

Continued Monitoring of Common Murres on Tatoosh Island

Final Report 1995

September 1996

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Acknowledgments

The author wishes to thank the Makah Tribal Nation and the U. S. Coast Guard for continued access to Tatoosh Island. As Makah college student intern, Neuee Vitalis helped collect field data as well as contribute to its analysis. Karen Jensen, Johanna Salatas, Trista Patterson and Jennifer Ruesink provided needed field and laboratory assistance. Dr. Robert T. Paine assisted with logistics and accommodations, and graciously provided data on Common Murre raft sizes and Bald Eagle visitation. Additional logistical support was provided by the Olympic Coast National Marine Sanctuary (OCNMS) research vessel TATOOSH and its captain, George Galasso. Fred Felleman provided prints of Common Murres nesting in crevices on Rainbow Rock (#035) in August. Tom Owens of WDFW provided data principally collected by Anita MacMillan on Bald Eagle nesting territories in the vicinity of Tatoosh Island. Roy Lowe and David Pitkin of the USF&WS kindly provided detailed comments on Common Murre-Bald Eagle interactions on Three Arch Rocks, Oregon. Ian Jones and Fred Cooke provided information and the opportunity to visit Triangle Island, British Columbia. Ed Bowlby of the OCNMS provided information on Common Murre-Bald Eagle interactions on Tatoosh in mid-July. Mary Mahaffy reported on Common Murre censuses conducted by USFWS personnel at the 13 December 1995 meeting of the *Tenyo Maru* Trustee's Council. Earlier drafts of this report were improved by Mary Mahaffy and Ken Warheit. Funding for this project was provided by the *Tenyo Maru* Trustee's Council to the University of Washington in conjunction with the Makah Tribal Nation.

Table of Contents

Cover Page	i
Acknowledgments	ii
Table of Contents	iii
List of Figures and Tables	iv
Introduction	1
Methods	2
Attendance	2
Phenology	5
Reproduction	6
Eagles	6
Results	6
Attendance	6
Phenology	13
Reproductive Success	16
Mitigating Factors - Eagles	22
Discussion	28
Conclusions	30
Citations	30

List of Figures and Tables

Figure 1. Diurnal pattern of attendance of Tatoosh Island Common Murres, 1995.

Figure 2. Annual attendance of Tatoosh Island Common Murres, 1995.

Figure 3. Distribution of attending Tatoosh Island Common Murres by subcolony size and habitat type, 1995.

Figure 4. Annual attendance of Tatoosh Island Common Murres on nine multiply-censused crevice subcolonies, 1991-1995.

Figure 5. Approximate phenology of Tatoosh Island Common Murres, 1995.

Figure 6. The relative presence of Tatoosh Island Common Murre crevice subcolonies as compared to cliff-top subcolonies, 1993-1995.

Figure 7. Active Bald Eagle territories within 25 km of Tatoosh Island, 1971-1994.

Figure 8. Average annual maximum Bald Eagle sightings on Tatoosh Island, 1981-1995.

Table 1. Average annual attendance of Tatoosh Island Common Murres, 1991-1995.

Table 2. Average annual attendance counts from BBPT of Tatoosh Island Common Murre crevice subcolonies, 1991-1995.

Table 3. Comparison of aerial versus land-based attendance estimates of Tatoosh Island Common Murres, 1995.

Table 4. Comparison of crevice and cliff-top subcolony Tatoosh Island Common Murre daily attendance patterns, 1993-1995.

Table 5. Reproductive output of Tatoosh Island Common Murres nesting in multiply-censused crevice subcolonies as a function of time of day, 1992-1995.

Table 6. Tatoosh Island Common Murre egg loss, 1994-1995.

Table 7. Disturbance factors causing Tatoosh Island Common Murre temporary abandonment of the MCT subcolony, 1992-1995.

Table 8. Amount of time Tatoosh Island Common Murre nesting on the MCT spent off the subcolony as a function of known disturbance source, 1995.

Table 9. Witnessed attack and kills by Bald Eagles of Tatoosh Island Common Murres, 1991-1995.

Table 10. Life table parameters used to model extinction time of Tatoosh Island Common Murre population as a function of Bald Eagle direct and indirect effects.

Table 11. Results of the life table model used to model extinction time of Tatoosh Island Common Murre population as a function of Bald Eagle direct and indirect effects.

Introduction

In July of 1991, the sinking of the *Tenyo Maru* released an estimated 100,000 gallons of oil into the waters immediately north of Tatoosh Island. At the time of the spill, over 4,000 Common Murres, *Uria aalge*, were nesting on the island, in addition to four other species of alcids, two species of cormorants, two species of storm-petrels, and one species of gull (Glaucous-winged Gulls, *Larus glaucescens*). Tatoosh Island (48° 24' N, 124° 44' W), is actually a collection of rocky islets connected by boulder and cobble beaches at low tide. There are five main islets, three of which - North Island (Rock #022), Pole Island (Rock #023), and Main Island (Rock #021) - have vertical cliff faces with ledge or crevice habitat suitable for murre nesting. Oil began to wash past Tatoosh Island on 26 July 1991, covering patches of intertidal on the western and northern parts of the island (Parrish pers. obs.). During the next three days (while researchers were present on the island), 70 severely oiled Common Murres were observed swimming to shore and beaching themselves around the island (R. Paine unpub. data). In total, 3,157 murres were recovered from a number of locations along the Washington coast during the spill, the majority of these were carcasses.

Attempts to determine whether the spill resulted in injury to the Tatoosh Island murre colony were hampered by a lack of specific data on reproductive success of the colony in years prior to the spill, as well as several confounding factors following the spill. Chief among these were a persistent El Niño-Southern Oscillation (ENSO) event in the years following the spill (1992-1993), and an escalating interaction between murres and their chief predators: Bald Eagles, *Haliaeetus leucocephalus* (on adults), and Glaucous-winged Gulls (on eggs). Despite these problems, colony monitoring in the years following the spill revealed several patterns:

1. Island-wide attendance declined following the spill (1991 to 1993), but began to rise again in 1994.
2. The colony is divided into many subcolonies which can be loosely grouped by habitat type into: cliff-top (5-6 subcolonies) and crevice (>25 subcolonies). Cliff-top subcolonies are, on average, orders of magnitude larger than crevice subcolonies, and house a disproportionately large percentage of the Tatoosh Island population (75-80%).
3. Reproductive success of monitored subcolonies was lowest in 1993 and also rebounded in 1994.
4. Murres nesting in cliff-top subcolonies experienced lower reproductive success than conspecifics nesting in crevice subcolonies in all specifically monitored years. Some cliff-top subcolonies experienced total breeding failures.

5. Cliff-top subcolony failures are apparently the result of disturbance by eagles, causing adult murres to temporarily abandon their breeding areas. During evacuation periods, gulls are able to remove undefended murre eggs. In years of subcolony failure, no eggs last long enough to hatch into chicks. In cliff-top subcolonies which do produce chicks/fledglings, the timing of reproduction (phenology) is one-two weeks later than adjacent crevice subcolonies.

In 1995, Common Murre attendance, phenology, and reproductive success was monitored. In addition, interactions between murres, eagles, and gulls were examined in a continuing effort to predict the degree to which the murre population on Tatoosh Island may be negatively affected. This report documents the data collected during the 1995 field season and provides an analysis of the patterns of murre demography relative to previous years.

Methods

Data documenting murre attendance, phenology, and breeding success by subcolony, were collected on Tatoosh Island during the April-September period. Research trips spanned 3-5 days. All data were collected from remote observation sites with the aid of binoculars, a spotting scope, and a remote 35 mm camera. The majority of the behavioral data were collected from a single location which afforded a simultaneous view of eleven separate subcolonies, operationally defined as a group of nesting murres, spatially separate from any other group (Burning Barrel Point, BBPT). From this location, observations were made in 1/2 hr. blocks, evenly spaced over each trip, starting at 0500H and ending at 2200H (approximately 55 hrs in total). Additional attendance data were collected from several locations around the island which afforded unimpeded views of various subcolonies. Early in the season, before the murres had colonized the Island (April), estimates were made of the cumulative number of murres attending three rafts traditionally located just offshore of the three largest cliff-top subcolonies (MCT, Pole Island, Petrified). These data were collected by Dr. Robert T. Paine. Annual raft counts were used as an additional index of population size.

Attendance

Subcolony attendance was assessed at least once during every trip, and several times for those subcolonies visually accessible by land. Attendance was defined as the number of murres on the subcolony (direct count), after eggs had been laid but before chicks had started to fledge. Attendance counts were limited to after 1200H and before dusk (approximately 2000H), when accurate counting became more difficult. Earlier counts

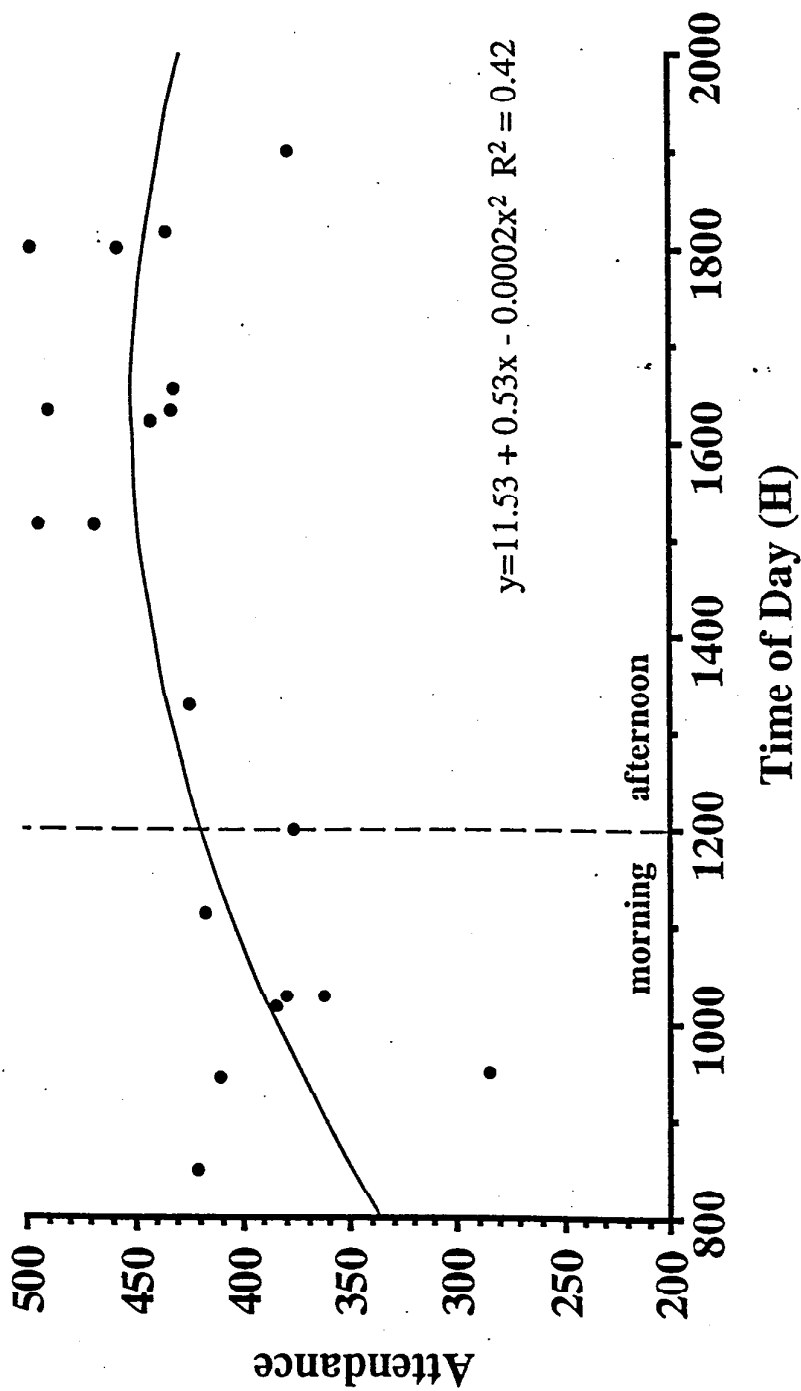


Figure 1. The pattern of diurnal variation in attendance in Common Murre crevice subcolonies in 1995. Data are from the egg and chick period and are cumulative over CCI-5 and TCI-4, as counted from the BBPT location. The dashed line indicates the split between morning and afternoon classification in this report.

were smaller (Figure 1), probably due to a larger percentage of foraging birds earlier in the morning. Because several subcolonies could only be counted in the morning due to tidal constraints, a morning to afternoon correction factor has been calculated for each monitored year (see Table 1) and applied to the morning-only subcolonies such that a total afternoon attendance figure could be reported. Therefore, unless otherwise stated, attendance is reported as afternoon figures.

For small subcolonies (e.g. <200 birds attending) direct counts were always made. Occasionally, a subcolony could not be counted from a single location (e.g. Crisscross 4 and 5, CC4-5). In these cases, repeated counts were made from all possible venues in order to estimate a correction factor for out-of-sight birds when counting from the BBPT location. This difference is reflected in direct count totals from the BBPT location (i.e. Table 2) and the overall island attendance estimates (i.e. Table 1). For larger subcolonies attendance was estimated by counting a subplot, usually not less than 20% of the total, and extrapolating total attendance by estimating the area of the subplot relative to the area of the entire subcolony (e.g. Pole Island). On occasion, a direct count of large subcolony attendance was made when the murres resettled after rafting on the water (e.g. MCT). Because this method may underestimate attendance, annual maximum values are reported rather than seasonal averages. Several subcolonies were not visually accessible, or only partially so. In these cases, attendance was estimated by measuring the areal extent of the subcolony and extrapolating attendance using density figures obtained from subcolonies with similar topography (e.g. Petrified). In two cliff-top subcolonies (Toad Point Cliff-top 1 and 2, TPCT1-2), only visible birds lining the cliff's edge were counted directly from a location beneath the cliff, even though more murres, at least 100 on TPCT1 were definitely nesting there.

Island-wide attendance is presented as an amalgam of these methods; thus this figure does not have confidence intervals and is meant as a gross indicator of population size, comparable with Tatoosh attendance estimates collected in previous years. More statistically valid attendance counts were made of 9 crevice subcolonies (CC1-5; TC1-4) by repeatedly counting murres throughout the nesting season. For these subcolonies, data are constrained by time of day (morning versus afternoon) and phenology (during egg and chick period only), and presented in both graphic and tabular form as mean and standard deviation.

Phenology

The timing of murre reproduction on Tatoosh Island was divided into several periods: Egg - when eggs only are present; Chick - when eggs begin to hatch but no fledging has occurred; and Fledging - when chicks begin to fledge. Because subcolonies did not always begin periods synchronously, but did tend to synchronize within habitat type (i.e. cliff-top versus crevice), phenology is reported by habitat type. During each visit to the island, the presence of eggs and chicks were noted daily for all visible colonies. Later in the season, nightly checks were made for the presence of fledglings, which are difficult to see but can easily be heard calling. Phenology is presented as a combination of these observations plus inference about likely onset times of each period based on an average egg residence time of 30 days and a minimum chick residence time of 15 days.

To determine daily attendance patterns as a function of subcolony habitat type (crevice versus cliff-top), a remote time-lapse 35 mm Nikon F3 camera with a 28mm lens, a 250 frame back, and a motor drive was installed on Strawberry Island (Rock #035). The camera faced east, photographing the crevice subcolonies from Lighthouse 4 (LH4) to TC4 and included the cliff-top subcolony MCT. Pictures were taken every hour from 0600H to 2000H, until all frames had been used. An intervalometer was used to set the frame rate (one frame per hour) and a modified garden hose timer was used to turn the intervalometer on and off so that no pictures were taken at night. Film used was Fuji Professional 100 ASA bulk film. All equipment was housed in a water tight Pelican box with a clear Plexiglas window through which the camera was focused. The Plexiglas was protected by a metal shade to minimize rain streaking, bird guano, and glare. The camera was reset with new film and batteries four times throughout the season.

Usable frames provided general information about when subcolonies were occupied. For each day, the total number of visible hours (defined as slides in which murre presence can be detected on the subcolonies), the number of hours murres are present on the crevices, and the number of hours murres are present on the clifftop are summed. Only days in which the total number of visible hours equaled or exceeded 7 were used. From these data, the percent of total time each habitat was occupied (per day) was calculated. The difference between these two values is relative presence, in percent. For example, if there were 9 visible hours, the crevices were occupied 5 hours and the clifftop 3 hours, percent time occupied would be crevice = 55% and clifftop = 33%. Relative presence would be 22% towards the crevice subcolonies. Relative presence is graphed by day, where the x-axis is positive from 0 to 100% in both directions. Thus, this index indicates whether there was a

discrepancy in attendance as a function of habitat type. A separate table presents data on the amount of time per day subcolonies were occupied.

Reproduction

Reproductive success was estimated as the number of fledglings per pair for four crevice subcolonies (CC1-4) where pairs could be mapped and the fate of eggs/chicks could be followed. Chicks were defined as fledglings and likely fledgers (i.e. healthy chicks greater than 15 days of age). The fate of mapped chicks was followed through fledging when possible. The number of pairs is reported as a minimum because staggered visits compromised an accurate assessment of egg loss, number of pairs re-laying, and/or number of pairs abandoning for the season. For other subcolonies, reproductive success was noted (e.g. produced eggs, chicks, or fledglings) if possible.

Eagles

Data on eagles comes from a variety of sources in addition to that collected by the principal investigator. Data on the number of active eagle territories (defined as those territories with nests that produce at least eggs) within 25 km of Tatoosh is collected by the Washington Department of Fisheries and Wildlife (WDFW) and provided by the WDFW non-game data base manager, Tom Owens. The maximum number of eagles seen simultaneously on Tatoosh per research trip during the murre breeding season is collected and provided by Dr. Robert T. Paine. In addition, data are collected on the number of attacks and kills made by eagles on murres, as well as the number of murre carcasses thought to have been the victim of eagles. Finally, the number of witnessed temporary evacuations by murres nesting in the MCT subcolony are counted and ascribed to a specific disturbance, when possible.

Results

Attendance

In 1995, the number of murres attending Tatoosh Island dropped below 1994 levels by almost 12% (Figure 2; Table 1). This drop appears to have been driven by significant declines in cliff-top subcolony attendance. Cliff-top attendance dropped 30% from 2757 in 1994 to a 5-year record low of 1915 in 1995 (Table 1). On the MCT, attendance was cut in half from 1200 in 1994 to 600 in 1995. There were also declines in the Pole Island subplot (down 12%) and the Petrified subcolony (down 33%; Table 1). The drop in cliff-top attendance was offset, to some degree, by an inverse trend in the crevice subcolonies. Fifteen of the 25 crevice subcolonies in existence in 1994 increased in size and 6 new crevice subcolonies were born (Table 1). This brought crevice subcolony attendance to a

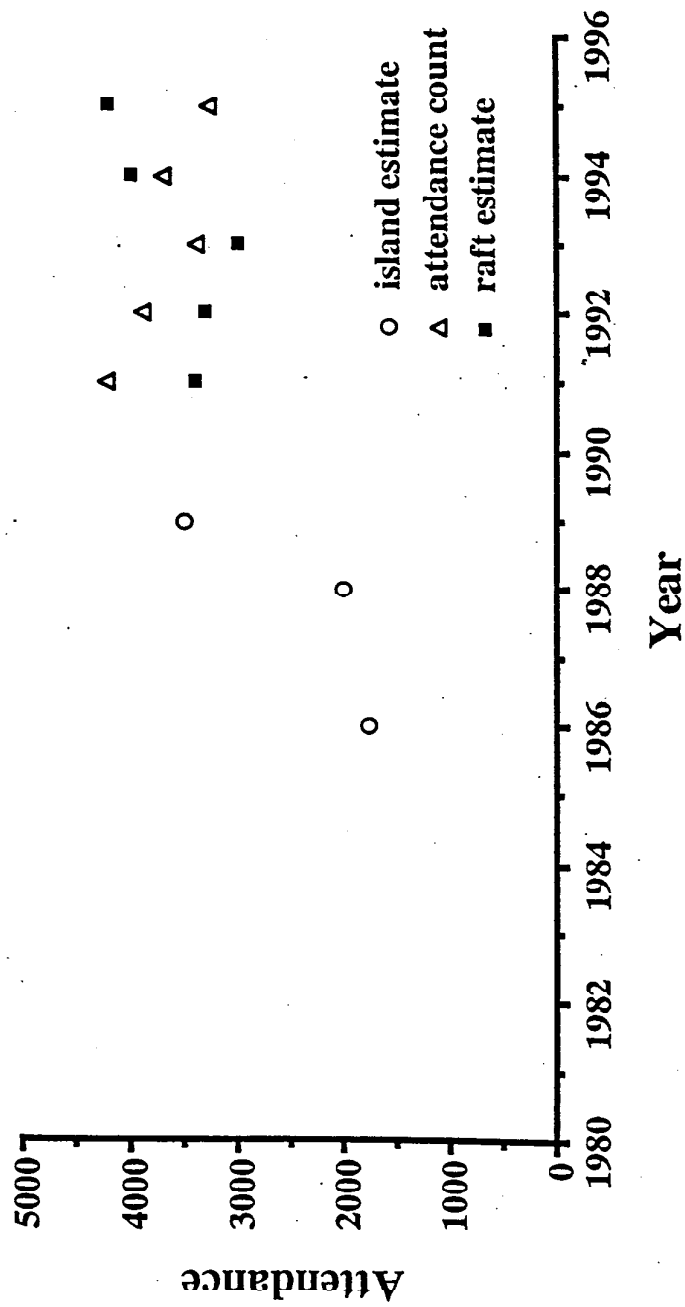


Figure 2. Annual attendance estimate of Common murres of Tatoosh Island. Circles are island estimates made by Robert T. Paine, triangles are estimates derived from averaged annual attendance counts after eggs were laid and before chicks began fledging made by Julia K. Parrish, and filled squares are raft estimates made by Robert T. Paine. Estimates and counts within a single year were made independently. See Table 1 for detailed attendance data.

Table 1 Average estimated annual attendance (afternoon counts during the egg/chick period) - Tatoosh Island Common Murres.

	Subcolony	Rock #	Habitat	1991	1992	1993	1994	1995	Comments
a	rainbow rock - u	035	crevice					212	born in 1995
a	rainbow rock - l	035	crevice	50	63	24	35	38	
a	boom	021	cliff-top	50	0	0	0	0	died in 1991
m	north island	022	crevice	99	134	100	150	136	
m	north island ridge	022	cliff-top				22	0	born in 1993
m	north island 2	022	crevice					27	born in 1995
m	finger	022	crevice				31	16	born in 1994
m	pole island	023	cliff-top	1300	1532	1176	1264	1108	plot est. @ 25%
m	lighthouse 1	021	crevice	89	75	27	101	110	
m	lighthouse 2	021	crevice	3	0	1	8	6	
m	lighthouse 3	021	crevice	23	15	0	25	19	
m	lighthouse 4	021	crevice	11	25	8	6	28	
m	lighthouse 5	021	crevice					17	born in 1995
m	submarine	021	crevice	50	30	42	43	44	
m	burning barrel	021	crevice	6	9	0	6	2	
m	burning barrel 2	021	crevice					32	born in 1995
m	burning barrel 3	021	crevice					2	born in 1995
m	above crisscross	021	crevice				3	6	born in 1994
a	crisscross 1	021	crevice	39	32	28	29	38	
a	crisscross 2	021	crevice	45	37	30	36	54	
a	crisscross 3	021	crevice	27	31	17	27	57	
a/m	crisscross 4	021	crevice	60	35	34	52	50	
a/m	crisscross 5	021	crevice	173	94	85	104	141	
m	r-crisscross	021	crevice	15	21	10	26	36	
m	fr-crisscross	021	crevice	20	19	12	22	12	
a	tennis court 1	021	crevice	79	36	30	29	40	
a	tennis court 2	021	crevice	50	29	23	20	26	
a	tennis court 3	021	crevice	82	91	71	64	77	
a	tennis court 4	021	crevice	25	23	21	21	19	
m	moustache	021	crevice					3	born in 1995
a	toadpoint 1	021	crevice	50	27	25	43	60	
a	toadpoint 2	021	crevice	50	22	35	24	24	
a	toadpoint 3	021	crevice	50	15	15	19	23	
a	tpcliff-top 1	021	cliff-top	48	30	26	7	15	partial count
a	tpcliff-top 2	021	cliff-top	24	46	30	4	17	partial count
a	main cliff-top	021	cliff-top	1500	1200	1300	1200	600	max count
a	below mct	021	crevice				10	0	born in 1994
a	petrified	021	cliff-top	200	200	200	260	175	visit est.
total				4214	3871	3370	3691	3270	
morn-aft multiplier				1.6	1.5	1.2	1.3	1.13	
crev total				1092	863	638	934	1355	
ct total				3122	3008	2732	2757	1915	
crevice %				26	22	19	25	41	

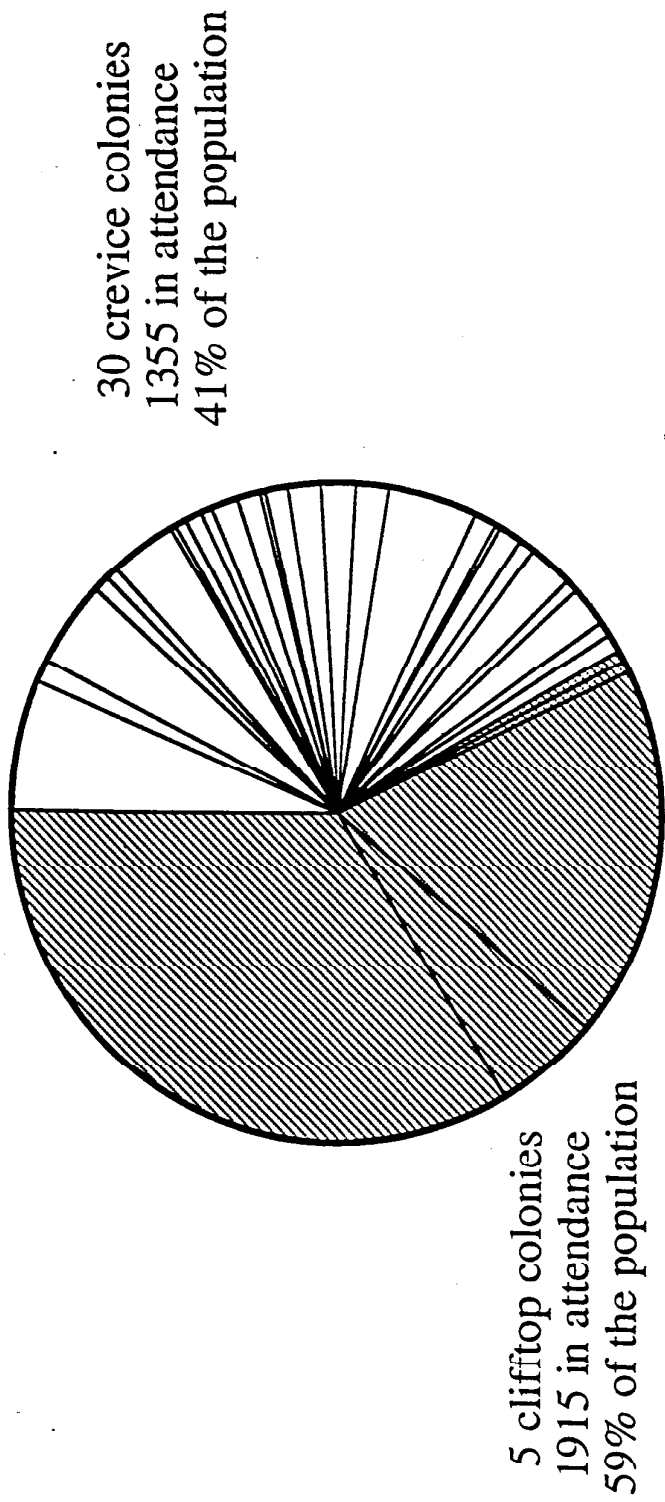


Figure 3. Distribution of Tatoosh Island Common Murre subcolonies in 1995 as a function of habitat type: crevice (open) versus cliff-top (filled).

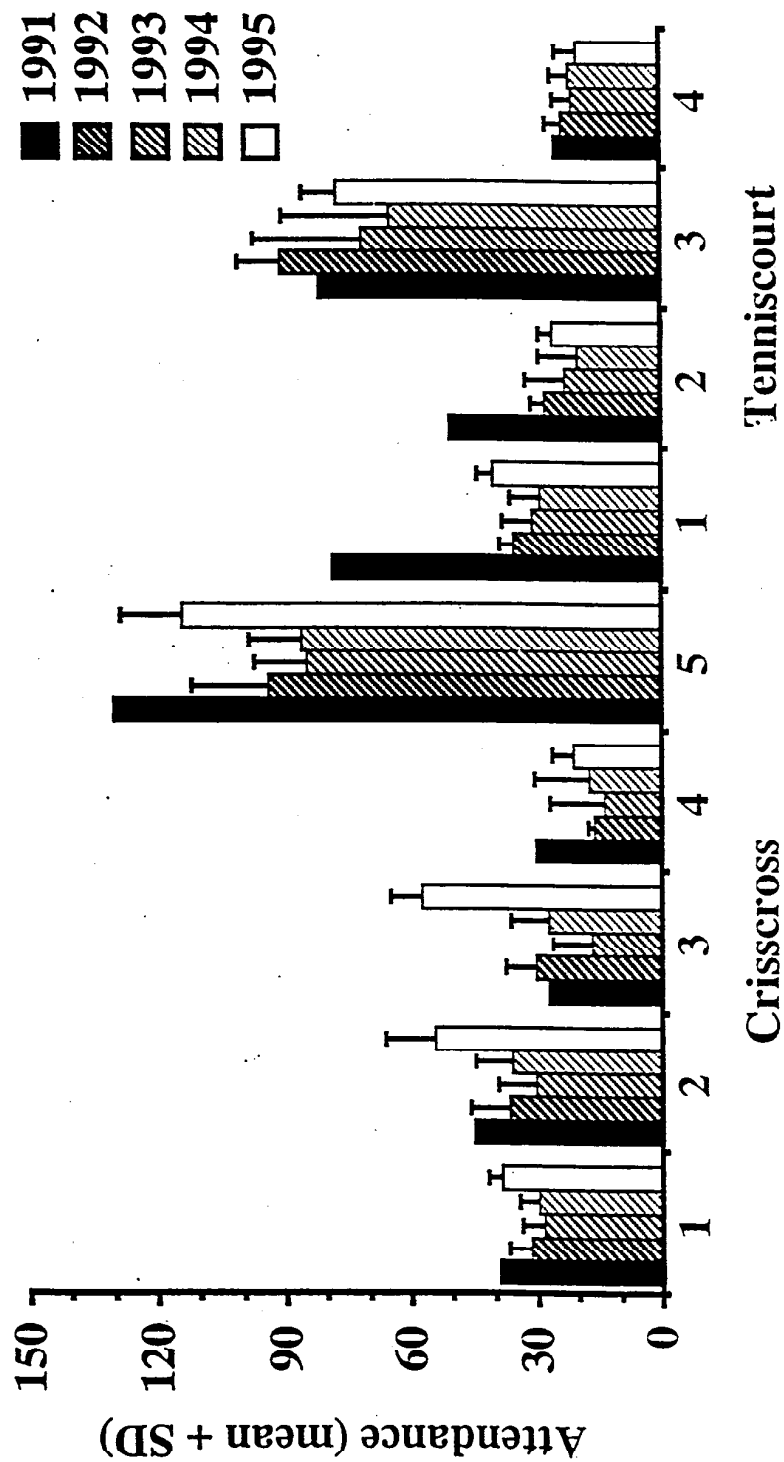


Figure 4. Annual attendance (mean + standard deviation) of Common Murres on Tatoosh Island in nine crevice subcolonies as counted directly from the BBPT location, after eggs were laid and before chicks began fledging, and between the hours of 1200 and 2000 (i.e. afternoon; see Figure 1). Refer to Table 2 for sample sizes.

Table 2 - Average attendance counts from BBPT (1991-1995) during egg/chick period for monitored crevice subcolonies.

Note that counts for CC4 and CC5 are lower than in Table 1 because neither crevice was entirely visible from BBPT.

		Morn av	Morn SD	Morn N	Aft av	Aft SD	Aft N
1991	crisscross 1	24.50	8.67	3	38.50	16.26	2
	crisscross 2	16.83	4.54	3	44.83	28.06	3
	crisscross 3				27.00		1
	crisscross 4	42.00	19.67	3	59.75	14.50	2
	crisscross 5	110.00	8.66	3	173.33	66.82	3
	tenniscourt 1	30.00		1	78.50	30.41	2
	tenniscourt 2	30.00		1	50.00		1
	tenniscourt 3	60.00		1	81.50	26.16	2
	tenniscourt 4	10.00		1	25.00	7.07	2
	TOTAL	323.33			578.42		
	ADJUSTED	291.73			505.21		
<i>Note: The 1991 counts were made from SB and TP NOT BBPT; pre-spll only</i>							
<i>Adjusted totals: BBPTCC4=CC4*.5; BBPTCC5=CC5*.75; AFT=MORN*1.6</i>							
1992	crisscross 1	21.20	9.36	5	31.25	5.73	8
	crisscross 2	25.20	7.46	5	36.00	9.74	8
	crisscross 3	15.80	9.36	5	30.25	6.86	8
	crisscross 4	10.60	3.13	5	15.88	1.81	8
	crisscross 5	76.40	22.81	5	93.88	18.14	8
	tenniscourt 1	26.40	12.10	5	34.88	3.40	8
	tenniscourt 2	19.60	10.24	5	27.50	3.42	8
	tenniscourt 3	66.40	34.26	5	90.88	10.26	8
	tenniscourt 4	17.00	7.07	5	23.38	4.00	8
	TOTAL	278.60			383.88		
1993	crisscross 1	19.00		1	28.43	5.13	7
	crisscross 2	5.00		1	30.29	11.76	7
	crisscross 3	0.00		1	16.71	11.00	7
	crisscross 4	8.00		1	13.43	2.99	7
	crisscross 5	56.00		1	84.71	16.85	7
	tenniscourt 1	28.00		1	30.33	5.28	6
	tenniscourt 2	14.00		1	22.50	5.17	6
	tenniscourt 3	49.00		1	70.83	9.41	6
	tenniscourt 4	19.00		1	21.00	2.76	6

Table 2 - Average attendance counts from BBPT (1991-1995) during egg/chick period for monitored crevice subcolonies.

TOTAL		198.00			318.24	
1994	crisscross 1	27.13	4.64	15	29.31	5.25 16
	crisscross 2	31.50	13.75	14	35.50	9.17 16
	crisscross 3	21.07	8.18	15	26.69	9.67 16
	crisscross 4	11.33	5.42	15	17.35	13.53 17
	crisscross 5	76.47	16.17	15	85.53	12.80 15
	tenniscourt 1	20.43	8.71	14	28.53	7.76 17
	tenniscourt 2	12.71	8.43	14	19.53	9.68 17
	tenniscourt 3	35.29	23.45	14	64.35	26.34 17
	tenniscourt 4	18.77	4.51	13	21.25	4.80 16
TOTAL		254.70			328.05	
1995	crisscross 1	36.57	4.72	7	37.82	3.84 11
	crisscross 2	41.43	8.62	7	53.82	12.29 11
	crisscross 3	49.71	11.79	7	57.09	8.07 11
	crisscross 4	19.57	5.09	7	21.00	5.51 11
	crisscross 5	100.52	13.61	7	114.00	14.81 11
	tenniscourt 1	35.57	6.21	7	40.09	3.94 11
	tenniscourt 2	20.86	3.98	7	25.73	3.44 11
	tenniscourt 3	72.00	12.68	7	77.00	8.45 11
	tenniscourt 4	15.86	2.97	7	19.45	5.57 11
TOTAL		392.10			446.00	

5-year high of 1355 and significantly altered the dynamic between crevice and cliff-top habitat. Prior to 1995, cliff-top nesters had comprised 75-80% of the attending population; however in 1995 cliff-top attendance dropped to 59% (Table 1; Figure 3).

Eight of the nine multiple-count crevice subcolonies experienced an increase in attendance (Figure 4; Table 2). Two of subcolonies (CC2,3) had attendance counts higher than the 1991 pre-spill counts. The only subcolony which declined (TC4) was taken over by Pelagic Cormorants (Parrish, pers. obs.). Despite this interspecific nesting habitat competition, murres managed to attend, if not nest, in nearly equal numbers as in previous years (Figure 4, Table 2).

During the 1995 nesting season, four aerial surveys were conducted by Ulrich Wilson of the U. S. Fish and Wildlife Service Coastal Refuge Office. University of Washington personnel were present for three of the four overflights such that groundtruths could be made (Table 3). In all cases, land-based counts were higher than aerial counts. Excluding zeros, aerial counts ranged from 14 to 89% of land-based counts. In general, differences were smaller as a function of total subcolony size (compare Pole Island #023 to North Island #022; Table 3) and time of season (e.g. late July counts were closer together than June counts). The Main Island (#021) counts had the lowest correspondence; aerial counts were 14-43% of land-based counts; however, this is understandable as there were 5 cliff-top subcolonies and 25 crevice subcolonies on this part of Tatoosh spread over the southwest to southeast facing cliffs. Furthermore, land-based counts were integrated over several days, minimizing the chance of incorporating anomalies (e.g. temporary subcolony abandonment).

Phenology

In 1995, eggs appeared on both the crevice and cliff-top subcolonies by mid-June (Figure 5). This is at least 7-10 days later than 1992 and 1993, when eggs were present in early June. However, the onset of egg production does not seem to determine in large part the onset of hatching, probably because early eggs are victims of egg predation (Parrish pers. obs.). Although the timing of egg laying did not appear to be habitat specific in 1995 (compare with 1993; Figure 5), chick hatching was. This pattern is also typical of previous years (Figure 5); crevice eggs hatch before cliff-top eggs. Although this could be because cliff-top nesters brood longer, it is more probably due to a more intensive cycle of laying and loosing eggs early in the season in the cliff-top subcolonies (see below), such that chicks are hatching from relays and/or first eggs laid relatively late. The discrepancy in

Table 3 - Comparison of USFS aerial censuses with land-based Tatoosh Island Common Murre attendance counts -(afternoon only); 1995.
USFS data are from Wilson 1995.

Island Name (USF&WS#)	6/17-6/19 AFTERNOON	6/19/95 USF&WS	6/25-6/27 AFTERNOON	6/25/95 USF&WS	7/27-7/29 AFTERNOON	7/27/95 USF&WS
Pole Island (023)	1520	660	1238	0	1042	925
North Island (022)	137	110	160	70	165	60
Rainbow Rock (035)	ND	165	ND	190	240	200
Main Island (021)	1272		1213		1097	
<i>italics indicate partial count</i>						
ND = no data						
Missing from Main Island:						
	LH1-U		LH1-U		ACC	
	BSUB		BB3		TP1-3	
	BB2		ACC		TPCT1	
	BB3		TP1-3		PETCOL	
	ACC		TPCT1-2		(MCT IS MT)	
	CC5-RT BIT		PETCOL			
	TP1-3					
	TPCT1-2					
	PETCOL					
Estimate of missing subcolonies:	354		321		120	
Estimated Main Island total	1626	550	1534	220	1217	520

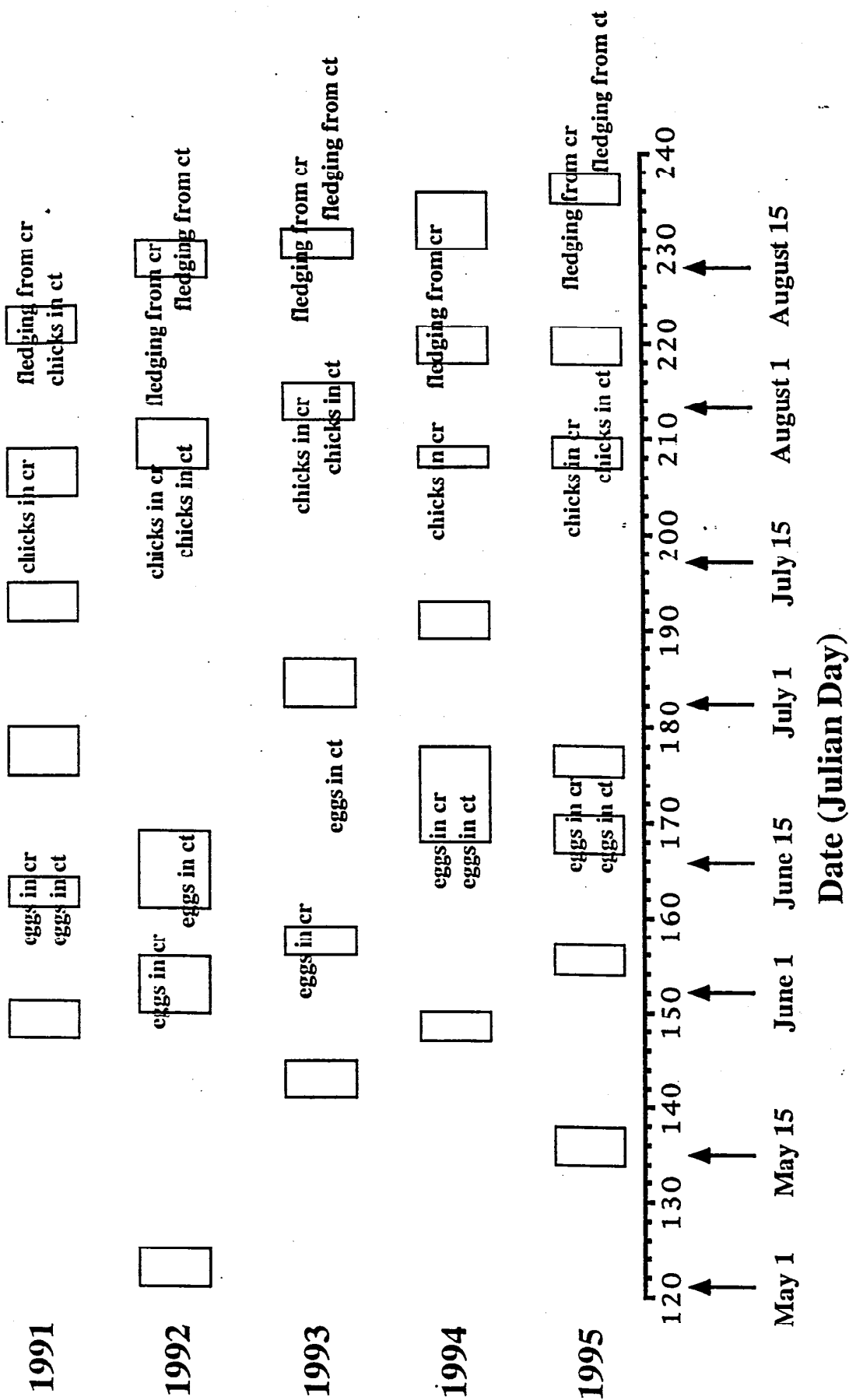


Figure 5. Approximate phenology as assessed by the appearance of eggs, chicks, and the departure of fledglings, respectively. Open bars indicate research trips to Tatoosh Island. Placement of egg, chick, and fledgling period initiation is based on actual sightings (eggs), or sightings plus size at age estimates (chicks, fledglings). For the chick period, the assumption has been made that chicks will remain on the subcolony at least 15 days. ct=crevice; ct=cliff-top.

chick hatching is accentuated at fledging. In 1995, cliff-top fledging did not begin until after the final research trip of the season, while crevice fledging was nearly complete (Figure 5).

Delays in phenology may also be the result of laying opportunities. Data from the time-lapse camera indicate that while cliff-top nesters (as exemplified by the MCT) and crevice nesters (as exemplified by CC1-5, TC1-4) are present on their respective breeding areas an equal portion of the day early in the season, crevice nesters begin to occupy the nesting area full time by mid-June while cliff-top nesters do not (Table 4). In 1995, murres on the MCT were visible on the cliff 100% of the visible hours on only 2 out of 31 monitored days after mid-June. On 13 of those days, murres were completely absent from the subcolony. Annual comparisons indicate that later in the season when murres should be attending full-time (that is, assuming they have chicks), crevice-nesting murres always spend more time on their breeding areas than cliff-top nesters (Figure 6). In 1994, attendance patterns appeared more similar between habitat types (that is, cliff-top nesters were present more often); however, this appears to be the exception rather than the rule.

Reproductive Success

In 1995 monitored crevice subcolonies (CC1-4) had the highest reproductive success recorded during the 1992-1995 interval (Table 5). With the exception of CC2, reproductive success was equal to or greater than 0.85 chicks per pair. CC2 would probably have experienced higher reproductive success as well; however, early in the season, (18 June 1995) a juvenile Bald Eagle landed on CC2, causing the destruction of 12 eggs (as a result of breakage as well as predation by gulls once the eagle had left). It is not known whether this incident was repeated but Olympic Coast National Marine Sanctuary personnel reported sighting an eagle remove a murre from the CC subcolonies during mid-July (E. Bowlby, pers. comm.).

Reproduction on the cliff-top subcolonies was lower than in the crevices. The MCT failed to hatch any eggs. This subcolony has now failed 4 out of the last 6 years. TPCT1 failed to hatch any eggs. Pole Island probably fledged chicks, although no visits were made to this subcolony in 1995. However, a small number of chicks (10-12) were seen on the Pole Island subplot counting area during mid-late August. Petrified and TPCT2 had 1-2 week-old chicks during the last research trip of the season (22-24 August 1995); barring an unknown disaster, these chicks probably fledged. Adults were seen bringing fish back to Pole Island and Petrified.

Table 4 -Percent of visible hours attended by Common Murres on the Crisscross subcolonies (CC1-5; RCC, FRCC) and the MCT as assessed by the timelapse camera, Tatoosh Island, 1993-1995. Blanks are no pictures taken.

	1993			1994			1995		
	Vis. Hrs	CREV %	MCT %	Vis. Hrs	CREV %	MCT %	Vis. Hrs	CREV %	MCT %
16-May							9	22	0
17-May							13	23	23
18-May							14	0	0
19-May							14	14	14
20-May							14	21	21
21-May							13	0	0
22-May							13	0	0
23-May							14	0	0
24-May							14	7	0
25-May							6		
26-May							15	40	33
27-May							14	71	43
28-May							8	63	63
29-May							13	100	31
30-May							14	36	14
31-May				9	55	33			
1-Jun				11	36	27			
2-Jun				15	80	53			
3-Jun				12	50	17			
4-Jun				12	17	33			
5-Jun				13	30	8			
6-Jun				12	25	25			
7-Jun				11	63	27			
8-Jun				13	76	62			
9-Jun				14	86	50			
10-Jun				14	86	43			
11-Jun				8	100	25			
12-Jun				11	100	36			
13-Jun				10	90	40			
14-Jun				11	100	55			
15-Jun									
16-Jun									
17-Jun							8	100	100
18-Jun							13	100	77
19-Jun							14	93	64
20-Jun							9	100	100
21-Jun							10	100	70
22-Jun							10	100	80
23-Jun							14	100	43
24-Jun							14	100	21
25-Jun							12	100	42

Table 4 -Percent of visible hours attended by Common Murres on the Crisscross subcolonies (CC1-5; RCC, FRCC) and the MCT as assessed by the timelapse camera, Tatoosh Island, 1993-1995. Blanks are no pictures taken.

26-Jun						
27-Jun						
28-Jun				8	100	63
29-Jun				13	100	38
30-Jun				13	85	69
1-Jul				10	100	40
2-Jul				15	100	27
3-Jul				13	100	31
4-Jul				10	100	0
5-Jul				10	100	10
6-Jul				14	100	0
7-Jul				14	100	0
8-Jul				12	100	8
9-Jul				12	100	8
10-Jul				12	100	0
11-Jul				6		
12-Jul			8	100	88	
13-Jul			11	100	72	
14-Jul			11	100	82	
15-Jul			6			
16-Jul			9	100	22	
17-Jul			11	91	55	
18-Jul			1			
19-Jul			4			
20-Jul			13	100	46	
21-Jul			11	100	36	
22-Jul			2			
23-Jul			11	100	55	
24-Jul			5			
25-Jul			7	100	86	
26-Jul			11	100	82	
27-Jul						
28-Jul			7	100	71	
29-Jul			13	85	85	
30-Jul			9	100	89	
31-Jul			13	92	46	
1-Aug			13	100	33	
2-Aug	7	100	29	2		
3-Aug	13	100	38	11	100	91
4-Aug	14	100	79	10	100	100
5-Aug	12	100	42	13	100	100
6-Aug	9	100	44	12	100	92
7-Aug	14	100	14	10	100	100

Table 4 -Percent of visible hours attended by Common Murres on the Crisscross subcolonies (CC1-5; RCC, FRCC) and the MCT as assessed by the timelapse camera, Tatoosh Island, 1993-1995. Blanks are no pictures taken.

8-Aug	13	100	23			
9-Aug	12	100	0		11	100
10-Aug	13	100	0		0	0
11-Aug	12	100	0		11	100
12-Aug	12	100	8		12	100
13-Aug	13	100	0		12	92
14-Aug	8	100	0		10	50
15-Aug					11	100
16-Aug					11	100
17-Aug					12	67
18-Aug					0	0
19-Aug					13	92

Relative Presence (%)

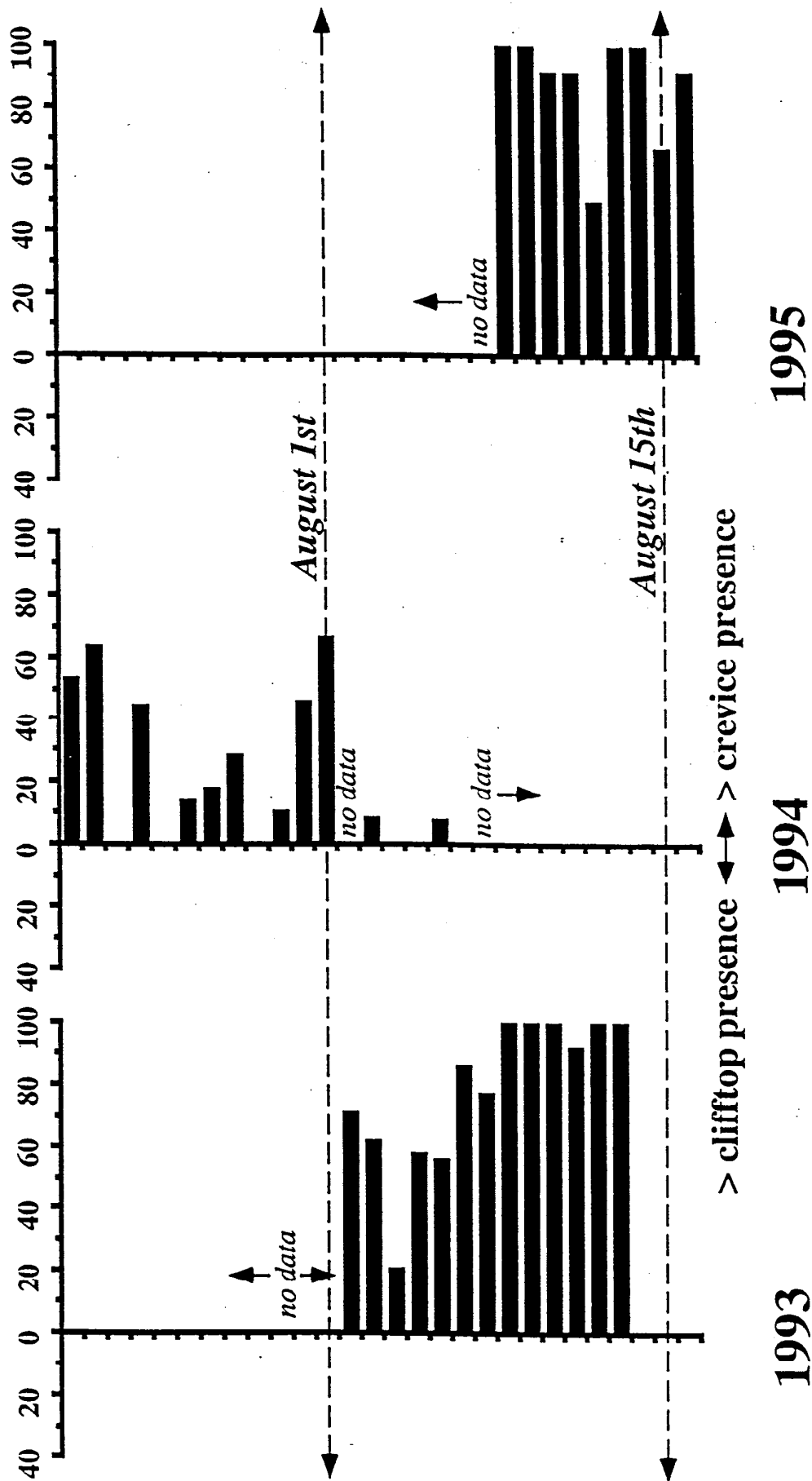


Figure 6. The discrepancy in percent of visible hours Tatoosh Island Common Murres nesting in crevice subcolonies (crev) versus a cliff-top subcolony (ct; MCT) were observed. See Table 4 for more detail. In general, shorter bars indicate more equal presence between habitat types, where 0 (that is, no bar) would indicate equal presence (e.g. 4 and 5 August 1994).

Table 5 - Tatoosh Island Common Murre reproductive output in monitored crevice subcolonies (1992-1995). Known pairs are defined as all pairs (assessed by location) which did or were suspected to have eggs. Known lost eggs were either observed abandoned, stolen, smashed, or failing to hatch. Because researchers were not continuously present on the Island, known pairs and known lost eggs are minimum estimates of pairs and lost eggs, respectively.

	1992	1993	1994	1995
CC1				
Attendance (aft)	31	28	29	38
Known Pairs	15	11	22	18
Known Lost Eggs	2	1	1	1
Chicks > 15D	11	7	20	17
Chicks/Pair	0.73	0.64	0.91	0.94
Chicks/Attendance	0.35	0.25	0.69	0.45
CC2				
Attendance (aft)	36	30	35	54
Known Pairs	17	9	21	15
Known Lost Eggs	2	4	2	12
Chicks > 15D	16	2	18	11
Chicks/Pair	0.94	0.22	0.86	0.73
Chicks/Attendance	0.44	0.07	0.51	0.20
CC3				
Attendance (aft)	30	17	27	57
Known Pairs	11	2	7	20
Known Lost Eggs	0	2	6	3
Chicks > 15D	7	0	1	17
Chicks/Pair	0.64	0.0	0.14	0.85
Chicks/Attendance	0.23	0.0	0.04	0.30
CC4				
Attendance (aft)		13	17	21
Known Pairs		6	7	7
Known Lost Eggs		1	0	0
Chicks > 15D		3	6	7
Chicks/Pair		0.50	0.86	1.00
Chicks/Attendance		0.23	0.35	0.33

Mitigating Factors - Eagles

Common Murre reproductive success on Tatoosh Island is influenced by two major forces: food availability and predators. In 1995, food appeared to be sufficient; however, reproductive success was still low on the cliff-top subcolonies, primarily due to Bald Eagle facilitated egg predation by gulls and crows. In 1995, 174 murre eggs were either observed being removed by gulls and crows, or found broken in traditional gull/crow areas (Parrish pers. obs.; Table 6). In both 1994 and 1995, the majority of lost eggs were from the MCT: counting eggs on and under this subcolony, 68% (1994) and 55% (1995) of all observed eggs (Table 6). Although there may be significant egg loss from other cliff-top subcolonies, this is difficult to determine as eggs are not directly visible without visitation. It is not known to what degree these totals (particularly the "other" category which includes eggs lost from crevice subcolonies) reflect relaying.

Egg loss is correlated with daily attendance patterns (i.e. Table 4, Figure 6). Cliff-top nesters, exemplified by the MCT, rarely spent an entire day on the subcolony. Eggs which had been laid the previous evening/early morning, were lost when adults left the breeding area. Murres evacuated from the MCT primarily in response to overflights by Bald Eagles (Table 7). From 1992-1995, 71 partial and 34 total evacuations have been witnessed. Of these, the majority have been associated with the presence of eagles. Once murres left the subcolony, resettlement was gradual, occasionally lasting overnight if ensuing eagle overflights occurred (Parrish pers. obs.). For resettlements which were completed without interruption (defined as timed from the point of evacuation to the point at which murres began to enter the salmonberry cover - usually at 1/4 to 1/3 of total attendance) the average time to salmonberry entry was 44.8 ± 36.5 minutes ($X \pm SD$, $N=7$, range 16-120; data from 1991-1993). Thus, even in the best circumstances following a single eagle overflight, eggs were left undefended for almost 3/4 of an hour.

Murres temporarily evacuated the MCT in response to a variety of disturbance events including eagle overflights, researcher effects, and unknown events. In order to quantify these events and calculate the relative effects of researchers on murre behavior and reproductive success, the amount of time the subcolony was full, partially full, and empty was recorded and categorized by disturbance causing murres to leave, if known.

Comparisons were made during two trips in June when eggs were being laid. (Before these trips murres had not yet started to lay and afterwards murres on the MCT had given up laying for the season.) Out of a total 1115 minutes watched, the subcolony was full

Table 6 - Common Murre eggs lost from/ found on a variety of locations around Tatoosh Island, 1994-1995.

	on MCT	under MCT	under TP/TPC T	on Island top	Other	Total
1994 (#)	178	12	19	44	25	278
(%)	64	4	7	16	9	
1995 (#)	77	19	11	40	27	174
(%)	44	11	6	23	16	

Table 7 - Disturbance factors causing Common Murres nesting on the MCT subcolony on Tatoosh Island to partially or totally evacuate, 1992-1995. These totals exclude researcher disturbance (see Table 9). Unk=unknown.

	Unk	Partial Eagle	Not Eagle	Unk	Total Eagle	Not Eagle
1992	5	3	2	1	13	0
1993	0	5	4	0	1	0
1994	8	26	10	0	7	4
1995	2	1	5	0	8	0
Total	15	35	21	1	29	4
% excluding unknowns		62	38		88	12

Table 8 - Total amount of observed time (in minutes) MCT Common Murres spent on and off the subcolony as a function of known disturbance. Data are from 16-19 and 25-27 June 1995.

	Empty	Partial	Full	Total
Eagles	343	60	-	403
Sound Experiment	5	10	-	15
Aircraft	0	15	-	15
Unknown	140	460	-	600
	-	-	82	82
Total	488	545	82	1115

Table 9 - Witnessed attacks and kills by Bald Eagles on/of Common Murres on Tatoosh Island, 1991-1995.

	1991	1992	1993	1994	1995
Attacks	5	5	1	5	4
Kills	1	1	0	5	2
Bodies found*	12	12	4	20	19
Observation hrs	60	80	46	90	55

* includes witnessed kills

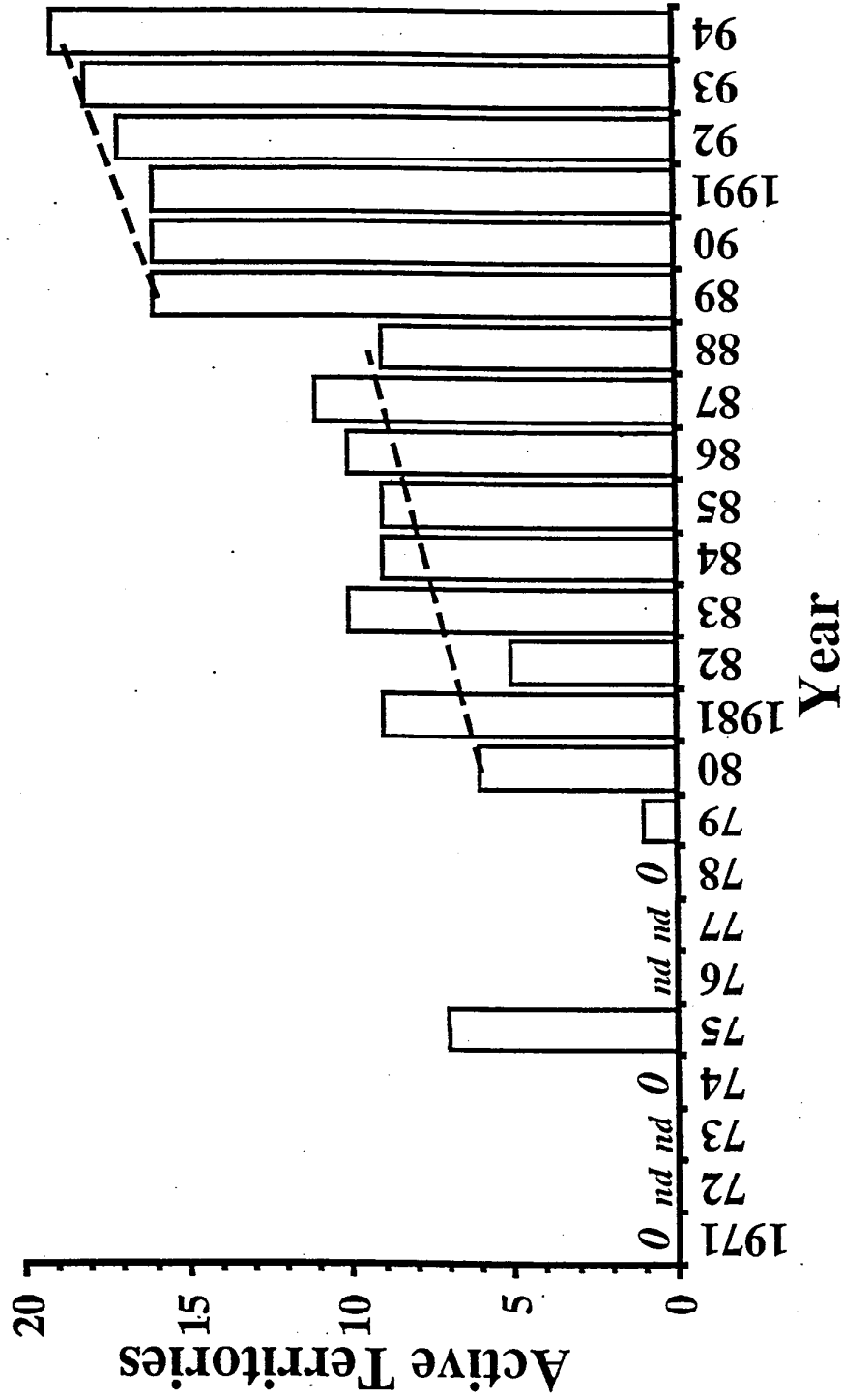


Figure 7. The number of Bald Eagle territories with offspring within a 25 km radius of Tatoosh Island (1971-1995). Data were provided by Anita MacMillan and Tom Owens, Wildlife Survey Management - WDFW. This figure is reproduced from Parrish and Paine (manuscript).

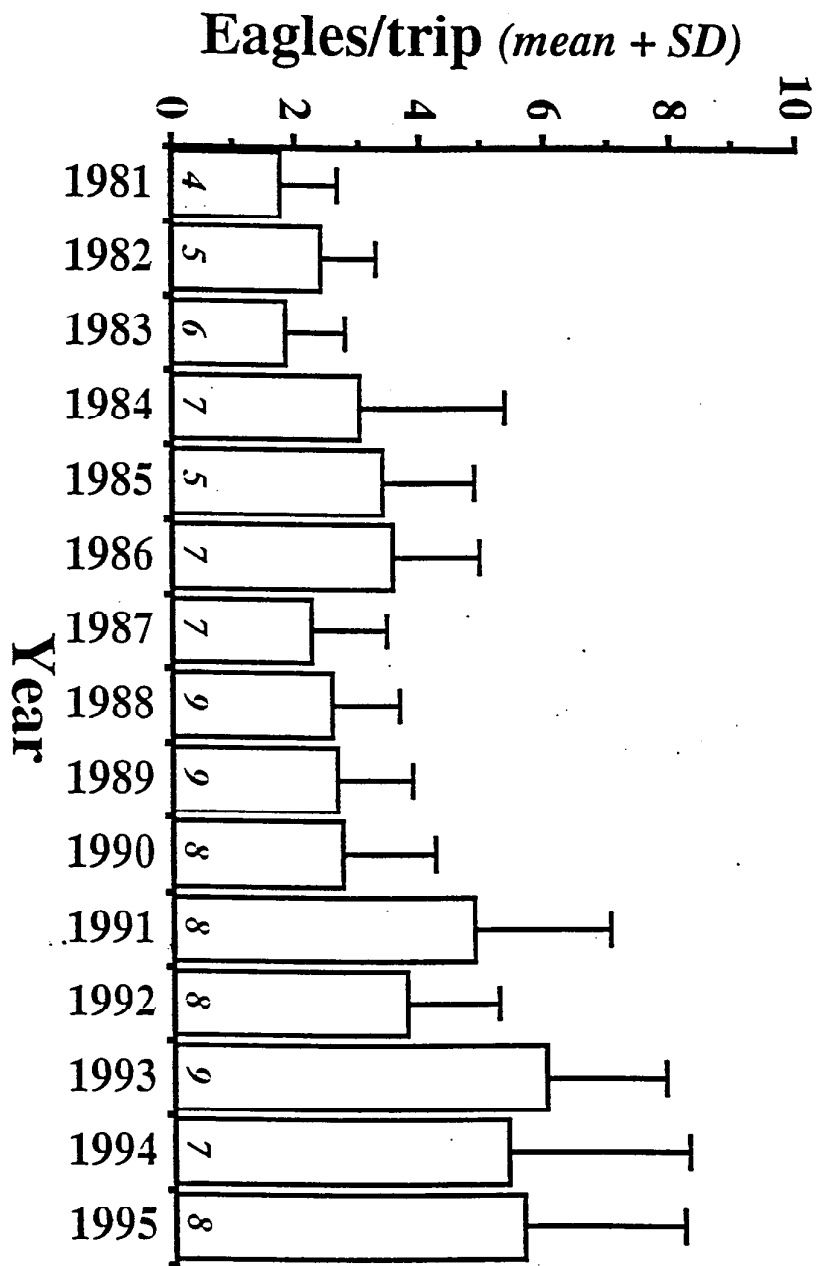


Figure 8. The maximum number of Bald Eagles sighted concurrently per research trip to Tatoosh, averaged over the periods of March-July, 1981-1995. Numbers inside each bar are research trips. Data provided by Dr. Robert T. Paine. This figure is reproduced from Parrish and Paine (manuscript).

only 7% of the time (Table 8). Almost 44% of the time, the subcolony was empty. During these visits a minimum of 37 temporarily abandoned eggs were stolen by gulls and crows. It is important to determine which disturbance factors are primarily responsible, especially as experiments were conducted during these visits which resulted in temporary abandonment. Of 488 minutes in which the MCT was empty, 70% were the direct result of eagle overflights. Researcher experiments resulted in a total of 5 minutes (1% of total) of abandonment. In total, researcher experiments caused the murres to partially or totally evacuate for 15 minutes (1% of the total observation time) and resettlement, defined as the time elapsed until the murres resumed their original positions and behavior, was approximately one hour in total. Aircraft caused a similar amount of disturbance, although never total abandonment.

Although eagles appear to influence murre demography on Tatoosh primarily through their facilitation of gull and crow egg predation, they also prey on adult murres. In all years (1991-1995), eagles were witnessed attacking murres. In 1994 and 1995, the success rate and the body count are higher than previous years (Table 9) perhaps indicating that the direct effect exerted by eagles is rising. In 1995, a juvenile eagle was successful in capturing a murre for the first time (as a function of all witnessed events), and eagles were witnessed landing in crevice subcolonies for the first time (see above - Reproduction; Table 5). Over the long term, eagle numbers in the vicinity of Tatoosh are increasing. The number of active Bald Eagle territories (defined as nests with offspring) within 25 km of Tatoosh is close to 20 (Figure 7; Data from WDFW) and the maximum number of eagles seen simultaneously per research trip to Tatoosh has also steadily increased (Figure 8; data from Dr. Robert T. Paine).

The influence of eagles on the Tatoosh Island Common Murre colony is difficult to predict accurately; however, using general assumptions about the distribution of murres on the island and standard murre life history parameters from other banded colonies, a life table can be constructed illustrating the relative impact of direct (i.e. predation on adults) versus indirect (i.e. egg predator facilitation) effects (Tables 10 and 11). Four age-specific parameters (in the absence of eagles) were estimated using information from banded Common and Thick-billed Murre colonies: percent surviving, percent of those returning to the breeding colony, percent of those attempting to breed, and reproductive success (data from Boekelheide et. al. 1990, Gaston et. al. 1994, Hedgren 1980, Hudson 1985). A stable age distribution was constructed with murres were aged 0 to 31. The rate of population increase was set at 0.8% annually ($\lambda = 1.008$; Table 11) to account for

Table 10. Parameter estimates for simulating Tatoosh murre population growth. Population is started with a stable age distribution and a total population size (i.e. on-colony + at-sea pool) of 10,331 of which 5,400 are attending Tatoosh (i.e. the 1995 estimated population), 25% in crevices and 75% on cliff-tops. Bald Eagle direct effects are simulated by decrementing survivorship of on-colony birds. Initial reproductive success is set at the 1991-1995 average at known crevice subcolonies (0.85 fledglings/pair). Bald Eagle indirect effects are simulated by decrementing reproductive success to match the 1991-1995 average at known cliff-top subcolonies (0.35 fledglings/pair).

Age	Return		Breed		Survival		Reproductive Success	
					Initial Predation @ 1%	Predation @ 2%	Initial (0.85 flg/pr)	Depressed (0.35 flg/pr)
0	0	0	0	0.71	0.71	0.71	0	0
1	0	0	0	0.81	0.81	0.81	0	0
2	0.08	0	0	0.81	0.81	0.81	0	0
3	0.36	0.05	0.83	0.83	0.83	0.83	0.20	0
4	0.58	0.28	0.86	0.86	0.86	0.85	0.30	0.08
5	0.85	0.65	0.87	0.86	0.86	0.85	0.45	0.10
6	0.96	0.87	0.88	0.87	0.87	0.86	0.75	0.30
7	0.96	1.00	0.89	0.87	0.87	0.86	0.90	0.35
8	0.96	1.00	0.90	0.89	0.89	0.88	0.91	0.35
9	0.96	1.00	0.91	0.90	0.90	0.89	0.92	0.40
10+	0.96	1.00	0.92	0.91	0.91	0.90	0.92	0.40
15+	0.97	1.00	0.92	0.91	0.91	0.90	0.92	0.40
20+	0.97	1.00	0.93	0.92	0.92	0.91	0.92	0.40

Table 11. Theoretical rate of Tatoosh murre population growth by habitat type, as a function of Bald Eagle direct and indirect effects. Numbers in parentheses following λ are years to extinction (defined as total within habitat population < 100). Plus signs following λ indicate a value slightly greater than 1.0 (i.e. growing population).

Habitat	Eagle Effects		λ	Population in 100 years
Crevice	none		1.008	5772
	direct (1%)		1.000+	2542
	direct (2%)		0.993 (435)	1218
Cliff-top	none		1.008	17316
	direct (1%)		1.000+	7786
	direct (2%)		0.993 (599)	3734
	direct (1%) + indirect		0.947 (80)	0
	direct (2%) + indirect		0.939 (70)	0

growth patterns on Tatoosh experienced during the 1980's. Tatoosh Island parameters, specifically total attendance in 1995, estimated eagle predation, and reductions in reproductive success as a function of habitat type (crevice versus cliff-top) estimated over the 1991-1995 period were substituted into the model. Thus, eagle effects did not affect either returns at age or breeding at age. Island attendance (3270) was multiplied by 1.67 (Harris 1989) to estimate the on-colony population (approximately 5400). This total was multiplied by age-specific on-colony percentages to estimate the number of murres at age on Tatoosh. These figures were then used to back calculate the total number of murres (that is, on-colony plus non-breeding pool) in the Tatoosh population. The model was then run with this initial, stable age distribution, where survivorship and reproductive success of on-colony birds was systematically adjusted to mimic estimated eagle effects. Population growth rate (λ), population size after 100 years, and the number of years to extinction (defined as population size < 100) were calculated iteratively as a function of habitat type.

Both direct and indirect eagle effects cause the population to decline (Table 11). Eagle predation at 2% of the on-colony cliff-top population will cause extinction in 599 years, whereas the cliff-top population will extinct itself in only 70 years if the influence of eagle-facilitated egg predation is included. In this simple model, the ratio of murres nesting in crevices versus cliff-tops was kept constant, even though this ratio would likely change if birds in one habitat were differentially affected, as was the case on Tatoosh in 1995. Nevertheless, as a broad comparative tool this simulation underscores the importance of indirect effects in regulating the Tatoosh murre population.

Discussion

It is clear from the 1995 season on Tatoosh Island that Common Murre demographics are difficult, if not impossible, to accurately predict from previous years. Although the murres appeared to be in "recovery" from the combined effects of the *Tenyo Maru* oil spill and the 1992-93 ENSO event in 1994, 1995 saw a drop in whole-island attendance combined with extremely high reproductive success in the monitored crevice subcolonies. The drop in attendance is therefore probably not the result of nearshore oceanographic changes in food supply. There are no known (to the author) seabird mortality events which would have caused such an attendance decline. Furthermore, Common Murre censuses along coastal Washington and Oregon were the highest recorded since 1988 (Mahaffy pers. comm. of data collected by U. Wilson and R. Lowe). Finally, the 1995 drop in Tatoosh Island attendance was accompanied by a dramatic switch in the pattern of island colonization. Murres joined crevice subcolonies and 6 new crevice subcolonies were born, both factors

leading to the highest crevice subcolony attendance on record: 1355 or 41% of total attendance. Furthermore, fledging occurred in at least one of these new subcolonies (Rainbow Rock - upper; RR-U). It seems likely that Tatoosh murre may have been switching breeding areas within the colony, although without banded individuals this conclusion is only based on correlative evidence. In any event, the patterns of attendance and reproduction in 1995 indicate that murre may be more flexible than a highly philopatric behavioral model would suggest (see also Halley & Harris 1993).

Behavioral flexibility may be a response to continued, perhaps escalating, direct and indirect pressure by Bald Eagles. With eagle visits, attacks, and captures rising, murre would at least continue to experience widespread reproductive failure and even loss of life, if the distribution between habitats remained predominantly cliff-top nesters. Simple life table models indicate that the Tatoosh colony could be substantially reduced in size by continued eagle pressure. It is too early to say whether the apparent movement towards crevice colonization will allow the Tatoosh Island population to circumvent the indirect effects of eagles. As eagles landed on at least one crevice for the first time this year, the movement by murre towards crevices may not be sufficient to ensure adequate survival and reproduction.

The incidence of eagle-induced disturbance of murre colonies does not appear limited to Tatoosh Island. Early in the murre nesting season, juvenile Bald Eagles apparently prevented breeding area colonization on Oregon's largest murre colony - Three Arch Rocks (Lowe pers. comm.). On Triangle Island, the largest stable Common Murre breeding colony in British Columbia and the nearest large colony north of Tatoosh, Bald Eagles exert a serious direct effect (predation on adults) as well as indirect effect (eagle-facilitated egg predation; Parrish pers. obs.). In addition, on this colony Glaucous-winged Gulls appear to be much more aggressive, stealing eggs and even chicks from attended subcolonies (J. Salatas pers. obs.). Comparisons between murre colonies might help indicate those factors which are regionally, versus locally, important in determining the survivorship and reproductive success necessary to produce "source" rather than "sink" colonies.

Attempts to elucidate the behavioral interactions between eagles, murre, and egg predators have proved fruitful. Parrish (1995b) has documented the effect eagle overflights have on murre behavior as a function of nesting habitat (i.e. crevice versus cliff-top). Parrish and Paine (1996) showed that temporary habitat manipulations on a cliff-top subcolony (MCT)

(in the form of added cover mimicking natural vegetation) increased egg production and were inversely proportional to percent of murres leaving (see also Figure 6, Table 4). Finally, Parrish (manuscript) has shown that murres not only respond to the actual presence of eagles, but more importantly to audio cues given by Glaucous-winged Gulls. In concert, these experiments suggest that the interactions between these community members are complex and need to be considered when attempting to influence murre demographics, particularly reproductive success.

Conclusions

If the present patterns of attendance and reproductive success of the Tatoosh Island Common Murres continue (assuming minimal immigration), the population may become smaller and eventually reside mostly in crevices. Whether a reduced population size will be viable in light of the factors affecting adult mortality (i.e. oil spills, gillnet by-catch, ENSO and other oceanographically-induced changes in food supply) is unknown. The rapidity of this habitat "switch" will probably be strongly influenced by immigration rate. In the 1980's, the Tatoosh population increased dramatically as a function of immigration - almost all of which went into the creation of cliff-top subcolonies. At present, these same birds may be in the process of moving into crevices and/or abandoning Tatoosh as a viable nesting colony. However, another wave of immigrants may change this pattern yet again. As murre colonies south of Tatoosh appear to be increasing in size, immigration may again become an important determinant of Tatoosh murre population size.

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