Inlet and surrounding waters. Observations were conducted from a 6 meter (m) boat.

### *Diurnal distribution surveys:*

Marine surveys were designed to document the fine scale distribution of grebes throughout the daily period in Saanich Inlet. Diurnal distribution surveys in 1994/1995 followed a polygonal transect course (Fig. 10) which began in the center of Saanich Inlet and sampled both shallow and deep water habitat. Each transect was 11.4 km long and was completed in approximately 1.3 hours. Water depths on the route ranged from 6 to 200 m. Observations were made from a boat traveling at constant speed (8.6 km/h). The

area scanned was defined by a 180° arc centered on the boat's heading with a radius of 150 m. The time of observation, species, behaviour, and group size was recorded for each group of birds encountered. During the transects, a 200 k Hz Lowrance sounder was used to obtain a record of water depths and prey distribution. On each sampling day, transects were conducted at intervals throughout the daylight period. The number of transects varied with seasonal changes in day length. The first transect began as soon as light conditions allowed the detection of birds and the last transect was conducted as late as possible. The remaining portion of the day was divided equally among either 2 or 3 transects (total = 4 or 5 surveys per day).



**Figure 10.** Site plan showing the location of diurnal distribution surveys conducted in both 1994/1995 (solid line) and in 1995/1996 (dotted line).

In 1995/1996 the diurnal distribution survey design was changed to allow a maximum surface area of Saanich Inlet to be covered (Fig. 10). The transect began north of Warrior Point on Saanich Peninsula (48° 40.2 N , 128° 29.0 W), crossed the inlet several times and ended off the south boundary of Bamberton Park (48° 36.2 N, 123° 31.0 W). The route was covered as quickly as conditions would allow so that swimming birds were not encountered more than once. Observations were made from a 6 m boat traveling at constant speed (~ 19.2 km/h). The area scanned was defined by a 180° arc centered on the boat's heading with a radius of 150 m. The time of observation and group size was logged for each group of birds encountered. On each survey day either 4 or 5 surveys were conducted depending seasonal differences in daylength.

*Behavioral observations:*

Behavioral scans of the roosting flock were conducted on 19 days in the 1994/1995 and on 2 days in the 1995/1996 season. The flock was scanned using binoculars. Counts of the number of birds performing the following behaviors were made: "resting", "alert", or "diving". Birds were recorded as resting when motionless with their heads on their back. Birds were recorded as alert when their heads were upright.

Flock dispersal and aggregation was observed on 30 occasions during the two wintering seasons from November 1994 to May 1996. On one occasion I recorded flock size and dispersal of 3 separate roosting flocks during the same time period. These flocks were located off Mill Bay in Saanich Inlet, in Fulford Harbour (Saltspring Island), and off Esquimalt Lagoon in the strait of Juan de Fuca.

*Analysis:*

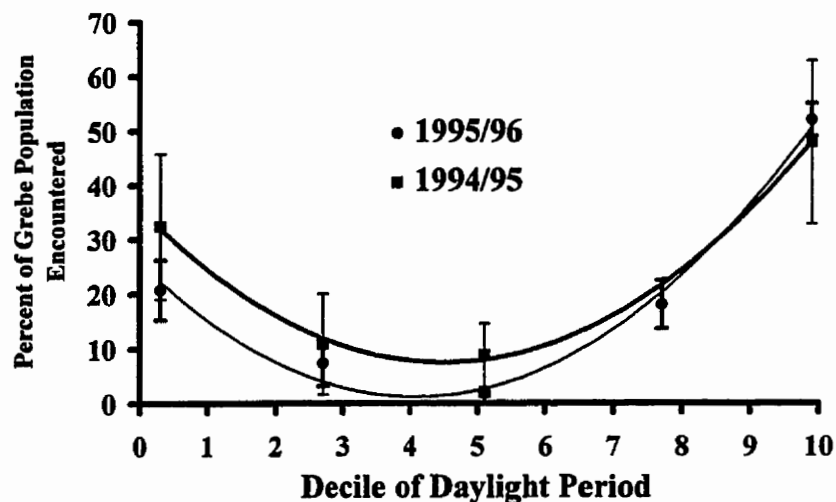
All observations have been adjusted to Pacific Standard Time. Sun rise and sunset times were calculated at Patricia Bay, Saanich Inlet, Lat. 48° 39' N , Long. 123° 30' W. Field observations of sunrise and sunset differ because of surrounding hills. Day

observation times are expressed in deciles (tenths) of daylight hours to allow for seasonal differences in sunrise and sunset times, and day lengths. Sunrise is the start of the 1st decile and sunset is the end of the 10th decile of daylight hours. Night observations are expressed in deciles of nighttime hours where the start of the 1st decile is sunset and the end of the 10th decile is sunrise.

## RESULTS

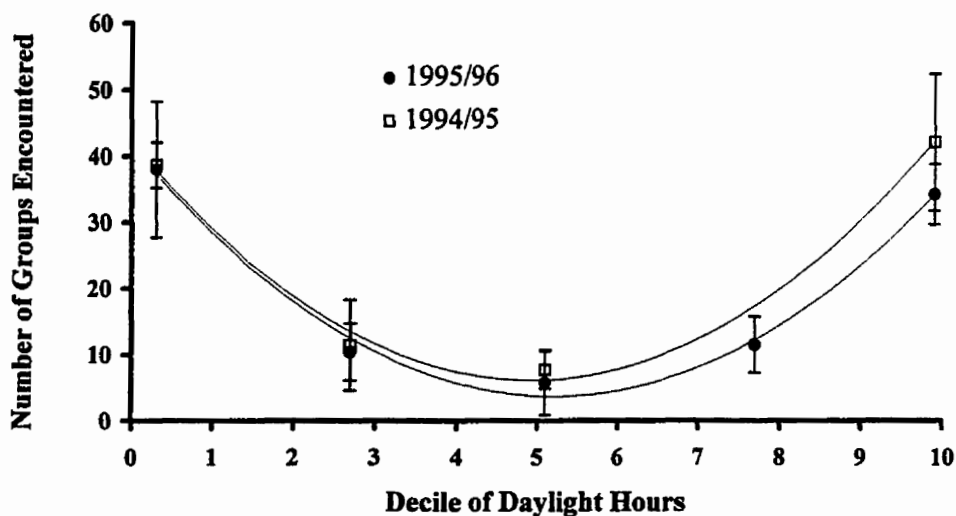
### *Diurnal distribution surveys:*

In diurnal distribution surveys grebes were encountered outside of the roosting flock most often at dawn and dusk (Fig. 11).

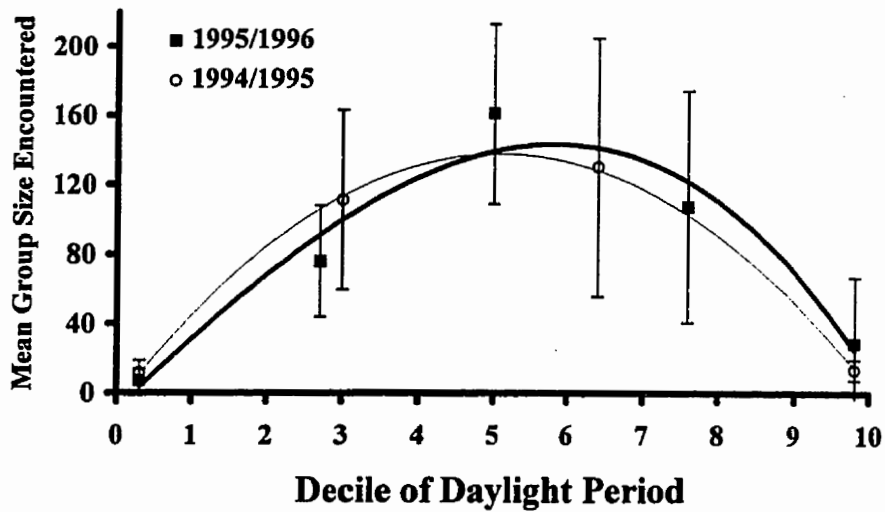


**Figure 11.** Percent of Western Grebe population encountered outside of the roosting flock in distribution surveys conducted throughout the daylight period. Figures are means and standard deviations of diurnal surveys conducted on 4 days in 1994/95 and 3 days in the 1995/95 season. X axis is in deciles of daylight hours where 0 is sunrise and 10 is sunset.

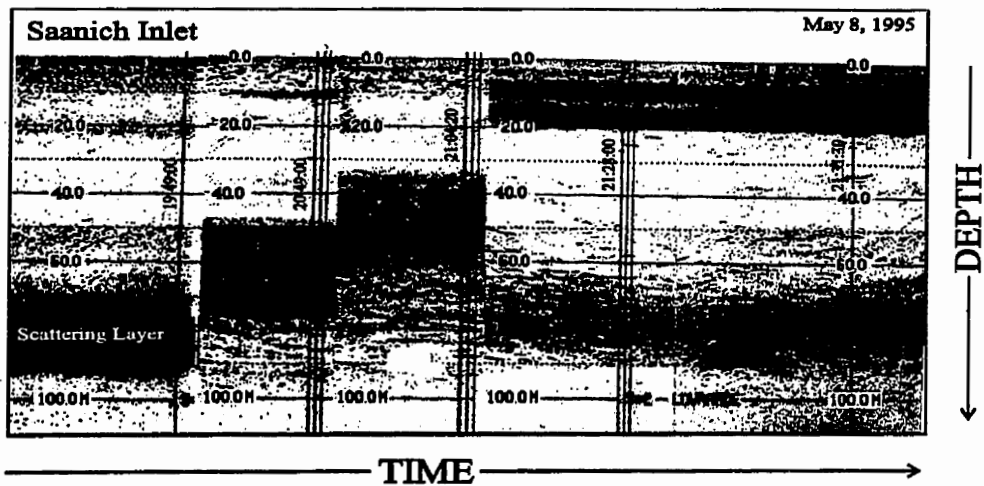
They disperse from the roosting flock in large groups which subsequently decrease in size as smaller groups of grebes leave the traveling flocks. In the morning grebes aggregate in the opposite way, as single or small groups combine with others as they travel to the roosting location. The result of this dispersal and aggregation pattern is that the number of groups encountered in surveys is greater near dawn and dusk than at midday (Fig. 12). Group size of grebes encountered is larger at midday than at dawn or dusk (Fig. 13). While conducting surveys of diurnal bird distribution, I simultaneously recorded the depth of the submarine scattering layer, which vertically migrated to surface waters at dusk (Fig. 14).



**Figure 12.** Number of groups of Western Grebes encountered in distribution surveys conducted throughout the daylight period. Figures are means and standard deviations of diurnal surveys conducted on 4 days in 1994/95 and 3 days in the 1995/95 season. X axis is in deciles of daylight hours where 0 is sunrise and 10 is sunset.



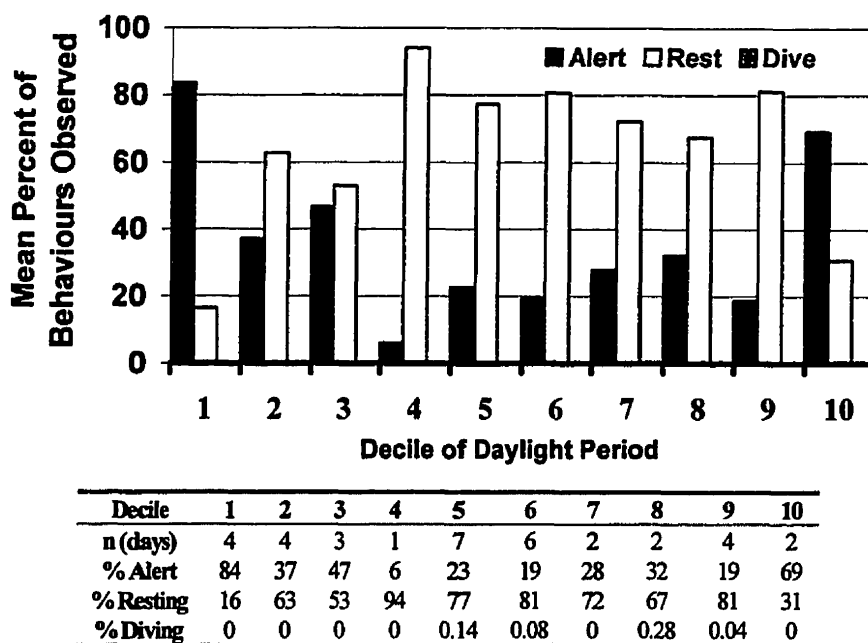
**Figure 13.** Mean group size of grebes encountered in distribution surveys. Figures are means and standard deviations of diurnal surveys conducted on 4 days in 1994/95 and 3 days in the 1995/95 season. X axis is in deciles of daylight hours where 0 is sunrise and 10 is sunset.



**Figure 14.** Sounder trace of scattering layer comprised of euphausiids, copepods, and fish on the evening of May 8, 1995, showing vertical migration to surface waters.

*Behavioral scans of Roosting Flocks:*

Wintering Western Grebes spend most of the daylight period in large roosting flocks. Early in the day grebes travel to the roosting locations and in late afternoon grebes disperse from roosting locations. While in the roosting flock grebes do not dive (Fig. 15). Western grebes are more alert in the morning and evening and spend most of the daylight period in resting posture (Fig. 15).



**Figure 15.** Summary of behaviors observed in behavioral scans of roosting flock in two wintering seasons from 1994 to 1996. X axis is in decile (tenths) of daylight hours where 0 is sunrise and 10 is sunset.

I observed single Western Grebes diving at night on 53 occasions in the winters of 1994 to 1996 (Table 4, Appendix 1). While I was able to observe grebes diving at night, it was very difficult to get dive duration data because of the limited range and small field of view of the night vision scope.

On March 16, 1995 and on March 12, 1996 I observed the first pair bonding displays that continued within the roosting flock until the grebes left for the breeding grounds in May. The displays I observed were "ratchet-pointing", "dip-shaking", "rushing", "barge-trilling", "neck-stretching", "bob-preening", and "high arch" (Nuechterlein and Storer 1982). On one occasion on March 24 1995 I recorded 81 social displays in 3.5 hours. On April 3, 1996 I sampled 7 - 5 minute periods in which I recorded all social "pair-bond" behaviours by birds in the roosting flock. The mean number of behaviours observed was 17 per 5 minute period (n=7), the range was 0 to 59 behaviours in 5 minutes.

I did not observe any predation of Western Grebes, but Dr. Fred Cooke collected a freshly killed Western Grebe from a Bald Eagle (*Haliaeetus leucocephalus*) that was feeding at Boundary Bay. On 5 occasions I saw Western Grebes respond by panic dives as other birds (2), aircraft (2), or eagles (1) flew over. On 2 occasions grebes watched eagles that approached. On one occasion I observed an eagle circling over a foraging grebe.

*Observations of dispersal:*

In addition to the diurnal surveys, I followed grebes dispersing from the roosting flock. The birds traveled up to 5 km. Only 0.7% (18 of 2731) of all grebes watched while dispersing were observed diving. In our study site grebes dispersed both north and south of the roosting flock location.



## DISCUSSION

Birds flock to exploit resources, for social interaction, or to avoid predation (Vine 1971). Flocking may also result from a combination of these factors. Which of these factors influence the behaviour of grebes? Western Grebe flocking behaviour is not directly a feeding strategy, since grebes do not usually feed while in the flock (Fig. 15).

Are winter grebe flocks formed to allow social interaction and mate evaluation? I observed grebes perform mating displays while in wintering roosting flocks, but these displays only occurred in spring, after March 12, and did not form a significant component of behaviours observed in flock scans at other times (Fig. 15). If winter flocks form for social display and mate evaluation, the flocks would likely not form until spring as the birds gather to migrate to the breeding grounds. This is the pattern observed for the sympatric Red-necked Grebes which form large flocks in spring but during the winter are solitary (pers. obs.).

It appears that Western Grebe flocks are not formed primarily for feeding or social display. Are they formed to resist predation? There are few animals that model the flocking and distribution behaviour of grebes better than the schooling behaviour of pelagic fish. The Pacific Herring (*Clupea harengus*) is a particularly good example since it is also the primary prey of the Western Grebe (Table 2). Pelagic fish commonly school during the day and disperse at night (Hobson 1979, Huntsman 1979). They do this as an anti-predator defense since they lack the advantage of proximity to cover that benthic (near bottom) fish have. At night, predation pressure is reduced because they are less detectable by predators under the cover of darkness. The flocking pattern of Western Grebes is unlike other fish eating marine birds because they have an additional problem that diurnal species don't encounter. Since Western Grebes are nocturnal foragers they have the additional difficulty of sleeping during the time of day when their predators are most active and when they are most visible to predators. Just like pelagic

fish, grebes can find little cover in the marine environment, so they form roosting flocks to reduce the risk of predation and to share the cost of vigilance while they rest.

If grebes form flocks as an anti-predation tactic, then why disperse to feed?

Many marine birds adopt group foraging strategies (Porter and Sealy 1981, Schenkeveld and Ydenberg 1985). The choice of foraging group size is ultimately determined by the distribution, abundance, and behaviour of the prey. It is likely that juvenile herring are the preferred prey of grebes (Table 2), so as well as mimicking the schooling behaviour of herring, grebes should also mimic their pattern of distribution. Both herring (Brawn 1960, Hobson 1968, 1986) and Western Grebes form large inactive schools during the day and then disperse at night to feed.

**Table 2.** Summary of necropsy data for Western Grebes collected from marine waters (Munro 1941, Chatwin 1956, Phillips and Carter 1957, Herman 1973, Robertson 1973, Vermeer and Ydenberg 1989, Monique Wilson U.S. Dept. Fish & Wildl. unpublished data 1995). Data are counts of stomachs that contained prey type categories. Weights of contents were not available.

<b>Stomach content data for Western Grebes</b>		
<b>collected in marine waters</b>		
<b>Prey Items</b>	<b>Counts of stomachs</b>	<b>Percent of stomachs</b>
herring	19	59.4%
other fish	11	34.4%
other	2	6.2%
<b>Total</b>	<b>32</b>	<b>100%</b>
<b>Total fish</b>	<b>30</b>	<b>94%</b>
<b>Total other</b>	<b>2</b>	<b>6%</b>

Although grebes disperse from large roosting flocks to feed at night, are they solitary foragers or do they forage in small groups? My nighttime observations of foraging Western Grebes suggest that they are likely solitary foragers. There are anecdotal observations of group and synchronous foraging by Western Grebes feeding during the day. To understand why grebes are solitary foragers at night, we must examine the distribution and behaviour of their prey.

If I assume that Western Grebes feed on herring and research shows that herring in Saanich Inlet feed on euphausiids (Barraclough and Fulton 1968, Robinson *et al.* 1968), I can predict the distribution of food for grebes. The dense layer of euphausiids in the inlet, although described as patchy in distribution, often maintains consistent horizontal distribution over periods of one to two weeks (Bary 1966). Phytoplankton on which the euphausiids feed occupy the upper 5 meters (m) of the water during winter months (Takahashi *et al.* 1978). Euphausiids, which form a layer tens of meters thick at depth, become concentrated as they migrate to feed in the upper 5 meters of the water column at night (Fig. 14). Near the surface at night we could then expect the food available to herring to be somewhat patchy with respect to the inlet's surface area, but very numerous within large patches. Herring feeding at night would be dispersed with respect to their daytime schooling behaviour, but likely numerous in surface waters. Bohl (1980) measured the horizontal distribution of four species of vertically migrating planktivorous fish in several lakes in Bavaria. He found that the fish dispersed from schools at night and were randomly distributed over the lake in a pattern indistinguishable from a Poisson distribution. If herring disperse in darkness to feed on euphausiids, it is likely that they would be randomly distributed with respect to a foraging grebe.

In summary, it is likely that zooplankton occur in large dense patches that are consistent in their horizontal distribution, but only appear in surface waters at night. Juvenile herring which stay in dense schools near the bottom during the day, are

numerous, but likely randomly distributed near the surface while feeding on euphausiids at night.

I will now predict, based on prey distribution, whether grebes should be solitary or group foragers. Optimal foraging theory suggests that if prey distribution is patchy and scarce, but numerous within a patch, then grebes may benefit from foraging in groups since all may benefit when one member encounters prey (Pulliam and Millikan 1982, Clark and Mangel 1984). This theory requires that the prey patch discovered is more than one grebe can consume and that the prey cannot flee before adjacent grebes arrive to feed. From what we know about herring dispersal at night, it is likely that a grebe would encounter only a single or a few herring at a time. A grebe encountering a patch would have only a single chance of capturing a fish before it flees to deeper water. Since grebes feed on prey that will quickly flee the approaching predator then there is no advantage to group foraging (Hamilton and Watt 1970, Clark and Mangel 1984, Pulliam and Millikan 1982, Ward and Zahavi 1973). Additionally, a grebe may suffer a cost if an adjacent grebe encounters the prey first. The limited direct observations of Western Grebes at night support the theory that they are indeed solitary foragers.

The overall pattern of flocking, dispersal, and roost location fits extremely well with Hamilton and Watt's theory of refuging (Hamilton and Watt 1970). Just as Hamilton *et al.*'s (1967) starlings wait until sunrise to disperse over the countryside to forage, Western Grebes wait until dark to disperse over Saanich Inlet. Refuging systems develop where resources occur in high abundance within scattered patches (Wiens 1976). The theory predicts that, as interspecific competition increases, foragers will travel further from the core (roost site) to less heavily exploited areas. As numbers of Western Grebes increase in Saanich Inlet we see the formation of smaller adjacent roosting flocks (Fig. 7).

Core roosting flocks probably form within traditionally productive foraging areas. This is why larger roosting flocks consistently appear in the same locations from year to

year. If the prey base is consistent from year to year, and the habitat remains the same, then the core roosting flock should remain centrally located within the foraging habitat. There should also be at least two kinds of roosting flocks, 1) large traditionally located roosting flocks that persist in the same locations year to year and throughout the wintering period, and 2) smaller flocks that appear only when numbers increase at the core sites. By combining Ideal Free Distribution theory with Hamilton's refuging system, we can predict that grebes dispersing further from the core flock site do equally as well as those choosing not to travel (Milinski and Parker 1991). If the prey base was consistent from year to year, we would expect that adjacent flocks would form at a similar threshold population size in each year. With further investigation, this may allow managers to estimate the maximum density tolerable to foraging grebes. Under the assumption that competition increases with a reduction in prey numbers, we may expect adjacent flocks to form at lower core population sizes. If this pattern can be successfully modeled then it may provide an index to monitor ecosystem health.

In summary, Western Grebes are marine predators specializing on vertically migrating fish. They form daytime roosting flocks within a traditional foraging area as an anti-predator defense while resting. The locations of roosting flocks are intimately linked to the abundance of juvenile fish populations. Seasonal changes in numbers within the roosting flock are the result of both transitional migrants as well as dispersal to adjacent foraging areas (chapter 1). It is likely that there are three kinds of winter roosting flocks, 1) the core roosting flock, 2) seasonal adjacent core flocks that form when population size increases, and 3) flocks that opportunistically form to take advantage of seasonal abundances of prey like spawning adult herring. Core roosting flocks disperse at night to take advantage of vertically migrating prey that are numerous but randomly distributed in surface waters. Nocturnal feeding Western Grebes are solitary foragers.

## CHAPTER 3 - NOCTURNAL FORAGING

### INTRODUCTION

There are many animals that have refined sensory and behavioral strategies that allow them to be active at night (McNeil *et al.* in press). It is not uncommon for birds to be occasionally active at night (Martin 1990a), but fewer than 3% are strictly nocturnal, completing all aspects of their life cycle after dark. A few birds have specialized sensory abilities. The Oilbird (*Steatornis caripensis*) (Snow 1961) and several species of swiftlets (*Apodidae*) (Griffin and Thompson 1982) have developed the ability to echolocate, whereas others are specialized to use different senses to exploit the night environment (Martin 1990b, Martin and Brooke 1990, McNeil *et al.* in press). It is likely however, that most birds use a synthesis of sensory inputs to allow them to be active at night and do not possess a single superior sensory ability (Martin 1990a).

One of the more suitable environments for nocturnal activity is the open water. Aquatic birds can receive the full illumination provided by the moon and starlight, without interception by foliage. Other than nest arrival and departure, the primary nocturnal activity of waterbirds is feeding (Brooke and Prince 1990, Owen 1990). But why would a bird choose to feed at night? McNeil *et al.* (1993) presented three hypotheses to explain nocturnal foraging in aquatic birds: (1) the supplementary hypothesis, (2) the predator avoidance hypothesis, and (3) the preference hypothesis.

The supplementary hypothesis suggests that night feeding occurs when daytime feeding has been inadequate to meet the bird's requirements. For wintering birds in northern latitudes, the short daylight period may not provide enough time to acquire the needed energetic stores. The predator avoidance hypothesis proposes that birds may feed at night to avoid attack from predators. Some predators may be strictly diurnal hunters or darkness may make foraging birds harder to locate. Finally, the preference

hypothesis suggests nighttime feeding opportunities are more profitable. This could arise from variation in availability, density, or quality of prey.

There are several ways that night foraging may be profitable for birds. When low tides occur at night, intertidal organisms will only be exposed after dark. For diving birds, vertically migrating prey are closer to the surface at night. For species which seize prey from the surface, prey may be available only at night. Nocturnal foragers can also take advantage of bioluminescent organisms which are visible in darkness (Imber 1973). Although several species of fish are likely available in daytime, the species available at night may be larger or higher in energetic content. Juvenile herring (*Clupeidae*) which migrate to surface waters at night contain twice the energetic density (kJ/g) of species such as sculpins (*Cottidae*), gunnels (*Pholidae*), and cod (*Gadidae*) available during the day (Roby *et al.* 1995).

Although diving birds feeding on molluscs or other benthic organisms can feed at night using tactile foraging techniques, those specializing on agile and elusive fish, seldom feed at night. Birds pursuing fish underwater are visually oriented predators that would suffer a great disadvantage foraging at night when elusive prey would be more difficult to see. In some instances, a temporary abundance of prey may provide the motivation for pursuit diving birds to forage at night. Marbled Murrelets (*Brachyramphus marmoratus*) (Carter and Sealy 1986), Rhinoceros Auklets (*Cerorhinca monocerata*) (Vermeer *et al.* 1987), Common Mergansers (*Mergus merganser*) (Sjoberg 1985), and King Penguins (*Aptenodytes patagonicus*) (Kooyman *et al.* 1992) are all known to take fish at night in response to increased availability of prey. King Penguins specialize on bioluminescent lanternfish (*Myctophidae*) which are likely visible in darkness (Kooyman *et al.* 1992, Hart 1973). Common Mergansers are suspected of using a tactile strategy while foraging nocturnally for salmon fry (Sjoberg 1985). Marbled Murrelets and Rhinoceros Auklets feed on juvenile herring and sandlance (*Ammodytidae*) which are often available in dense schools but are not bioluminescent. If

schools of fish are forced against the surface by predators, alcids may locate these disturbances on relatively clear bright nights. In most instances, however, it remains a mystery how diving birds could locate and capture cryptic active prey in dark waters.

The foraging behaviour of the Great Crested Grebe (*Podiceps cristatus*) is well documented from its wintering grounds on Lake IJsselmeer in the Netherlands (Piersma 1987, 1988, Piersma *et al.* 1988, Eerden 1993). Great Crested Grebes are crepuscular foragers and disperse from roosting flocks to feed at dusk and at dawn while there is still sufficient light to detect prey (Piersma *et al.* 1988).

Many of the accounts of Western Grebe foraging behaviour are from the breeding grounds where they appear to be daytime feeders (Lawrence 1950, Forbes 1985, Ratti 1985, Forbes and Sealy 1988, Ydenberg and Forbes 1988, Ydenberg and Clark 1989). There are a couple of anecdotal accounts of grebes feeding at night on the wintering grounds (Hatler *et al.* 1978, Chatwin 1956), but nocturnal foraging has not been scientifically documented for Western Grebes. Since Western Grebes are fish specialists, it raises the question why they would choose to feed at night, and additionally, how would they find and capture such elusive cryptic prey in darkness. If Western Grebes are nocturnal foragers, then how can they continue to feed after dark unlike the Great Crested Grebe which seems to be restricted by available light.

Because of the difficulties in observing behaviors at night, I approached the investigation of nocturnal foraging by Western Grebes by gathering evidence to show that grebes seldom forage during the day. This evidence is supplemented by direct observations, using a night vision scope, of birds diving at night. Although the primary question addressed in this discussion is: "Are Western Grebes nocturnal foragers?", the more challenging questions may be "Why do grebes choose to be nocturnal?" and "How can grebes find their prey in darkness?".



## *METHODS*

### *Study site:*

Wintering Western Grebes were observed in the waters off southern Vancouver Island, British Columbia (Fig. 2) from August 1994 to May 1995 and from August 1995 to May 1996. The study site was located in Saanich Inlet and surrounding waters.

Observations were conducted from a 6 meter (m) boat.

Grebes found foraging during the day were followed. Dive and pause durations were recorded and water depth recorded. Night observations of Western Grebes were made by positioning the boat at random locations in Saanich Inlet, turning off the motor and lights and waiting for grebes to approach close enough to view with a night vision scope.

### *Diurnal distribution surveys:*

See Methods Chapter 2.

### *Analysis:*

All observations have been adjusted to Pacific Standard Time. Sun rise and sunset times were calculated at Patricia Bay, Saanich Inlet, Lat. 48° 39' N , Long. 123° 30' W. Field observations of sunrise and sunset differ because of surrounding hills. Day observation times are expressed in deciles (tenths) of daylight hours to allow for seasonal differences in sunrise and sunset times, and daylengths. Sunrise is the start of the 1st decile and sunset is the end of the 10th decile of daylight hours. Night observations are expressed in deciles of nighttime hours where the start of the 1st decile is sunset and the end of the 10th decile is sunrise

### *Dissections:*

Two fresh Western Grebe specimens were dissected and the morphology of the bill, palate, and tongue examined. In addition, I examined museum specimens of Western Grebes, Great Crested Grebes (*Podiceps cristatus*), Red-necked Grebes, (*Podiceps grisegena*), Horned Grebes (*Podiceps auritus*), Anhingas (*Anhinga anhinga*), Great Blue Herons (*Ardea herodias*), Red Breasted Mergansers (*Mergus serrator*) and Common Mergansers (*Mergus merganser*).

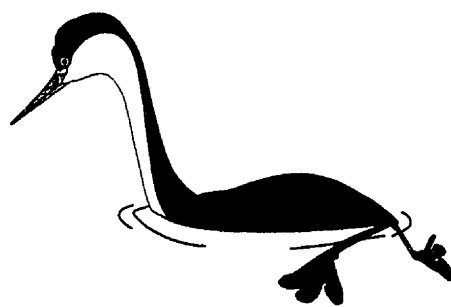
### **RESULTS**

A small portion of the wintering Western Grebe flock (approximately 2%) dive during the day. Mean dive durations for the species were calculated from mean durations for individual birds. The mean dive duration of day foraging Western Grebes was 49 seconds (s.) (n = 124, sd = 14.64) while the mean dive duration of a day foraging Red-necked Grebe was 134 s. (n = 21, sd = 32.90)(Table 3).

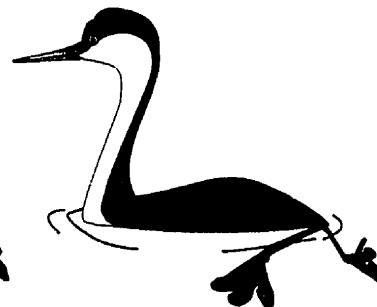
I observed Western Grebes diving at night on 53 occasions in the winters of 1994 to 1996 (Table 4, Appendix 1). While I was able to observe grebes diving at night, it was very difficult to get dive duration data because of the limited range and small field of view of the night vision scope. I encountered only single grebes at night. The posture of grebes foraging at night was different from that of grebes observed foraging during the day (Fig. 16). Grebes foraging at night had their neck angled forward and appeared to be looking into the water. Grebes foraging during the day would initiate a dive without appearing to look into the water.

**Table 3.** Summary of dive duration data for day foraging Western Grebes and Red-necked grebes. Number of birds is shown in brackets. Dive durations of alcids that specialize on epibenthic fish and pelagic schooling fish are shown for comparative purposes.

Species	Dive (sec.)		Source
	Mean	No. Dives	
<b>Western Grebe</b>	49	1603 (124)	this study
<b>Red-necked Grebe</b>	134	21 (1)	this study
<b>Black Guillemot:</b>	71		Cairns 1992
<b>Pigeon Guillemot:</b>			
Benthic foraging	86	140	Kuletz 1983
Pelagic foraging	47	125	Kuletz 1983
<b>Marbled Murrelet:</b>	28	119	Carter & Sealy 1990
	44	14	Thoresen 1989
	28	89	Clowater and Burger 1994
<b>Rhinoceros Auklet:</b>	37	46	Ainley <i>et al.</i> 1990
	45	75	Burger <i>et al.</i> 1993
	34	130	Clowater and Burger 1994



**Night Foraging**



**Day Foraging**

**Figure 16.** Grebes observed foraging at night appear to have a different posture than grebes seen feeding during the day.

*Diurnal distribution surveys:*

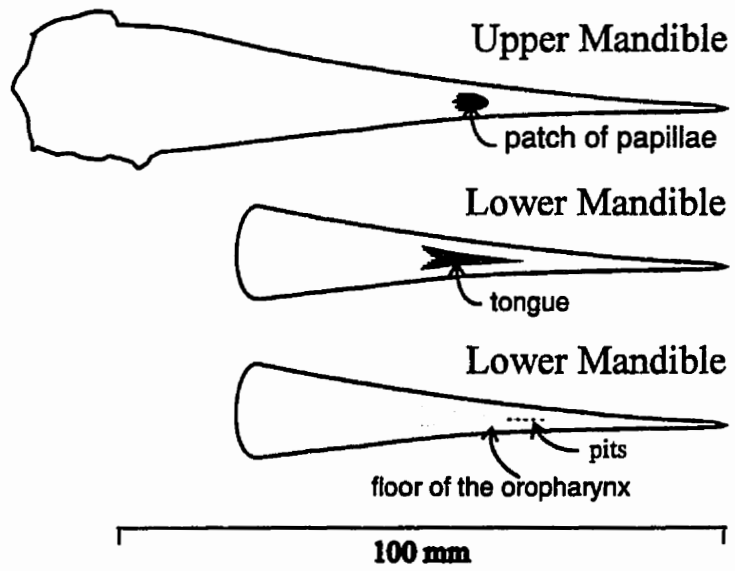
See Chapter 2.

*Diet:*

I researched necropsy evidence in the literature and summarized the data to present evidence to support diet specialization on pelagic fish (Table 2). I saw grebes with captured fish on only 4 occasions over 2 wintering seasons. The fish taken in 3 occasions were silver fish estimated to be less than 150 mm long. On April 3, 1996 a grebe forced a tight school of herring to the surface and I was able to net a sample of the prey fish. The fish captured were juvenile Pacific Herring (*Clupea harengus*), mean length of 111.4 mm and mean thickness of 22.3 mm (n=10).

*Dissections:*

I dissected 2 Western Grebe heads to look for specific adaptations of the bill and tongue that may facilitate nocturnal foraging. The rhambotheca of the Western Grebe forms a sharp knife-like surface along the edges of the bill, unlike either the anhinga's bill or the merganser's bill which both have serrated surfaces. The tongue is slender, pointed and much reduced with respect to the length of the bill. The upper surface of the palate has a patch of papillae that correspond to the position of the tongue (Fig. 17). I did not see any processes on the rhambotheca or the bill surface that resembled adaptations for tactile foraging. There were also no pits in the rhambotheca that may indicate chemosensors. There were however, a series of 6 pits in a line on the floor of the oropharynx just in front of the tongue.



**Figure 17.** Dissection examination of the Western Grebe bill and oral cavity.

## DISCUSSION

Although the research data on Western Grebes contains no reference to nocturnal foraging, there are a couple of anecdotal accounts of grebes seen diving at night. Hatler *et al.* (1978) report three occasions when grebes were seen hunting between the hours of 2210 and 2225 PST. On two of these occasions there were no significant light sources. Chatwin (1956) reports capturing grebes on a hook and line at midnight, 2:00 am, 3:30 am, and 4:50 am, where they were feeding near berthed ships in Seattle.

If the grebes in Saanich Inlet were feeding at night, then we should encounter few birds diving during the day. I designed surveys to record the daytime (diurnal) distribution and behaviour of grebes at the study site (Fig. 10). The data from two wintering seasons confirm that grebes spend the middle portion of the daylight period resting in large roosting flocks and the rest of the day traveling to and from roosting locations. Grebes are seldom observed diving while in the roosting flock (Fig. 15) or while traveling to or from that location. By providing evidence that grebes seldom forage during the day, I conclude that Western Grebes must be nocturnal foragers. Alternately, our observations could indicate that grebes perform a seasonal fast, such as was suggested by Piersma (1988) for molting Great Crested Grebes in the Netherlands. But since our observations span the full 8 month wintering period in two successive years it is unlikely that cessation of daytime foraging is a temporary event. In 1994/1995 I conducted synchronous observations on 3 roosting flocks 8-20 km apart and observed the same dispersal pattern that was documented at the study site. These observations suggest that nocturnal foraging is not a phenomenon restricted to the Saanich Inlet alone.

In addition to the diurnal surveys, I followed grebes that dispersed from the roosting flock. Since the group size diminishes over time, these observations sample the

behaviour of only a few birds. Our findings may be biased toward birds that disperse the greatest distance from the flock location. The diurnal surveys, as well as more casual observations at dusk indicate that grebes disperse over local waters and do not appear to congregate at localized foraging "hot spots".

It would be ideal to conduct night-time surveys to record the behaviours and distribution of grebes at night, but, because of the limited range of the night vision scope and the likelihood that bird behaviour would be disturbed by the sound of the boat, I could not continue the surveys after dark. To provide additional evidence and direct observations of grebes at night, I waited in a silent boat with lights off and I was able to observe grebes diving at night (Table 4, Appendix 1). Although these unsystematic observations alone would not present a convincing argument for nocturnal foraging at the population level, in addition to our diurnal survey evidence they provide a convincing confirmation.

Although casual observers may see birds feeding during the day, this is not the common strategy adopted by wintering Western Grebes. My evidence shows that Western Grebes are nocturnal foragers. Birds observed feeding during the day may be those that were unable to obtain their energetic requirements during the night-time period. Since flocks often roost far offshore it may not be apparent to observers on shore that the few birds they see foraging represent only a minor component of the population.

#### *Diet*

Before discussing alternate hypotheses of why grebes forage at night, I first address the problem that I lack necropsy data for the diet of grebes in this study. I did not obtain stomach samples, both because the birds are difficult to capture, and the study site is well populated and it was difficult to obtain shooting permits. I therefore provide evidence to support our hypothesis that Western Grebes feed exclusively on

pelagic schooling fish while on the wintering grounds. My evidence for an exclusive fish diet for wintering Western Grebes is in the form of a) direct observations of fish caught by grebes, b) published necropsy data, c) physiological adaptations, and d) diving behaviour.

Although most grebes are nocturnal foragers, in a large population it is possible to encounter a few birds foraging in daylight. In 1994/1995 I observed over 2,000 dives by grebes foraging during the day in Saanich Inlet, but fish were returned to the surface in only 5 of these dives. In all occasions the prey were slender silvery fish. It is likely that grebes are able to swallow most fish underwater. On one occasion, when a grebe forced a school of juvenile Pacific Herring (*Clupea harengus*) to the surface, I was able to obtain prey samples.

The necropsy data for birds wintering in marine waters indicate that in 32 stomach samples, 94% consumed fish, and 59.4% of fish were herring (Table 2). In 2 samples, stomach contents contained invertebrates as well as fish (Munro 1941). Although the sample size is small and I lack proportionate mass of individual prey items, these data suggests that grebes wintering in marine waters prefer fish over other food types and they prefer herring among available fish.

The alternative hypothesis is that grebes prey on pelagic or benthic invertebrates. Grebes in Saanich Inlet forage in water 200 m deep, it is unlikely that they dive to the bottom to feed on benthic invertebrates. In addition, the lower 100 m of the inlet is anoxic and would provide few species suitable for grebes.

Saanich Inlet, however, is well known for its high density of pelagic invertebrates, specifically euphausiids (Euphausiacea), copepods (Copepoda) and amphipods (Amphipoda) (Bary et al. 1962). In daytime the euphausiids are located just above the anoxic layer at 100 m, and migrate to the surface at dusk (Fig. 14). Several studies have documented fish associated with the dense layer of invertebrates in Saanich Inlet (Barraclough and Herlinveaux 1961, Bary et al. 1962, Boden and Kampa



1965, Bary 1967, Barraclough and Fulton 1968). The principal species are juvenile herring, hake (*Merluccius productus*), and dogfish (*Squalus suckleyi*) which appear to migrate to the surface at night. Nocturnal foraging grebes in Saanich Inlet may then be feeding on either pelagic fish or pelagic invertebrates (euphausiids) which move to the surface waters at night.

I have narrowed the possible prey choice of nocturnal foraging Western Grebes to either pelagic fish or invertebrates. I will now present evidence that grebes are morphologically adapted to feed on fish and not directly on euphausiids. By examining the bill and tongue shape of Western Grebes, I find additional evidence for specialization of fish and not invertebrates. Bedard (1969) explained that the structural stresses on the bill caused by feeding on krill occur nearer the tip of the bill, thus requiring that the bill be short and stout. In fish feeders, the stresses occur further away from the bill tip and allow a longer narrow bill. In addition, birds that specialize on euphausiids have large fleshy tongues, while fish eaters have reduced narrow cornified tongues. The Western grebe has a extremely long, narrow, sharp bill and a small narrow tongue (Fig. 17). Both of these adaptations are specific to a fish diet.

Another feature of the Western Grebe that suggests specialization on fish is an osteological adaptation of the neck which allows the sudden forward snap of the head for spearing prey (Storer 1960). Anhingas (*Anhingidae*), herons (*Ardeidae*), and to a lesser degree, the Great Cormorant (*Palacrocorax carbo*) are the only other species which share this adaptation (Bock 1956, Owre 1967, Payne and Rislely 1976, Storer and Nuechterlein 1992), which is specifically designed to capture elusive prey such as fish.

The foraging behaviour of a predator is intimately linked to the behaviour and ecology of its prey. By examining the dive duration data collected from daytime foraging Western Grebes I can provide additional evidence that they are pelagic fish specialists. Diving birds specializing on benthic solitary prey have different dive and recovery strategies from those birds specializing on pelagic schooling fish. The differences are

primarily due to optimal behaviour and not to physiological abilities. Ydenberg and Forbes (1988) showed that birds specializing on schooling fish may delay surface recovery times to exploit and remain in contact with a school of prey. Birds that feed on pelagic fish may not need to dive as deep as birds feeding on epibenthic fish or invertebrates. In general it appears that birds feeding on epibenthic fish will have longer mean dive durations than birds specializing on pelagic schooling fish (Kuletz 1983, Clowater and Burger 1994). Among alcids, both Pigeon Guillemots (*Cepphus columba*) and Black Guillemots (*Cepphus grylle*) tend to specialize on epibenthic organisms and have mean dive durations that are greater than species such as the Marbled Murrelets and the Rhinoceros Auklets that specialize on pelagic schooling fish (Table 3). Kuletz (1983) showed that benthic foraging Pigeon Guillemots had longer mean dive durations than pelagic foraging guillemots in the same colony (Table 3). A similar difference in diving behavior can be found by observing Red-necked Grebes and Western Grebes at our study site. I had the opportunity to compare a Western Grebe and a Red-necked Grebe feeding in the same bay. The mean dive duration of the Western Grebe was 49 seconds while the Red-necked Grebe had a mean dive duration of 134 seconds (Table 3). Longer mean dive durations are likely typical of species specializing on epibenthic fish while the shorter dive durations of Western Grebes are typical of birds specializing on pelagic schooling fish.

#### *Why feed at night*

If we accept that grebes feed on pelagic schooling fish, I must still present a hypothesis to explain why they would prefer to wait until darkness to feed. Considering McNeil *et al.*'s (1993) 3 hypotheses for nocturnal foraging, I can rule out the supplemental hypotheses since most grebes do not attempt to feed during the day. In fact, the inverse of this hypothesis may explain why a few grebes can be found feeding during the day, namely because night-time feeding has been inadequate to meet the

birds requirements. The second hypothesis suggests that grebes feed at night to avoid predation while foraging. In two years of observing grebes on the wintering grounds I saw no grebes taken by predators, however Dr. Fred Cooke (pers. comm.) encountered a Bald Eagle (*Haliaeetus leucocephalus*) with a freshly dead Western Grebe carcass. Even though grebes dive when Bald Eagles fly overhead, it is unlikely that predation pressure by eagles is enough to cause nocturnal foraging by Western Grebes. The final hypothesis suggests that night-time feeding opportunities are more profitable. This is likely a good explanation for nocturnal foraging by Western Grebes and I will now present a model to show how this could arise.

Foraging may become more profitable if either the energetic benefits of foraging are increased or the costs of foraging are decreased. The benefits of foraging at night may increase if larger or higher quality fish are available at night. This situation could easily arise with the natural distribution of prey species in Saanich Inlet. A summary of surface trawls in Saanich inlet in 1961 and 1966 indicate that fish are more numerous in surface water at night and that some species such as juvenile herring, and hake may only be available near the surface at night (Barraclough and Herlinveaux 1961, Barraclough and Fulton 1968). The mean energetic content of 1st and 2nd age class herring and sandlance are 160 kJ/fish and 65 kJ/fish respectively (Roby *et al.* 1995). In Saanich Inlet, herring, the more profitable species, may only be available to foraging birds at night, while other less profitable species, such as sandlance, are available during the day.

Diving is an energetically costly event, both because of the increase in muscle activity and because heat is lost to the cool water. The cost of foraging may be reduced if dive durations are shorter or because fewer dives are required to catch enough food. Dive durations can be shorter if prey is closer to the surface and travel time is reduced, or if prey is available in higher densities, the time until capture (search time) is reduced. It is likely that 80% of dives by birds feeding on schooling fish are search dives where no

prey is located (Kooyman and Davis 1982, Clowater and Burger 1994). If night feeding Western Grebes could reduce or eliminate search dives, they could vastly increase their net energy intake from foraging.

In summary, I suggest that Western Grebes feed at night because nocturnal foraging is energetically more profitable. Grebes may experience a greater net energy gain because the energetic content of prey fish available at night is much greater than the energetic content of fish available during the day. The energetic expense of diving may also be reduced at night because prey are closer to the surface.

#### *Mechanisms of prey capture*

Although I have presented several reasons why grebes would forage at night, the question of how they can find their prey in darkness remains a mystery. If grebes have a strategy that allows them to locate fish without conducting search dives, they could further reduce the cost of foraging. It is useful to speculate on the possible mechanisms of prey location and capture because it can lead to a more complete understanding of the predator-prey system and allow us to apply this knowledge to other species and systems.

How do birds find prey at night? The literature suggests several ways: birds may rely on the sensory inputs of 1) audition, 2) olfaction, 3) mechanoreception, 4) chemoreception, or 5) vision (Brooke and Prince 1990, Martin 1990a, 1990b, McNeil *et al.* 1992).

Auditory abilities important to nocturnal foraging birds consist of both sound sensitivity and sound localization (Knudsen 1980, McNeil *et al.* in press). Other than owls, most birds appear unspecialized for hunting by sound alone since their heads are small and they lack specialized external ear structures to help capture sound (for details see Knudsen 1980). Since Western Grebes, like other colonial waterbirds reviewed by

McNeil *et al.* (in press), lack specialized outer ear structures it is not likely that sound provides the sole mechanism for nocturnal prey capture.

In 1968 B.G. Bang and S. Cobb measured the size of the olfactory bulb in 108 species of birds. They assumed that proportional larger olfactory bulbs may indicate greater functional abilities between species. The largest olfactory bulbs were found in the Apterygiformes (Kiwi, *Apteryx australia*, n=1) followed by the Procellariiformes (n=15), and then the Podicipediformes (n=3) (Bang and Cobb 1968). The species measured were the Horned Grebe (*Podiceps auritus*, n=1) and the Little Grebe (*Podiceps rufficollis*, n=2). Although the sample sizes are very small, it is interesting to find that these two species of grebes appear to have well developed olfactory bulbs. Before we can infer functional ability from these observations we must first examine the phylogeny of the trait. If grebes are closely related to an ancestral species that had large olfactory bulbs they have inherited the trait without maintaining a current function. We still lack data on the Western Grebe.

Can olfaction aid Western Grebes in finding food? Most marine birds known to use olfaction to find food feed on floating refuse and carrion (Lequette *et al.* 1989), however, Nevitt *et al.* (1995) showed that Procellariiformes are attracted to dimethyl sulphide (DMS) which is released when zooplankton graze on phytoplankton. Detecting DMS may allow seabirds to locate and exploit zooplankton-rich areas (McNeil *et al.* 1992). Since herring may also be associated with zooplankton rich areas, Western Grebes may benefit if they can detect DMS. Although olfaction could help grebes find prey patches it is difficult to imagine how it could be useful in the capture of mobile prey.

If grebes use mechanoreception to detect prey, they would likely display some of the morphological adaptations seen in other species known to be tactile foragers (Martin 1990a, McNeil *et al.* 1992). Tactile foragers usually have specially adapted bill shapes and mechanoreceptors such as Herbst and Grandry's corpuscles in the bill and tongue.

Flamingos (*Phoenicopterus* spp.) and Mallards (*Anas platyrhynchos*) for example are tactile filter feeders that have very specialized bill structures. Many shorebirds use tactile foraging during day and night to probe for prey beneath the surface of the sand (Martin 1990a, McNeil *et al.* in press). Few tactile foragers specialize on large mobile prey (McNeil *et al.* in press). The Western Grebe's bill shape appears to be specialized for the grasping capture of fish (Bedard 1969) and a detailed microscopic examination of its bill did not reveal the pit structures expected in tactile foragers (Martin 1990a).

Chemoreception or taste detection of prey has been found only in species feeding on benthic or sedentary prey (Martin 1990a). Berkhoudt (1985) showed that a captive Great Crested Grebe was able to taste and reject a fish held in its bill. But can taste assist grebes to locate and capture prey? It is not likely that taste is a mechanism for prey capture of mobile prey, but just as olfaction may allow birds to detect zooplankton-rich patches in the ocean, it is possible that taste may allow birds to locate foraging patches.

There are several ways that birds could use vision to detect prey at night. They may have enhanced visual abilities, efficiently use available light, or they may select bioluminescent prey. The eyes of owls (*Tytonidae* and *Strigidae*) show adaptations for enhanced sensitivity in low light conditions. The visual sensitivity of owls was examined by Martin (1990a) who found that the mean absolute visual threshold of owls was lower than of humans by an average of 2.2 fold. The range of sensitivities in humans and owls overlap, however, so that one may expect to find individual people that have eyes that are more sensitive at night than some owls (Martin 1990a). Martin suggests that both human and owl retinas have attained the absolute limit of visual sensitivity for a vertebrate eye and that the difference in night vision capabilities is explained by owls being able to produce a brighter retinal image. Owls produce brighter images by having large pupils that can collect more light. If birds have enhanced night vision capabilities then we would expect them to have relatively large eyes.

Would enhanced visual abilities alone be sufficient to allow grebes to capture fish at night? If grebes had visual sensitivity similar to owls they should also have relatively large eyes. They don't appear to have large eyes. They also must be able to detect cryptic prey in dark waters. Martin (1990a) suggests that owls on dark nights or within the forest canopy are unable to hunt if restricted to sight alone. The nocturnal foraging ability of owls is better explained by their ability to use a synthesis of several sensory and behavioral strategies. Owl use not only hearing and vision but an intimate knowledge of the spatial structure of their hunting grounds. It is likely that grebes do not rely on enhanced visual abilities, but use several sensory and behavioural strategies to be successful foragers at night.

Grebes may efficiently use available light to forage at night. Diving birds and mammals dive deeply and use ambient light to silhouette prey against the surface (Hobson 1966). I observed grebes diving throughout the night-time period when there was very little ambient light and often cloudy skies and fog. I have no data, however, to determine whether these conditions allow sufficient light to silhouette prey against the surface. Grebes have been observed foraging at night near the lights of wharves and anchored ships (Chatwin 1956, Hatler *et al.* 1978, Clowater pers. Obs.), but very few birds were seen to do this. Prey taken in this way are likely a nearshore species that are not as energetically valuable as herring taken during the night (Roby *et al.* 1995). Birds that forage near ships may be those that are less successful at nocturnal foraging.

Do grebes feed on bioluminescent fish? There is some evidence that birds such as night feeding petrels select bioluminescent prey (Imber 1973), and King Penguins feed exclusively on bioluminescent lantern fish at night (Cherel and Ridoux 1992). Sampling of prey fish in Saanich Inlet include only 2 records of lanternfish (a total of 4 fish) (Barraclough & Herlinveaux 1961, Bary *et al.* 1962). Although lanternfish (Myctophidae) may be available in Saanich Inlet, necropsy data have not listed this species among the those taken from the stomachs of grebes. The stomach content data

for wintering grebes, however, were not collected with the knowledge that they may be nocturnal foragers. Samples taken during the day may not contain evidence of species taken at night. Without stomach content data, I cannot exclude that grebes could take bioluminescent lanternfish; however, samples taken of the pelagic fish population in Saanich Inlet list lanternfish as a very minor component.

In 1943, Birkenroad suggested that the light from disturbed bioluminescent organisms may betray the location of prey to their predators. He was specifically looking at invertebrates which emit light when attacked by predators. The burglar-alarm hypothesis suggests "an exhibition of light by the prey upon attack by a predator *might* attract an enemy of the predator (Burkenroad 1943)". Since then, Hobson *et al.* (1981) showed that predatory reef fish use the light from disturbed bioluminescence to detect prey fish in surface waters. No one has previously suggested that marine birds may do this as well. It is possible that Western Grebes use bioluminescence in two ways: 1) If a herring is feeding on euphausiids, the prey when disturbed, emit bioluminescent light which attracts the bird to consume the herring (the burglar-alarm hypothesis), and 2) if herring are feeding near the surface, and sense the approach of the secondary predator, they accelerate to flee and leave a bioluminescent wake (Burkenroad 1943) which betrays their location to the bird. Since I observed much bioluminescence in Saanich Inlet at night, it may be possible that grebes can use this technique to capture fish.

Considering the five sensory inputs that grebes may utilize to locate and capture fish, they do not appear to have specific morphological adaptations for either audition or mechanoreception. I have no data on chemoreception, but even if grebes were able to detect presence of prey in the water using taste, it would not likely be sufficient to aid in capturing mobile and elusive prey. There is some evidence that other grebe species have comparatively large olfactory bulbs, but again this mechanism would not likely be useful in prey capture. This leaves vision as the sensory basis of prey capture in foraging grebes. If their eyes are not specifically adapted for nocturnal vision and we



accept that lanternfish are not the primary prey species, then the two remaining mechanisms of prey capture are by using available surface light or by using ambient bioluminescence.

It is likely that grebes use an integration of sensory abilities to detect prey at night. Martin (1990a) explains that the night vision capability alone is insufficient to explain how owls are able to operate as nocturnal predators. Owls use a combination of vision, hearing, and an intimate knowledge of their foraging habitat to capture prey in darkness. Western Grebes probably utilize a wide range of techniques to locate fish in surface waters. In calm seas grebes may hear or see fish rippling the surface of the water, they may taste or smell patches rich in prey. To capture fish they may dive deep and look for prey silhouetted against the surface or they may look for bioluminescent wakes left by fleeing fish.

### *A bioluminating mechanism*

If Western Grebes use bioluminescence to locate fish, it would add another strategy to the options available to foraging grebes and help explain why they can rely on nocturnal foraging to provide their energetic requirements. I have no direct proof that grebes use bioluminescence to locate fish, but this unique mechanism may explain how grebes as well as other marine predators locate and capture fish at night. The reasons for suggesting this mechanism for Western Grebes are based on nocturnal observations of grebes as well as published theory. When observing grebes at night, there was a great abundance of ambient bioluminescence. When schools of fish were encountered by our slow moving boat, I could see bioluminescent wakes left by the fleeing fish. Grebes appear to be looking into the water at night. The posture of grebes observed at night was unlike that of grebes seen swimming during the day and unlike

those observed foraging during the day (Fig. 16). Grebes at night swim with their necks straight and angled ahead of their body, as though they are looking into the water.

Ultimately, natural selection should favor successful foraging strategies and many successful morphological and behavioral traits will appear across taxonomic boundaries by convergent evolution. Hobson *et al.* (1981) showed that nocturnal fish predators use bioluminescence to locate prey. They found that nocturnal fish have visual pigments that are particularly sensitive to bioluminescence and that differ from diurnal fish predators. Bioluminescence is likely a very effective way to detect predators and prey at night since luminescent organisms emit light when disturbed (Burkenroad 1943, Hobson *et al.* 1981). This may be why nocturnal planktivorous fishes are characteristically motionless while foraging at night (Hobson *et al.* 1981). Laboratory experiments indicate that the presence of bioluminescent dinoflagellates can increase the intake rate of primary predators (Mensing and Case 1992) as well as the foraging efficiency of secondary predators (Abrahams and Townsend 1993). If nocturnal foraging fish have evolved to take advantage of bioluminescence, then it is likely that other marine animals have done so as well. Several species of nocturnal fish spend the day in large inactive schools and disperse over the feeding grounds at night. This is strikingly similar to the flocking pattern I observed in Western Grebes and suggests that these are convergent behavioral adaptations suited specifically to nocturnal foraging.

If fish predators use bioluminescence to locate prey, then we would expect that other marine predators would use this strategy as well. Hobson (1966) suggests that seals and sea lions may locate and capture prey this way. Even humans, adapted to foraging in the marine environment, have used this technique. Nuu-chah-nulth fishermen in the 19th century used bioluminescence to locate Bluefin Tuna (*Thunnus thynnus*) and also attracted fish into harpooning range by creating a luminous wake with their canoe (Crockford 1994, 1997). Bioluminescent location of fish is such an effective strategy that aerial photographic techniques have been developed that utilize

the light from disturbed bioluminescent organisms to locate and assess fish stocks in surface waters (Cram and Hampton 1976).

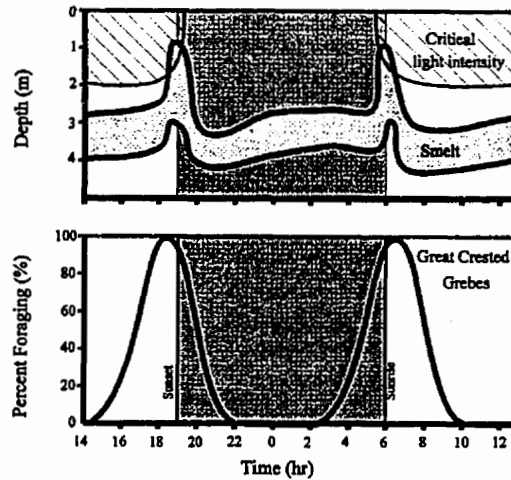
But is bioluminescence consistently available to nocturnal marine predators? Saanich Inlet has high densities of euphausiids, copepods, and amphipods, which are easily recorded as a vertically migrating scattering layer on sonograms throughout the year. The bioluminescent invertebrate community include microscopic dinoflagellates (*Dinoflagellata*), macroscopic euphausiids (*Euphausiacea*), ctenophores (*Ctenophora*), and cnidarian medusas (*Cnidaria*). The relative densities of these organisms likely vary throughout the year and it is generally considered that phytoplankton densities peak in summer months and lead to a complementary increase in numbers of predatory zooplankton at that time. A study of seasonal changes in bioluminescence in the Sargasso Sea, however, show that there is a higher density of bioluminescent organisms in the winter (Batchelder *et al.* 1990). Since bioluminescence involves many different kinds of organisms it is difficult to predict seasonal occurrence or extent of the phenomenon, it is likely, however, that bioluminescence is present throughout the seasonal cycle.

A foraging pattern similar to what I describe for Western Grebes was described by Piersma *et al.* (1988) for Great Crested Grebes on Lake IJsselmeer in the Netherlands. In that system, however, the prey fish, smelt (*Osmerus eperlanus*) was restricted by critical light intensity to fishing in the surface waters for a short period near dawn and dusk (Fig. 18). The smelt likely experience a tradeoff between the benefits of greater illumination for feeding and the cost of a greater vulnerability to predators with increasing light intensities. Piersma *et al.* (1988) found that the Great Crested Grebes responded to the vertical migration of their prey with a crepuscular foraging pattern that was synchronized with the increased availability of smelt in the surface waters.

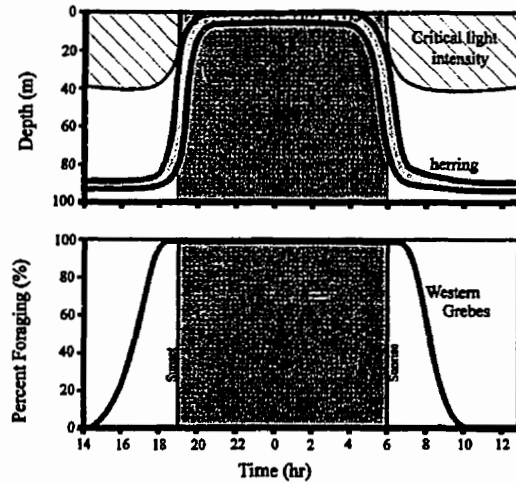
One might expect from this example that Western Grebes would respond to the vertical migration of their prey with crepuscular foraging and not nocturnal foraging. There are, however, some important differences between the predator-prey system described by Piersma *et al.* (1988) and the system I describe for Western Grebes in British Columbia. First of all, both systems are driven by the increased availability of prey in the surface waters. The smelt in Lake IJsselmeer are crepuscular foragers while juvenile herring are nocturnal foragers (Brawn 1960, Hobson 1968, 1986), and are likely available in the surface waters for a longer period of time than the smelt.

The second reason the systems differ is that Western Grebes have evolved to take advantage of the bioluminescence available in the marine environment. This mechanism allows grebes to extend their foraging time into the darkness period while the Great Crested Grebes in the Netherlands are restricted to foraging during a short period at dawn and dusk when there is sufficient daylight available to see prey (Fig. 18).

### Great Crested Grebes in the Netherlands



### Western Grebes in British Columbia



**Figure 18.** Comparison of diel changes in vertical distribution of prey and foraging behaviour of Great Crested Grebes on Lake IJsselmeer in the Netherlands (Piersma *et al.* 1988) and Western Grebes on Saanich Inlet. In the Netherlands, smelt are near the surface only at dawn and dusk while in Saanich Inlet herring remain at the surface during the night.

The final reason why the systems differ is that Great Crested Grebes and Western Grebes are morphologically dissimilar. The North American ecological counterpart to the Great Crested Grebe is the Red-necked Grebe (Fjeldsa 1983); they are similar in body weight, habitat preferences, and bill shape. The most important

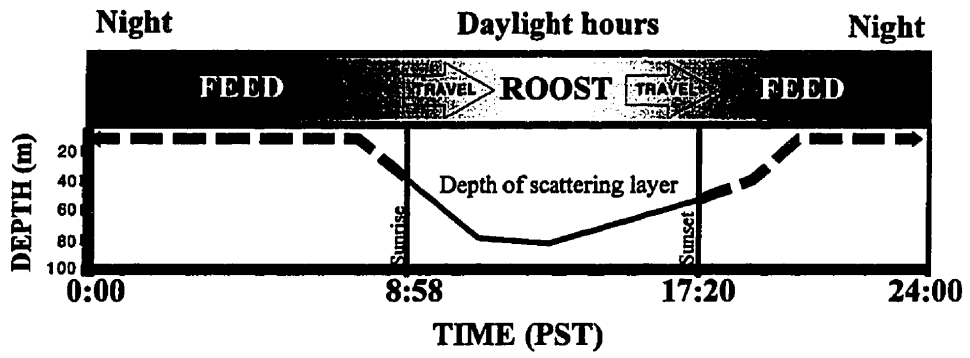
morphological difference is that Western Grebes have a long sharp pointed bill and are the only grebe species that has the osteological adaptation in the neck to allow spearing of fish (Storer 1960). When prey fish are detected by ambient bioluminescence, this adaptation, may allow Western Grebes to suddenly spear the fish, perhaps even from the surface. The spearing of prey may allow the Western Grebe to further reduce the cost of foraging, when compared to the Great Crested Grebe, by reducing the need for search or pursuit dives.

Although I have emphasized the differences between the behaviour of Great Crested Grebes and Western Grebes, the similarities between the systems indicate possible optimal solutions to similar problems and constraints faced by both species on the wintering grounds. The flocking and dispersal of both species appears to conform to a refuging system as described by Hamilton (1970). The distribution, flocking behaviour, and the dispersal pattern of both grebes is driven by the increased availability of vertically migrating prey. Since Great Crested Grebes and Western Grebes moult while on the wintering grounds, the energetic savings of pursuing prey in shallow rather than deep water may carry a greater survival value. The Great Crested Grebes are crepuscular foragers because 1) the smelt they prey on is only available at those times and vertically migrates to deeper waters both during mid-day and mid-night. 2) Great Crested Grebes are limited to foraging while there is sufficient daylight available to detect and capture prey. Since freshwater systems are deficient in numbers of bioluminescent organisms, grebes cannot use this mechanism to locate and capture prey after dark. Western Grebes are nocturnal foragers because 1) their prey are available in surface waters during the nighttime period. 2) They use ambient bioluminescence to locate and capture prey and are not restricted by the amount of daylight available to forage.

To offer convincing proof that Western Grebes utilize these strategies, I must develop a technique to better observe grebes foraging at night. By also devising a

method to capture grebes in the marine environment, I will have the opportunity to attach remote sensors which will allow us to determine dive durations and rate of prey capture. I may also have the opportunity to obtain fresh stomach contents. In the lab, I can test the response of grebes to simulated bioluminescence wakes and examine the structure and sensitivity of the Western Grebes eye in comparison to closely related diurnally foraging grebes.

In summary, grebes disperse from large diurnal roosting flocks to forage at night, much like nocturnal predatory fish (Fig. 19). It appears that they disperse to hunt individually over Saanich Inlet. They remain on the surface and search for signs of prey fish. Grebes may have several strategies for finding fish at night and will opportunistically select methods as conditions allow. If a searching grebe encounters a school of fish feeding near the surface, it may use the bioluminescent wakes of fleeing prey to locate and capture the fish. Nocturnal foraging may be energetically efficient because high quality fish are available at night, because fish move into surface waters, and because the grebes can locate fish without conducting search dives. The use of bioluminescence to locate and capture fish is a strategy that has not previously been suggested for marine birds, and may offer useful avenues of research to explain how other marine species find prey at night.



**Figure 19.** Summary of the dispersal and feeding of Western Grebes in Saanich Inlet in relation to the vertical migration of prey.



## **SYNTHESIS AND MANAGEMENT OPTIONS**

### *Synthesis*

The Western Grebe is a specialist among bird predators and displays three distinct degrees of specialization. A single degree of specialization adapts grebes for the pursuit of prey under water. Predators such as hawks, owls, and herons do not face the added difficulty of pursuing prey in an alien underwater environment. As a pursuit diver, the Western Grebe has acquired morphological adaptations that tradeoff terrestrial function for increased aquatic function. Among these adaptations are body size, bill shape, pelvis and hind limb structure, and foot structure. The second degree of specialization is to a diet of specific fish. On the wintering ground this may be further specialized to pelagic fish. Beyond this, our research suggests that wintering Western Grebes are also nocturnal foragers; a third degree of specialization.

Both the diurnal distribution pattern and the flocking behaviour of wintering Western Grebes are the direct result of specialization on vertically migrating prey which are most easily available at night. It is also likely that the consistent roosting flock locations are due to a historically consistent abundance of vertically migrating prey stocks. Although it appears that transient flocks may gather to take advantage of seasonally abundant prey such as spawning herring, many flocks persist at the same site throughout the wintering period.

If Western Grebes rely heavily on bioluminescence to capture prey, they represent an extremely specialized predator that is intimately dependent on a diurnal cycle of migrating predators and prey that begins with phytoplankton and zooplankton and ends with fish and grebes. It is more likely that the use of bioluminescence is just one of several strategies that grebes have to detect and capture fish at night. This is the first study to suggest that birds use bioluminescence to capture fish at night. Further research is required to provide conclusive evidence that grebes use bioluminescence and

to quantify how often they employ this tactic. We know that both nocturnal fish and aboriginal humans used bioluminescence to locate and capture prey; it is likely that other marine specialists including whales, dolphins, porpoises, seals and sealions use this technique as well.

### *Management*

Birds that are most susceptible to oil spills are those that form large flocks, since this means that a single spill can affect a greater proportion of the wintering population. In addition birds which dive for food tend to get the oil distributed over their entire body. Since Western Grebes are both diving birds and aggregate into large flocks, they are extremely vulnerable to oil spills. Because breeding populations at British Columbia's interior lakes are comprised of less than 200 birds, it is possible that a single oil spill could wipe out an entire breeding population.

Western Grebes are very specialized predators. Not only are they fish specialists, they may have evolved to specifically select pelagic, vertically migrating, juvenile fish. This extreme specialization puts them in a more precarious position than other generalist marine birds. If juvenile herring stocks are degraded due to habitat loss or over fishing of spawning adults, the grebes will find it more difficult to find food. Since there is a commercial fishery of herring, it would be prudent to expect over exploitation of the resource.

If Western Grebes are specialized predators of juvenile fish stocks, can we monitor grebe numbers as an indicator of ecosystem health? It likely depends on what scale our question encompasses. If bird populations can be used to monitor environmental change, the chosen species should be highly visible and widespread throughout the area of interest (Nysewander *et al.* 1993, 1994). Western Grebes have been selected on two occasions to examine bioaccumulation of toxic compounds acquired while wintering in coastal marine waters (Henny *et al.* 1990) (Vermeer *et al.*

1993). In Nysewander *et al.*'s (1993) Puget Sound Ambient Monitoring Program (PSAMP), the Western Grebe was not selected as a species to monitor environmental change because it was not evenly widespread throughout the study area. The PSAMP however, is mandated to monitor a very large area of coastal waters. If an interest was in monitoring the ecological health of a single inlet, such as Saanich inlet, then the Western Grebe may be a good candidate. Contrary to what was known about this grebe's distribution before this study was completed, the Western Grebe disperses quite widely over its foraging habitat at night. In a coastal habitat zone like Saanich Inlet, which is considered to be a nursery ground for juvenile fish (Barraclough and Herlinveaux 1961), the long-term monitoring of Western Grebe population numbers may provide a good index of juvenile fish populations.

The predictions of Hamilton's refuging theory and Ideal Free Distribution theory suggest that grebe populations should respond to variations in density of prey. In Saanich Inlet the seasonal occurrence of adjacent smaller roosting flocks may appear when the predator to prey ratio exceeds a threshold value. If we can establish a quantitative relationship between these population densities then we may easily monitor relative prey fish densities by recording when and at what population sizes adjacent flocks appear. With further investigation, this may allow managers to estimate the maximum density tolerable to foraging grebes and, under the assumption that competition increases with reductions of prey numbers, provide an index to monitor ecosystem health.

### *Recommendations*

1) Surveys which are intended to census numbers of wintering Western Grebes should be scheduled for January to avoid fluctuations in numbers due to migrant and dispersing birds.

2) Daylight surveys should be scheduled as close to the middle of the daylight period as possible so that most Western Grebes will be assembled in the roosting flock location.

3) The presentation of survey results should indicate roost locations and localized population numbers and avoid mathematically distributing the grebes encountered throughout the course route as "birds per kilometre".

4) Surveys intending to document habitat use must recognize that grebes disperse over deep water habitat to forage at night.

5) Managers interested in documenting diet of Western Grebes must obtain stomach samples at night or in early morning.

6) To protect British Columbia's low breeding populations of Western Grebes, the traditional winter roosting flock locations should be located and designated as sensitive wildlife areas.

## REFERENCES

- Abrahams, M.V., and L.D. Townsend. 1993. Bioluminescence in dinoflagellates: A test of the burglar alarm hypothesis. *Ecology* 74(1):258-260.
- Ainley, D.C., C.S. Strong, T.M. Penniman, and R.J. Boekelheide. 1990. The Feeding Ecology of Farallon Seabirds. *In* Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community. Edited by Ainley, D.C. and Boekelheide, R.J.. Stanford U Press, Stanford, Calif. pp. 51-127.
- Bang, B.G., and S. Cobb. 1968. The size of the olfactory bulb in 108 species of birds. *Auk* 85:55-61.
- Barracough, W.E., and J.D. Fulton. 1968. Data record: Food of larval and juvenile fish caught with a surface trawl in Saanich Inlet during June and July 1966. Manuscript Report Fisheries Research Board Canada 1003.
- Barracough, W.E., and R.H. Herlinveaux. 1961. Midwater trawling through the echo scattering layer in Saanich Inlet March 1-2 1961. Fisheries Research Board of Canada Manuscript Report 712.
- Bary, B.McK. 1966. Qualitative observations of scattering of 12 kc/s sound in Saanich Inlet, British Columbia. *Deep-Sea Research* 13:667-677.
- Bary, B.M. 1967. Diel vertical migrations of underwater scattering, mostly in Saanich Inlet, British Columbia. *Deep-Sea Research* 14:35-50.
- Bary, B.M., W.E. Barracough, and R. Herlinveaux. 1962. Scattering of underwater sound in Saanich Inlet, British Columbia. *Nature* 194:36-37.
- Batchelder, H.L., E. Swift, and J.R. Van Keuren. 1990. Pattern of planktonic bioluminescence in the northern Sargasso Sea: seasonal and vertical distribution. *Marine Biology* 104:153-164.
- B.C. Conservation Data Centre. 1997. Rare vertebrate animal tracking list, March 10, 1997. Wildlife Branch, British Columbia Ministry of Environment, Lands & Parks. pp.5
- Bedard, J. 1969. Adaptive radiation in Alcidae. *Ibis* 111:189-198.
- Berkhoudt, H. 1985. Structure and function of avian taste receptors. 463-496 in . *Form and Function in Birds*. Academic Press. London.
- Bock, W.J. 1956. A generic review of the Family Ardeidae (Aves). *American Museum Novitates* 1779:1-49.
- Boden, B.P., and E.M. Kampa. 1965. An aspect of euphausiid ecology revealed by echosounding in a fjord. *Crustaceana* 9:155-173.
- Bohl, E. 1980. Diel pattern of pelagic distribution and feeding in planktivorous fish. *Oecologia (Berl.)* 44:368-375.
- Bollens, S.M. 1996. Diel vertical migration in zooplankton: Trade-offs between predators and food. *Oceanus* 39:19.

- Brawn, V.M. 1960. Seasonal and diurnal vertical distribution of herring (*Clupea harengus L.*) in Passamaquoddy Bay, N.B., J. Fish. Res. Bd. Can. 17:699-711.
- Brooke, M.de L., and P.A. Prince. 1990. Nocturnality in seabirds. Acta XX Congressus Internationalis Ornithologici(II):1113-1121.
- Burger, A.E. 1997. Status of the Western Grebe in British Columbia. Wildlife Working Report WR-87:32.
- Burger, A.E., R.P. Wilson, D.G. Wilson, M-P.T. Wilson. 1993. Diving depths, diet, and underwater foraging of Rhinoceros Auklets in British Columbia. Can. J. Zool. 71:2528-2540.
- Burkenroad, M.D. 1943. A possible function of bioluminescence. J. marine Research 5:161-164.
- Cairns, D.K. 1992. Diving behaviour of Black Guillemots in Northeastern Hudson Bay. Colonial Waterbirds 15: 245-248.
- Campbell, R.W., N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser, and M.C.E. McNall. 1990. The Birds of British Columbia: Volume 1. Nonpasserines. Canadian Wildlife Service. Birds. p.178-181.
- Cannings, R.A., R.J. Cannings, and S.G. Cannings. 1987. Birds of the Okanagan Valley, British Columbia. Royal British Columbia Museum, Victoria.
- Carter, H.R., and S.G. Sealy. 1986. Year-round use of coastal lakes by Marbled Murrelets. Condor 88:473-477.
- Carter, H.R., and Sealy, S. G. 1990. Daily foraging behavior of Marbled Murrelets. In Auks at sea. Proceedings of an International symposium of the Pacific Seabird Group, Pacific Grove, California, 17 December, 1987. Edited by S. G. Sealy. Studies in Avian Biology No. 14: 93-102.
- Chatwin, S.L. 1956. The Western Grebe taken on hook and line. Condor 58:73-74.
- Cherel, Y., and V. Ridoux. 1992. Prey species and nutritive value of food fed during summer to King Penguin *Aptenodytes patagonicus* chicks at Possession Island, Crozet Archipelago. Ibis 134:118-127.
- Clark, C.W., and M. Mangel. 1984. Foraging and flocking strategies: information in an uncertain environment. American Naturalist 123:626-641.
- Clowater, J.S., and A.E. Burger. 1994. The feeding behaviour of Pigeon Guillemots (*Cepphus columba*) off southern Vancouver Island, British Columbia. Can. J. Zool. 72:863-872.
- Cram, D.L., and I. Hampton. 1976. A proposed aerial/acoustic strategy for pelagic fish stock assessment. J.Cons. int. Explor. Mer. 37(1):91-97.

- Crockford, S. (1994): New archaeological and ethnographic evidence of an extinct fishery for giant bluefin tuna (*Thunnus thynnus orientalis*) on the Pacific Northwest Coast of North America. *Fish Exploitation in the Past. Proceedings of the 7th meeting of the ICAZ Fish Remains Working Group.* Van Neer, W.(ed.), Annales du Musee Royal de l'Afrique Centrale, Sciences Zoologiques n.274, Tervuren, 1994. p.163-168.
- Crockford, S.J. 1997. Archeological evidence of large northern bluefin tuna, *Thunnus thynnus*, in coastal waters of British Columbia and northern Washington. *Fishery Bulletin* 95:11-24.
- Eichhorst, B.A., 1992. An analysis of Western Grebe banding and recovery data. *North American Bird Bander* 17(3): 108-115.
- Fjeldsa, J., 1983, Ecological character displacement and character release in grebes Podicipedidae. *Ibis* 125: 463-481.
- Forbes, L.S. 1985. The feeding ecology of Western Grebes breeding at Duck Lake, British Columbia. M.Sc. Thesis. University of Manitoba, Winnipeg
- Forbes, L.S., and S.G. Sealy. 1988. Diving behaviour of male and female Western Grebes. *Can. J. Zool.* 66:2695-2698.
- Fretwell, S.D., and H.J. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16-36.
- Gliwicz, M.Z. 1986. Predation and the evolution of vertical migration in zooplankton. *Nature* 320:746- 748.
- Griffin, D.R., and D. Thompson. 1982. Echolocation by cave swiftlets. *Behav. Ecol. Sociobiol.* 10: 119-123.
- Hamilton III, W.J. 1966. Social Aspects of Bird Orientation Mechanisms. 57-71 in . *Animal Orientation and Navigation: Proceedings of the Twenty-Seventh Annual Biology Colloquium, May 6-7, 1966.* Oregon State University Press. Corvallis.
- Hamilton III, W.J., and K.E.F. Watt. 1970. Refuging. *Ann. Rev. Ecol. Syst.* 1:263-287.
- Hamilton III, W.J., and W.M. Gilbert. 1969. Starling dispersal from a winter roost. *Ecology* 50(5):886-898.
- Hamilton III, W.J., and K.E.F. Watt. 1970. Refuging. *Ann. Rev. Ecol. Syst.* 1:263-287.
- Hamilton III, W.J., W.M. Gilbert, F.H. Heppner, and R.J. Planck. 1967. Starling roost dispersal and a hypothetical mechanism regulating rhythmical animal movement to and from dispersal centers. *Ecology* 48(5):825-833.
- Hart, J.L. 1973. *Pacific Fishes of Canada.* Fisheries Research Board of Canada, Ottawa.
- Hatler, D.F., R.W. Campbell, and A. Dorst. 1978. *Birds of Pacific Rim National Park.,* Victoria.

- Henny, C.J., L.J. Blus, and R.A. Grove. 1990. Western Grebe, *Aechmophorus occidentalis*, wintering biology and contaminant accumulation in Commencement Bay, Puget Sound, Washington. *The Can. Field Nat.* 104:460-472.
- Herman, S.G. 1973. Cyclic fluctuations in feeding rates and body weight in captive Western Grebes *Aechmophorus occidentalis*. Ph.D. Dissertation. University of California, Davis
- Hobson, E.S. 1966. Visual orientation and feeding in seals and Sea Lions. *Nature* 210:326-327.
- Hobson, E.S. 1968. Predatory behavior of some shore fishes in the Gulf of California. in . U.S. Dept. Interior Bureau of Sport Fish. and Wildl. Research Report 73. diurnal. nocturnal.
- . 1979. Interactions between piscivorous fishes and their prey. 231-242 in . Predator-prey systems in Fisheries management. Sport Fishing Institute. Washington, D.C.
- . 1986. Predation on Pacific Sandlance, *Ammodytes Hexapterus* (Pices: *Ammodytidae*) during the transition between day and night in southeastern Alaska. *Copeia* 1986 (1):223-226.
- Hobson, E.S., W.N. McFarland, and J.R. Chess. 1981. Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of their scotopic visual pigments and the photic environment. *Fishery Bulletin* 79:1-30.
- Holmgren, N., and A. Hedenstrom. 1995. The scheduling of molt in migratory birds. *Evolutionary Ecology* 9:354-368.
- Huntsman, G.R. 1979. Predation's role in structuring reef fish communities. 103-108 in . Predator-prey systems in Fisheries management. Sport Fishing Institute. Washington, D.C.
- Hutchinson, I., A.C. Prentice, and G. Bradfield. 1989. Aquatic plant resources of the Strait of Georgia. 50-60 in . The ecology and status of marine and shoreline birds in the Strait of Georgia, British Columbia. Spec. Publ. Can. Wildl. Serv. Ottawa.
- Imber, M.J. 1973. The food of the Grey-faced Petrels (*Pterodroma macroptera* Gouldi (Hutton)), with special reference to diurnal vertical migration of their prey. *Journal of Animal Ecology* 42:645-662.
- James, R.A. 1989. Mate feeding in wintering Western Grebes. *J. Field Ornithol.* 60:358-360.
- Jarman, P.J. 1974. The social Organisation of antelope in relation to their ecology. *Behaviour* 68:214-267.
- Jehl, J.R. 1990. Aspects of molt migration. in *Bird Migration*. E. Gwinner (Ed.) Springer-Verlag, Berlin. p. 102-113.



- Knudsen, E.I. 1980. Sound localization in birds. in . Comparative Studies of Hearing in Vertebrates. Springer-Verlag. New York.
- Kooyman, G.L., and R.W. Davis. 1982. Diving depths and energy requirements of King Penguins. *Science* 217:726-727.
- Kooyman, G.L., Y. Cherel, Y. Le Maho, J.P. Croxall, P.H. Thorson, V. Ridoux, and C.A. Kooyman. 1992. Diving behaviour and foraging energetics during foraging cycles in King Penguins. *Ecological Monographs* 61(1):143-163.
- Kuletz, K.J., 1983. Mechanisms and consequences of foraging behavior in a population of breeding Pigeon Guillemots. M.Sc. Thesis, University of California, Irvine.
- Lawrence, G.E. 1950. The diving and feeding activity of the Western Grebe on the breeding grounds. *Condor* 52:3-16.
- Lequette, B., C. Verheyden, and P. Jouventin. 1989. Olfaction in subantarctic seabirds: Its phylogenetic and ecological significance. *Condor* 91:732-735.
- Martin, G.R. 1990a. Birds by night. T & A D Poyster, London.
- Martin, G.R. 1990b. The sensory bases of nocturnal foraging in birds. *Acta XX Congressus Internationalis Ornithologici(II)*:1130-1135.
- Martin, G.R., and M.de L. Brooke. 1990. Introductory remarks: Nocturnality in birds. *Acta XX Congressus Internationalis Ornithologici(II)*:1091-1097.
- McNeil, R., P. Drapeau, and J.D. Goss-Custard. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. *Biol. Rev.* 67:381-419.
- McNeil, R., P. Drapeau, and R. Pierotti. 1993. Nocturnality in colonial waterbirds: occurrence, special adaptations, and suspected benefits. *Current Ornithology* 10:187-246.
- McNeil, R., F. Genevois, J.A. Kushlan, and G.R. Martin. in press. Foraging and nocturnality in colonial waterbirds. in . Colonial breeding in waterbirds: Evolutionary causes and functional consequences. Oxford University Press. Oxford.
- Mensingher, A.F., and J.F. Case. 1992. Dinoflagellate luminescence increases susceptibility of zooplankton to teleost predation. *Marine Biology* 112:207-210.
- Milinski, M., and G.A. Parker. 1991. Competition for resources. 137-168 in . Behavioural Ecology: An Evolutionary Approach. Blackwell Scientific Publications. London.
- Morgan, K.H. 1989. Marine birds of Saanich Inlet, a Vancouver Island fjord entering the Strait of Georgia. 158-165 in . The ecology and status of marine and shoreline birds in the Strait of Georgia, British Columbia. Spec. Publ. Can. Wildl. Serv. Ottawa.
- Munro, J.A. 1941. Studies of Waterfowl in British Columbia: The Grebes. British Columbia Provincial Museum, Victoria.

- Nevitt, G.A., R.R. Veit, P. Kareiva. 1995. Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds. *Nature* 376: 680-682.
- Nuechterlein, G.L., and R.W. Storer. 1982. The pair-formation displays of the western grebe. *Condor* 84:350-369.
- Nysewander, D., J. Stein, and S. Jeffries. 1993. Implementation plan for marine bird, waterfowl, and marine mammal monitoring in the Puget Sound Ambient Monitoring Program. Wash. Dept. of Wildlife, Olympia, Washington.
- Nysewander, D., M. Nixon, and J. Stein. 1994. Puget Sound Ambient Monitoring Program: Progress report of the marine bird, waterfowl, and marine mammal monitoring project. Wash. State Dept. Fish and Wildl. Birds.
- Ohman, M.D. 1990. The demographic benefits of diel vertical migration by zooplankton. *Ecological Monographs* 60(3):257-281.
- Owen, M. (1990): Nocturnal feeding in waterfowl. *Acta XX Congressus Internationalis Ornithologici(II)*:1105-1112.
- Owre, O.T. 1967. Adaptations for locomotion and feeding in the anhinga and the Double-crested Cormorant. *Ornithological Monographs* 6:1-137.
- Payne, R.B., and C.J. Risley. 1976. Systematics and evolutionary relationships among the herons (*Ardeidae*). *Miscellaneous publications Museum of Zoology, University of Michigan* 150:1-115.
- Phillips, R.E., and G.D. Carter. 1957. Winter food of Western Grebes. *Murrelet* 38(1):5-6.
- Piersma, T. 1987. Population turnover in groups of wing-moulting waterbirds: the use of a natural marker in Great Crested Grebes. *Wildfowl* 38: 37-45.
- Piersma, T. 1988. The annual moult cycle of Great Crested Grebes. *Ardea* 76:82-95.
- Piersma, T., Lindeboom, R., van Eerden, M.R. 1988. Foraging rhythm of Great Crested Grebes *Podiceps cristatus* adjusted to diel variations in the vertical distribution of their prey *Osmerus eperlanus* in a shallow eutrophic lake in the Netherlands. *Oecologia* 76: 481-486.
- Porter, J.M., and S.G. Sealy. 1981. Dynamics of seabird multispecies feeding flocks: Chronology of flocking in Barkley Sound, British Columbia, in 1979. *Colonial Waterbirds* 4:104-113.
- Pulliam, H.R., and G.C. Millikan. 1982. Social organization in the nonreproductive season. *Avian Biology* VI:169-197.
- Purdy, A. 1972. Whoever you are. *in Selected Poems*. McClelland and Stewart, Toronto. p.113.
- Ratti, J.T. 1985. A test of water depth niche partitioning by Western Grebe color morphs. *Auk* 102:635-637.

- Robertson, I. 1973. Predation by fish-eating birds on stocks of the Pacific Herring, *Clupea pallasii*, in the Gulf Islands of British Columbia. in . unpublished report Fish. Res. Board of Can. Nanaimo. Birds.
- Robinson, D.G., W.E. Barraclough, and J.D. Fulton. 1968. Data Record. Number, size composition. weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia June 5-9, 1967. Fisheries Research Board of Canada Manuscript Report 972:1-109.
- Roby, D.D., J.L. Ryder, G. Blundell, K.R. Turco, and A. Prichard. 1995. Diet composition, reproductive energetics and productivity of seabirds damaged by the Exxon Valdez oil spill. in . Annual Report Restoration Project 95163 G Alaska Cooperative F & W Res. Unit.
- Salomonsen, F. 1965. The moult migration. Wildfowl 19: 5-24.
- Schenkeveld, L.E., and R.C. Ydenberg. 1985. Synchronous diving by surf scoter flocks. Can. J. Zool. 63:2516-2519.
- Sibley, F.C. 1970. Winter wing molt in the Western Grebe. Condor 72: 373.
- Sjoberg, K. 1985. Foraging activity patterns in the Goosanger (*Mergus merganser*) and the red-breasted merganser (*M. serrator*) in relation to patterns of activity in their major prey species. Oecologia(Berlin) 67:35-39.
- Snow, D.W., 1961. The natural history of the Oilbird, *Steatornis caripensis*, in Trinidad. 1. General behaviour and breeding habits. Zoologica 46: 27-48.
- Storer, R.W. 1960. Evolution in the diving birds. Proceedings of the Twelfth International Ornithological Congress 12:694-707.
- Storer, R.W., and J.R. Jehl, Jr. 1985. Molt patterns and molt migration in the Black-necked Grebe *Podiceps nigricolis*. Ornithologica Scandinavica 16(4): 253-260.
- Storer, R.W., and G.L. Nuechterlein. 1985. An analysis of plumage and morphological characters of the two color forms of the Western Grebe. Auk 102: 102-119.
- Storer, R.W., and G.L. Nuechterlein. 1992. Western Grebe & Clark's Grebe. The Birds of North America 26:1-22.
- Takahashi, M., J. Barwell-Clark, F. Whitney, and P. Koeller. 1978. Winter condition of marine plankton populations in Saanich Inlet, B.C., Canada. I. Phytoplankton and its surrounding environment. Journal of experimental marine Biology and Ecology 31:283-301.
- Thoresen, C. 1989. Diving times and behavior of Pigeon Guillemots and Marbled Murrelets off Rosario Head, Washington. Western Birds 20: 33-37.
- van Eerden, M.R., T. Piersma, and R. Lindeboom. 1993. Competitive food exploitation of smelt *Osmerus eperlanus* by Great Crested Grebes *Podiceps cristatus* and perch *Perca fluviatilis* at Lake IJsselmeer. Oecologia 93:463-474.

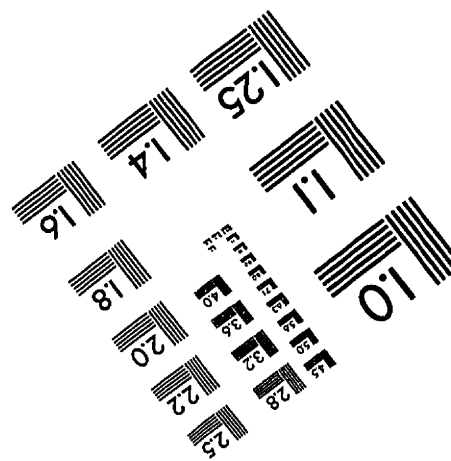
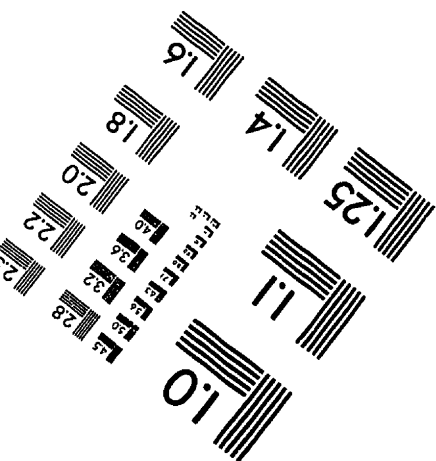
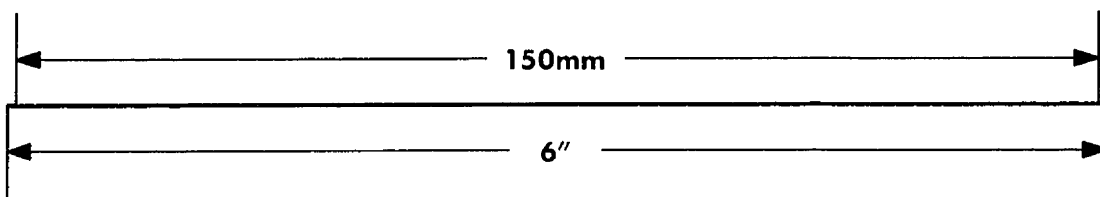
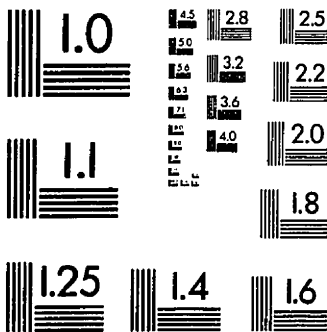
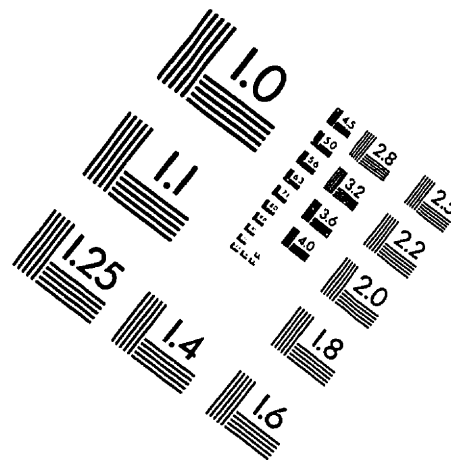
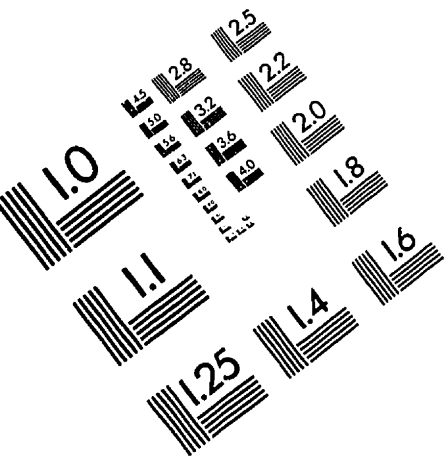
- Vermeer, K., and K.H. Morgan. 1992. Marine bird populations and habitat use in a fjord on the west coast of Vancouver Island. 86-96 in . The ecology, status, and conservation of marine and shoreline birds on the west coast of Vancouver Island. Canadian Wildlife Service. Ottawa.
- Vermeer, K., and R.C. Ydenberg. 1989. Feeding ecology of marine birds in the Strait of Georgia. 62-73 in . The ecology and status of marine and shoreline birds in the Strait of Georgia, British Columbia. Spec. Publ. Can. Wildl. Serv. Ottawa.
- Vermeer, K., K.H. Morgan, A. Dorst, and B. Whittington. 1992. Bird populations of estuaries on the southwest coast of Vancouver Island. 97-108 in . The ecology, status, and conservation of marine and shoreline birds on the west coast of Vancouver Island. Canadian Wildlife Service. Ottawa.
- Vermeer, K., W.J. Cretney, J.E. Elliott, R.J. Norstrom, and P.E. Whitehead. 1993. Elevated polychlorinated dibenzodioxin and dibenzofuran concentrations in grebes, ducks, and their prey near Port Alberni, British Columbia, Canada. *Marine Pollution Bulletin* 26(8):431-435.
- Vermeer, K., S.G. Sealy, and G.A. Sanger. 1987. Feeding ecology of Alcidae in the eastern North Pacific Ocean. 189-227 in . Cambridge University Press, London.
- Vine, I. 1971. Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *J. theor. Biol.* 30:405-422.
- Ward, P., and A. Zahavi. 1973. The importance of certain assemblages of birds as information-centres for food-finding. *Ibis* 115:517-534.
- Wetmore, A. 1924. Food and economic relations of North American grebes. United States Department of Agriculture Department Bulletin 1196:1-24.
- Wiens, J.A. 1976. Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* 7:81-120.
- Ydenberg, R.C., and C.W. Clark. 1989. Aerobiosis and anaerobiosis during diving by Western Grebes: An optimal foraging approach. *J. theor. Biol.* 139:437-449.
- Ydenberg, R.C., and L.S. Forbes. 1988. Diving and foraging in the Western Grebe. *Ornis Scandinavica* 19:129-133.

## **APPENDIX 1**

**Table 4.** Summary of observations of Western Grebes diving at night. Sunset is the beginning of 1st decile and sunrise is the end of 10th decile.

#	Date	Obs. Time	Decile	#	Date	Obs. Time	Decile
		STD	of			STD	of
			Night				Night
1	71294	16:30	1	27	120396	06:23	10
2	71294	16:45	1	28	120396	06:25	10
3	291294	07:09	10	29	120396	06:26	10
4	291294	16:30	1	30	120396	06:27	10
5	291294	16:36	1	31	120396	06:30	10
6	311294	16:40	1	32	50496	19:05	1
7	311294	16:49	1	33	50496	19:08	1
8	311294	17:08	1	34	50496	19:58	2
9	311294	17:12	1	35	50496	20:09	2
10	311294	17:12	1	36	50496	20:38	2
11	40195	07:53	10	37	100496	00:11	5
12	40195	16:46	1	38	100496	00:51	6
13	270395	06:00	10	39	120496	23:13	5
14	270395	06:01	10	40	130496	00:28	6
15	270395	19:02	1	41	130496	00:34	6
16	270395	19:04	1	42	130496	00:49	6
17	240495	04:56	10	43	130496	00:51	6
18	240495	19:29	1	44	130496	01:26	7
19	181095	17:19	1	45	130496	22:15	4
20	181095	17:27	1	46	130496	23:42	5
21	181095	17:28	1	47	190496	00:42	6
22	181095	20:10	3	48	190496	01:01	6
23	201195	07:22	10	49	190496	01:46	7
24	11295	07:40	10	50	190496	22:55	4
25	100296	07:10	10	51	190496	23:49	5
26	120396	06:21	10				

# IMAGE EVALUATION TEST TARGET (QA-3)



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