DYNAMICS OF MULTI-SPECIES FEEDING ASSOCIATIONS IN MARINE WATERS NEAR JUNEAU, ALASKA

TREVOR B. HAYNES[1,2], S. KIM NELSON[1] & VERONICA M. PADULA[1,2]

[1]*Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, Department of Fisheries and Wildlife, 104 Nash Hall, Corvallis, Oregon, 97331, USA*
[2]*Current address: School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, Alaska, 99775-7720, USA (t.haynes@alaska.edu)*

Received 16 March 2011, accepted 4 September 2011

SUMMARY

HAYNES, T.B., NELSON, S.K. & PADULA, V.M. 2011. Dynamics of multi-species feeding associations in marine waters near Juneau, Alaska. *Marine Ornithology* 39: 227–234.

During the summer of 2008, we examined the dynamics of multi-species feeding associations (MSFAs) in marine waters near Juneau, southeast Alaska. We conducted 1400 m wide strip transects to determine regional and seasonal differences in the composition of flocks. We conducted focal observations of 39 flocks to determine: (1) which bird species trapped prey at the surface, allowing for the initiation of the MSFA; (2) the roles of the numerically dominant species; and (3) how each flock terminated. Sixteen avian species participated in flocks, with flock size ranging from two to 543 individual birds (mean ± SD = 37 ± 63 birds). Bird species richness ranged from one to five species (3 ± 1 species). Capelin *Mallotus villosus*, sampled by dip net (n = 44 prey balls), were the only prey species found targeted by flocks. Mean flock densities on transects ranged from 0.21 ± 0.29 flocks/10 km^2 in Stevens Passage to 2.42 ± 1.93 flocks/10 km^2 in Tracy Arm. Of the 174 flocks surveyed, 172 were MSFAs and 170 of those involved at least one species of pursuit diving bird. Focal observations revealed that pursuit divers produced prey at the surface, leading to initiation of 16 of the 22 flocks, with murrelets *Brachyramphus* sp. producing 14 flocks, Pacific Loons *Gavia pacifica* producing one, and murrelets and Pacific Loons together producing one. Of the remaining six flocks, foraging salmonids produced prey at the surface at two, while the producers at four flocks were unobserved. Flock initiators included both small and large gull species as well as Bald Eagles *Haliaeetus leucocephalus*. Of the 39 focal observations, 31 terminated when pursuit divers stopped foraging and dispersed, subsequently followed by the dispersal of surface feeders. Eight focal observation flocks were terminated by Humpback Whales *Megaptera novaeangliae* lunge feeding at the center of the flock. Bald Eagles frequently participated in flocks in May and June but very infrequently in July and August, likely switching to a spawning salmon diet later in the season.

Key words: *Brachyramphus*, Bald Eagle, Capelin, foraging flocks, gull, Humpback Whale, Marbled Murrelet, seabirds

INTRODUCTION

Multi-species feeding associations (MSFAs) have been recognized as an important foraging adaptation for birds both in terrestrial (e.g. Morse 1970, 1977, Powell 1985) and marine environments (e.g. Hoffman et al. 1981, Camphuysen & Webb 1999). MSFAs offer two major advantages for birds: (1) reduced predation risk, and (2) increased foraging efficiency (Tubelis et *al.* 2006). For seabirds, increased foraging efficiency rather than reduced predation risk is likely the major benefit gained by participating in MSFAs. Seabirds and their prey are generally dispersed over large areas, and prey are spatially patchy. Once a prey patch is located, MSFAs often allow multiple species to exploit the prey resource. In these flocks, seabird species can interact at the scale of meters, providing an interesting opportunity to examine seabird interactions.

MSFAs generally include species with different foraging tactics, which can influence flock initiation and persistence through positive or negative inter- and intraspecific interactions (Tubelis *et al*. 2006). Positive interactions include information transfer among individuals, easier detection of prey, and access to prey that would otherwise be unavailable (Hoffman *et al.* 1981, Irons 1998, Camphuysen & Webb 1999, Goodale *et al.* 2010). Negative interactions include increased competition and kleptoparasitism (Jullien & Clobert 2000, Maniscalco *et al.* 2001, Catry *et al.* 2009). Fine-scale spatial and temporal interactions among species occurring in flocks have likely led to co-evolution of this type of feeding structure for several avian species (Hoffman *et al.* 1981). The roles of seabirds in MSFAs have been defined in multiple ways. For example, seabirds can be classified according to their feeding type: e.g. surface feeders, shallow plunge divers, deep plunge divers, and pursuit divers (Camphuysen & Webb 1999). Another approach is to classify species according to how their participation affects the dynamics of a flock. For example, Hoffman *et al.* (1981) classified birds as catalysts (highly visible birds that may attract others to the location), divers (pursuit or plunge divers that are key in flock production and persistence), kleptoparasites (birds that steal prey from others) and suppressors (species that cause a decrease in prey availability or break up the flock). Roles of species may vary spatially and temporally depending on the species present in a particular system, and the specific dynamics of that system.

In this study, we examined the dynamics of MSFAs near Juneau, southeast Alaska. We expected that flock composition would change across the summer season as the composition of bird species in the region changed. We expected murrelets would play an important role as producers in MSFAs because *Brachyramphus* murrelets are more abundant in the region than other pursuit diving birds. Additionally, because surface feeders require subsurface feeders (e.g. pursuit diving birds) to trap the prey at the surface, we expected that the participation and behavior of surface feeders, such as gulls, would depend on murrelet abundance and activity. To assess those ideas, we examined how species composition, abundance and behavior in MSFAs varied regionally, seasonally and over the duration of a flock event.

METHODS

Study area

We conducted our study along Stephens Passage from Gastineau Channel (58°11'N, 134°12'W) south to Port Snettisham (57°58'N, 133°53'W) and within the confluence of Holkham Bay (57°45'N, 133°37'W), Tracy Arm and Endicott Arm, a distance of more than 68 km (Fig. 1). These channels, passages and fjords are generally wide (up to 8.5 km) and deep (up to 380 m). The nearshore habitat includes features such as sand and gravel beaches, estuarine river mouths, tidal flats, rocky intertidal reef and steep cliffs. Although this area is distant from the open ocean and protected from the Gulf of Alaska by Admiralty and Chichagof Islands, tidal fluctuations reach 7.5 m and ocean currents can be swift. The channels and passages are fed by freshwater from bays, tidewater and hanging glaciers, and perennial and intermittent streams. Convergence zones occur where the cold, silty glacial waters meet the warmer, saline channels and inlets. The head of Tracy Arm contains two large glaciers, Sawyer and South Sawyer; during the summer, Holkham Bay and the adjoining inlets have considerable floating ice.

This area is surrounded by the steep, granite coastal mountains of the Tongass National Forest (USDA Forest Service) that range to over 2000 m in elevation. This rugged inland topography has helped maintain most of the surrounding forests in roadless, unharvested and relatively pristine condition. The northern temperate maritime climate in this region is characterized by high levels of precipitation and cloud cover, even in summer.

During the spring and summer months, the nutrient-rich waters of this area support populations of Steller Sea Lions *Eumetopias jubatus*, Harbor Seals *Phoca vitulina*, Humpback Whales *Megaptera novaeangliae*, Bald Eagles *Haliaeetus leucocephalus*, and a variety of piscivorous birds, including a large population of Marbled Murrelets *Brachyramphus marmoratus* (Haynes *et al.* 2011).

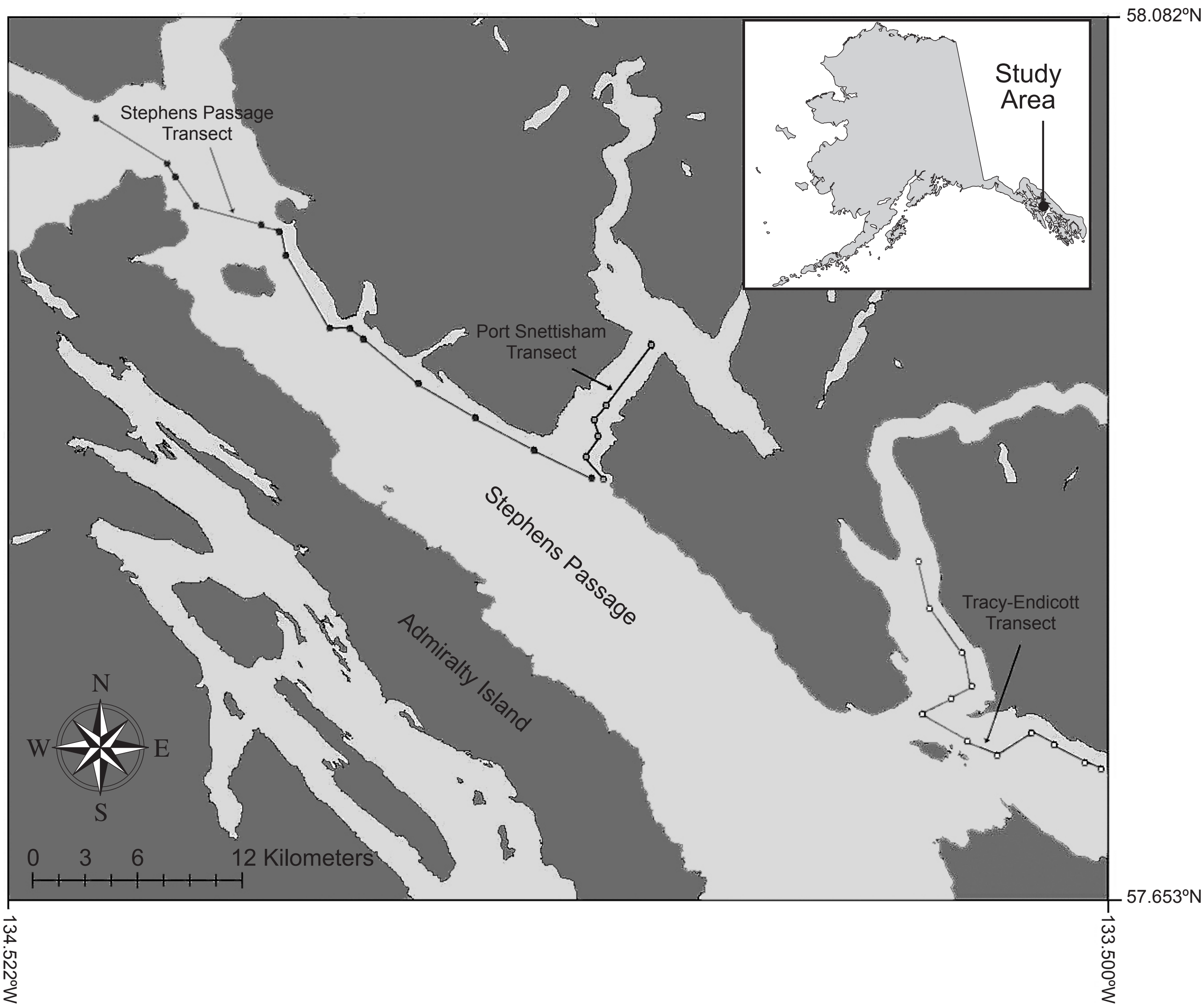

Fig. 1. Study area and locations of strip transects.

At-sea transects

We conducted strip transects in three regions during summer 2008 (5 June–2 August): Port Snettisham, Stephens Passage and Tracy-Endicott (Fig. 1). Transects were 700 m from the shoreline, except when they crossed water channels. We defined a flock as a group of two or more birds with surface feeders (i.e. gulls, terns, eagles) actively feeding. This definition purposely excludes flocks consisting strictly of pursuit diving birds because it is difficult to observe from the surface whether birds are diving to feed or prospecting for prey.

An observer stood on the bow of a 6.1 m vessel traveling at 15 knots (28 km/h), with an eye elevation of about 2.5 m, and scanned continuously for flocks in a 180° arc centered on the direction of travel. We conducted surveys when visibility was >1 km and on seas with a Beaufort index <4. Single species flocks and MSFAs were highly visible at great distances under these conditions. Any flocks located within 700 m of either side of the vessel were considered part of the observation area. When a flock was sighted, the boat traveled off the transect midline to the flock, stopping about 120 m away from the center. We defined the center of the flock as the position of foraging surface feeders. Two observers used binoculars to identify and count all birds within a 100 m radius of the center of the flock; a third person recorded the observations. We chose a 100 m radius because flocks were small, generally contained within this boundary, and because we wanted to focus on birds that were actively participating. Also, it gave us a logistically feasible boundary to standardize focal observation counts of birds moving in and out of flocks (see below). We also occasionally sampled the prey targeted by flocks using a long-handled dip net. Once information on the flock was recorded, the vessel returned to the transect midline and continued the survey.

We tested for differences in daily mean flock size and mean number of species per flock among transects using Kruskal–Wallis tests and post hoc multiple comparison tests of the average ranks for each pair of groups. We ran tests in Statistica 7.0 (Statsoft Inc.) and considered tests significant at a P value of 0.05. All values in the text are presented as the mean ± standard deviation.

We also opportunistically sampled flocks while conducting other sampling activities. We recorded the same information as was recorded for the flocks on transects and sampled prey with a dip net when possible. During fieldwork in 2007, we sampled prey opportunistically at flocks but did not record bird observations.

Focal observations

One observer monitored the number of diving birds sitting on the water or diving within the 100 m radius, and flying into (landing on the water) or out of (taking off from the water) the radius. Birds flying in and out were monitored continuously while scan counts of diving birds on the water or diving were conducted about every 3 min. The second observer monitored surface feeder abundance within the 100 m radius. Gulls spent much of the time on the wing when feeding, often hovering over the prey ball and making shallow plunge dives from the air when an opportunity arose. The second observer counted the number of gulls flying and on the water separately at 1–3 minute intervals. All birds were identified to species when possible. Because Kittlitz's *Brachyramphus brevirostris* and Marbled murrelets are sometimes difficult to distinguish on the water, and because forage flocks often contained large numbers of birds, some Kittlitz's Murrelets were likely identified as Marbled Murrelets. However, Kittlitz's Murrelet numbers were low in the region and thus this did not greatly inflate Marbled Murrelet counts. Rather, we likely underestimated the frequency and abundance of Kittlitz's Murrelets taking part in MSFAs.

While flocks had often already initiated when we began observations, we also saw flocks initiate. In those cases, we observed flocks from start to finish and noted which pursuit diving species produced the prey at the surface ("producer" species, after Camphuysen & Webb 1999). All flocks were observed until they broke up, which we determined as the point when surface feeders had not been observed feeding for three minutes. Because flocks were not all seen at initiation, we analyzed only the last 12 minutes of the flock duration to examine how counts and behavior of surface and subsurface feeders changed as flocks ended.

RESULTS

At-sea transects

We found 123 flocks on 1044 km of transect surveys (Table 1). We were unable to count birds in 17 of the 123 flocks because of rapid flock break-up. We sampled an additional 68 flocks opportunistically. All opportunistic sampling occurred in the general area of, but not necessarily on, transects. Of the 174 flocks in which birds were counted (transect and opportunistic combined), 172 were multi-species flocks and 170 involved at least one species of pursuit diving bird. Although almost all flocks observed were MSFAs, we probably underestimated the number of single-species flocks because of the definitional exclusion of single species flocks of diving birds (see Methods). Sixteen species of birds participated in MSFAs, with flock sizes ranging from two to 543 individuals (37 ± 63 birds) and bird species richness ranging from one to five species per flock (3 ± 1 species) (Table 2). Marbled Murrelets were by far the most frequent and numerous pursuit divers in the MSFAs (Table 2) and were the only pursuit diving species in the majority (71%) of MSFAs that had pursuit diving birds present. Four species of gulls, Arctic Terns *Sterna paradisaea* and Bald Eagles made up

TABLE 1
Summary of three strip transects and opportunistically sampled multi-species flocks

Transect	Transect length (km)	Sampling events	Total flocks	Flocks/10 km^2 (mean ± SD)	Total species	Species/flock (mean ± SD)
Port Snettisham	9.6	14	19	1.00 ± 0.86	9	4 ± 1
Stephens Passage	37.2	16	20	0.21 ± 0.29	8	4 ± 1
Endicott-Tracy	22.9	10	79	2.42 ± 1.93	11	3 ± 1
Opportunistic	NA	68	68	NA	14	3 ± 1

the majority of surface feeders (Table 2). Gulls and eagles were often active in the flocks over their duration, whereas Arctic Terns often participated only for short periods or on the periphery.

Mean flock size per day differed significantly among transects (Kruskal–Wallis $H = 18.71$, n = 32, $P = 0.0001$), with Tracy-Endicott having a significantly higher mean flock size than Port Snettisham or Stephens Passage, which did not differ (Table 1). Nine species were found on the Port Snettisham transect, eight on the Stephens Passage transect and 11 on the Tracy-Endicott transect. However, no significant differences were found in the mean number of species per flock among transects ($H = 3.87$, n = 23, $P = 0.145$).

TABLE 2
Bird species found in flocks recorded on strip transects and opportunistically sampled

Taxa	Frequency of presence in flocks, %	Birds/flock (mean ± SD)
Diving Birds		
Alcids[d]	97.4	31 ± 73
Brachyramphus marmoratus	96.0	31 ± 73
Brachyramphus brevirostris	5.2	4 ± 5
Uria aalge	7.5	5 ± 6
Cepphus columba[a]	3.4	1 ± 1
Synthliboramphus antiquus[c]	NA	NA
Loons[d]	17.8	8 ± 12
Gavia pacifica	13.2	9 ± 11
Gavia immer	2.4	1 ± 1
Other		
Scoters[b]	4.6	3 ± 3
Mergus serrator[c]	NA	NA
Surface feeders		
Gulls[d]	98.9	14 ± 10
Chroicocephalus philadelphia	73.7	9 ± 9
Larus canus	47.1	7 ± 8
Larus smithsonianus	16.3	4 ± 6
Larus glaucescens	15.0	4 ± 4
Other		
Haliaeetus leucocephalus	25.9	4 ± 4
Sterna paradisaea	16.1	4 ± 3
Stercorarius parasiticus[c]	NA	NA

[a] Recorded within the 100 m radius of forage flock but not seen participating in flock.
[b] Not identified to species.
[c] Not recorded during flock surveys but were noted at other instances participating in flocks.
[d] Values represent totals for the taxa, including birds that were only identified to major group.

There were seasonal differences in MSFA participation for several species, including Bald Eagles, loon *Gavia* sp. and scoter *Melanitta* sp. species. During June, Bald Eagles were involved in 64% of all MSFAs. However, after June, their participation was much lower (17% of all MSFAs, Fig. 2). Loons also showed strong seasonal occurrence, participating in 42% of MSFAs in June but only 8% of MSFAs in July and August. Scoters were not found in MSFAs until August, when they began gathering in higher numbers in the area to molt. The participated infrequently even then, but we did observe scoters targeting fish trapped by the MSFAs. Conversely, Pigeon Guillemots *Cepphus columba*, found within the 100 m observation radius at six MSFAs, did not appear to be feeding on the prey ball, as they have been seen to do elsewhere (Maniscalco *et al.* 2001). We noted that Marbled Murrelets frequently performed courtship displays at MSFAs, but this occurred only toward the end of the season.

According to the three-type classification system of Hoffman *et al.* (1981), all MSFAs in this study were type I: small, ephemeral flocks occurring over dense concentrations of prey. As seen elsewhere (Hoffman *et al.* 1981, Porter & Sealy 1982, Grover & Olla 1983, Mahon *et al.*1992, Ostrand 1999), gulls and other surface feeders were concentrated near the center of the forage flock, while murrelets and other pursuit diving birds generally remained around the periphery. The largest gulls generally held the central position over the prey ball.

Capelin *Mallotus villosus* was the only prey species found to be targeted by MSFAs (n = 44 prey balls, with 20 prey balls sampled in 2007 and 24, in 2008). The average Capelin fork length was 87 ± 12 mm (n = 548, range 39–121 mm). Based on estimated age–size values (Brown 2002), approximately 2% of the Capelin sampled from MSFAs were age-0 (<50 mm), 61% were age-1 (60–90 mm) and 8% were age-2 (100–130 mm). The remainder (29%) fell between those age–size classes. No Capelin older than two years were present according to this classification.

Focal observations

We conducted focal observations of 39 MSFAs. The point of flock initiation was generally difficult to observe; thus, we observed only

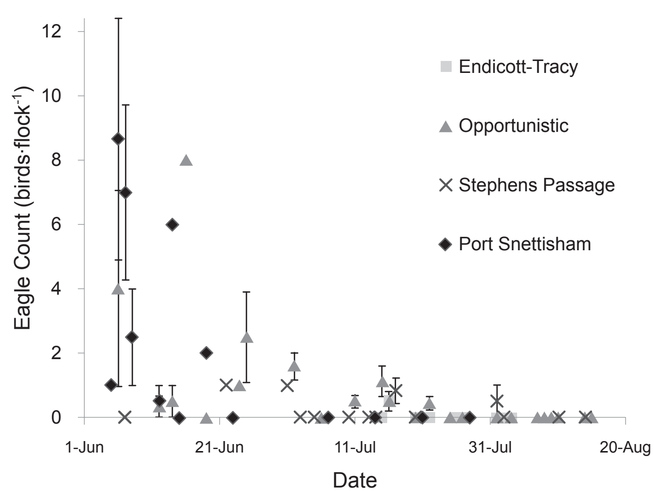

Fig. 2. Bald Eagle counts in MSFAs over the 2008 season from the three transect surveys and opportunistically observed flocks. Counts from flocks sampled on the same transect type on the same day were averaged. Error bars represent standard error.

22 MSFAs from initiation and 17 MSFAs after initiation. Diving birds produced 16 of the 22 MSFAs, with murrelets producing 14, Pacific Loons *Gavia pacifica* producing one and murrelets and Pacific Loons producing one. Six MSFAs were initiated without pursuit diving birds present. At 19 MSFAs, we identified the species that initiated flocks. For six of 19 MSFAs, multiple species initiated surface feeding at approximately the same time. Smaller gulls, including Bonaparte's Gulls *Chroicocephalus philadelphia* and Mew Gulls *Larus canus*, were involved with initiation of surface feeding in most MSFAs (10 and four MSFAs, respectively), whereas Glaucous-winged Gulls *Larus glaucescens* and Herring Gulls *Larus smithsonianus* were involved in initiation of only three (two and one MSFA, respectively). Bald Eagles were involved in initiation at seven MSFAs. At two of the MSFAs initiated without pursuit diving birds present, we noted salmonids attacking the prey ball before the MSFAs were initiated.

Because murrelets were the numerically dominant pursuit diver and gulls were the predominant surface feeders, we focused our analysis of flock termination dynamics on those species. Twelve minutes before flock termination, almost all of the murrelets observed flying were joining the flock (Fig. 3a). From that point, the proportion of murrelets flying in declined. Between 6 to 10 min before flock termination, the proportion of murrelets flying out became greater than the proportion flying in. At the point of termination, about 25% of the murrelets were flying in, while 75% were flying out. The changes in the rates that murrelets recruited to or left the flocks corresponded with changes in the numbers of murrelets in the flock, with murrelet numbers decreasing as the proportion flying out increased (Fig. 4).

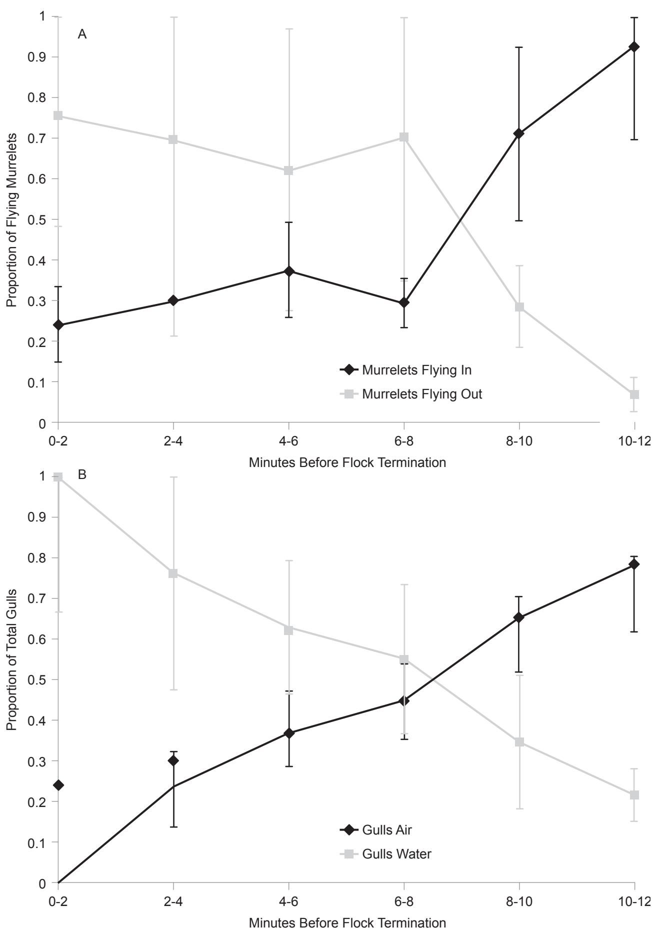

Fig. 3. Focal observations of MSFAs 12 min before flock termination: (a) proportion of murrelets flying into the flock compared to the proportion flying out, and (b) proportion of gulls on the water versus the proportion of gulls flying above the prey ball.

Gull behavior changed dramatically during the last 12 min before MSFA termination (Fig. 3b). At 12 min before MSFA termination, 80% of gulls observed were in the air, indicating that most birds were actively foraging. Closer to flock termination, the proportion of gulls in the air decreased. By 2 min before termination, all gulls were observed on the water, suggesting that the prey had become unavailable by moving beyond the reach of surface seizers and shallow plunge feeders. Unlike murrelets, gull numbers did not change substantially as the MSFAs approached termination (Fig. 4).

Eight of the 39 focal observation MSFAs, as well as six MSFAs observed during transect surveys, were suppressed by Humpback Whales lunge feeding at the center of the flock. Whales targeted prey that had been trapped at the surface by the flock. We did not note any discernible behavioral changes among the birds at the surface before the whales fed. Whales came up with their mouths open directly under birds at the surface, startling the birds. On two occasions, it appeared that whales ingested murrelets at the surface.

DISCUSSION

For at least some seabirds, joining a MSFA can provide a substantial increase in foraging efficiency. However, seabird flocking behavior may not confer a predator avoidance advantage (Hoffman *et al.* 1981, Ballance *et al.* 1997), as is thought for terrestrial multi-species flocks. This was substantiated by our observations of predators and avian prey feeding together in close proximity (within meters) in MSFAs. Bald Eagles, gulls and murrelets were found foraging in the same flocks, despite eagles being known predators of murrelets (Murie 1940, Anthony *et al.* 2008) and gulls (e.g. Buchanan & Watson 2010). We observed Bald Eagles preying on Marbled Murrelets and gulls within the study region; however, these events did not occur at MSFAs. If avoidance of predators was a factor in MSFA formation, we would expect that flocks would rapidly disperse when eagles were present. However, MSFAs

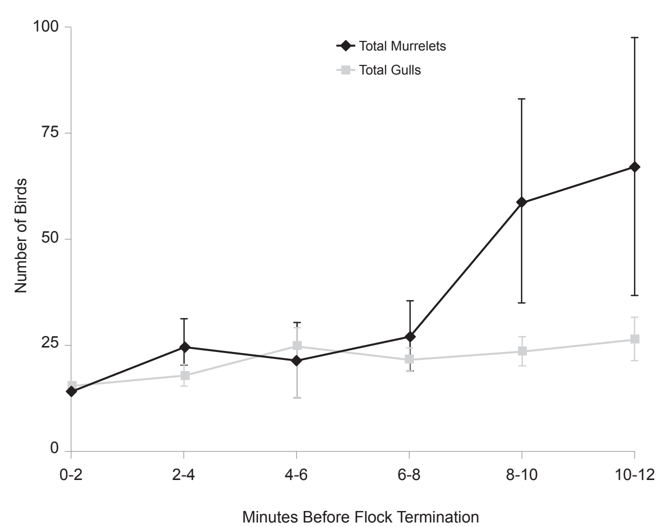

Fig. 4. Numbers of murrelets and gulls in MSFAs 12 min before flock termination.

persisted when eagles participated, suggesting the seabirds were not threatened enough to give up the feeding opportunity.

To understand the dynamics of MSFAs, it is crucial to delineate the role of important species (Hoffman *et al.* 1981, Camphuysen & Webb 1999). Diving birds and other subsurface predators drive prey to the surface and affect the horizontal and vertical movements and shape of the prey school, making it more accessible to surface feeders (Vaughn *et al.* 2008). Diving birds may also make prey available to surface feeders by injuring prey below the surface, causing the injured organisms to swim toward the surface (Hunt *et al.* 1988).

Marbled Murrelets were key producers, although other diving birds and piscivorous fishes initiated a small proportion of the MSFAs. Of the 22 MSFA initiations we observed, the majority were produced by Marbled Murrelets. Also, many of the flocks that were not seen at initiation were likely produced by Marbled Murrelets, as they were the only pursuit diving species present at the majority of MSFAs.

Both small and large gulls featured prominently in MSFAs, but their influence on the flocks was difficult to discern. Although our low number of observed initiations limits our inference, Bonaparte's Gulls initiated the most MSFAs and thus may play a role similar to that of Black-legged Kittiwakes *Rissa tridactyla* in the North Sea as key initiators (Camphuysen & Webb 1999). Similarly to Camphuysen & Webb (1999), we found larger gulls were typically "joiners" but also sometimes initiated MSFAs. Hoffman *et al.* (1981) suggested that highly visible gull species could act as catalysts, attracting other birds to the MSFAs. Camphuysen & Webb (1999) found that the participation of large gulls quickly led to flock termination. We did not find that the presence of large gulls noticeably disrupted the MSFAs as reported elsewhere, but we may have missed this in our observations because of our small sample size. Gulls often attempted to kleptoparasitize other gulls or Bald Eagles, but such attempts on murrelets were uncommon or unlikely to succeed, as murrelets consume fish mainly underwater, except when holding prey for inland flights to feed chicks.

MSFA termination appeared to be linked to a shift from murrelets recruiting to murrelets leaving the flock. Between 6 to 10 min before termination, we observed a rapid decline in murrelets flying in, a rise in murrelets flying out, and a decline in murrelet on the water. It is unclear whether murrelets left the flock in large numbers because they were satiated, had exhausted the prey supply or were unable to keep prey trapped at the surface. Murrelets generally dove in synchrony when initially "producing" the prey ball at the surface (also seen in alcids taking part in MSFAs in the North Sea, Camphuysen & Webb 1999). However, if high numbers of murrelets joined the flock, as was often the case as the MSFA progressed, this synchrony may have broken down, allowing prey to escape from the surface. We noted on occasion that after murrelets left the flocks or stopped diving, a prey ball was still visible from the surface (but no longer available to surface feeders), supporting the idea that satiation sometimes affected murrelet activity at flocks.

Gulls did not leave MSFAs when murrelets did; their numbers remained relatively stable right up to flock termination. Although their numbers remained constant toward the end, most gulls began to sit on the water rather than fly, and feeding attempts decreased. Shortly after murrelets began to leave, feeding opportunities likely decreased because prey were no longer trapped at the surface and thus were unavailable for surface-feeding gulls.

Previous studies of MSFAs in Alaska have been reported (e.g. Hoffman *et al.* 1981, Bayer 1983, Hunt *et al.* 1988, Ostrand 1999). However, the ecosystem characteristics, species composition and target prey differ from study to study, and consequently the MSFAs we observed have both similarities to and differences in dynamics from other studies. This is best exemplified in regional differences in flock participation found for certain species. For example, in British Columbia, Mahon *et al.* (1992) found loons did not participate in MSFAs, despite being present in the area. In our study, Common *Gavia immer* and Pacific loons participated in MSFAs as initiators and joiners. Another species which shows high variation in MSFA participation across its range is the Marbled Murrelet. In general, Marbled Murrelets are more likely to participate in MSFAs in sheltered waters than in the more exposed waters of the open coast (Hunt 1995). For example, on the outer coast of Vancouver Island, British Columbia (Porter & Sealy 1981, 1982) and in exposed coastal regions in the Gulf of Alaska (Hoffman *et al.* 1981), Marbled Murrelets were rare participants in MSFAs despite being present. Conversely, in more sheltered coastal waters, they were key producers of flocks (e.g. Mahon *et al.* 1992, Ostrand 1999, this study). It is unclear why Marbled Murrelets are key producers in some areas but not others. One possible reason they avoid flocks in some areas is to avoid interference competition from larger diving birds, such as Common Murres (Chilton & Sealy 1987, Mahon *et al.* 1992, Ronconi & Burger 2011). This has been demonstrated or suspected in the context of MSFAs for other species (Henkel 2009). For example, Ballance *et al.* (1997) suggested that the potential for competition in MSFAs, described as a function of body size, was a major factor structuring broad-scale community patterns of seabirds in the tropics. Furthermore, Maniscalco *et al.* (2001) found that Black-legged Kittiwakes avoided flocks with large numbers of Glaucous-winged Gulls and made fewer feeding attempts when joining flocks with greater numbers of gulls. Larger diving birds were relatively rare in our study area (Haynes *et al.* 2008); therefore, murrelets were not regularly exposed to potential interference competition from larger pursuit divers.

Eagles were documented participating in MSFAs by Sealy (1973) but have not been reported to participate in flocks to the degree seen in our study. For example, on 8 June, we noted 39 eagles feeding at a single flock. Eagles initiated MSFAs but also joined flocks after initiation by other species (classified as "joiners" or "scroungers," Camphuysen & Webb 1999). As a top predator, eagles may have suppressed flock activity by affecting the behavior of pursuit divers and initiators, but we did not see any obvious evidence of that.

The degree to which Bald Eagles participated in MSFAs varied within the season. We noted a sharp decrease in participation by eagles at the end of June, coinciding with the beginning of local salmon runs in rivers and streams, salmon being an important seasonal food source for eagles in the region (Ofelt 1975, Cain 1985). Until late June, eagles generally target a diversity of prey, including forage fish (Gende 2008). When Pink Salmon *Oncorhynchus gorbuscha* become regionally available in rivers and streams in early July, eagles begin to congregate at key feeding areas to exploit salmon, which become their main prey (Gende 2008). Because salmon are unavailable at the beginning of the breeding season, MSFAs likely serve to supply breeding eagles with an important prey source that would otherwise be unavailable.

Seabirds often associate with subsurface predators that drive prey to the surface, including marine mammals (Harrison 1979, Evans

1982, Au & Pitman 1986, Obst & Hunt 1990, Harrison *et al.* 1991, Grebmeier & Harrison 1992, Hawke 1994, Bräger 1998, Ballance *et al.* 1997, Clua & Grosvalet 2001, Vaughn *et al.* 2008, Henkel 2009). Less well documented is flocking seabirds acting as indicators of prey for marine mammals (Hoelzel *et al.* 1989, Herman 1991, Anderwald *et al.* 2011). In our study, Humpback Whales targeted prey located and trapped by seabirds. Humpback Whales often moved from flock to flock, targeting Capelin prey schools trapped at the surface by the flock even when flocks were over 150 m away. This suggests that seabird flocks may have provided visual cues for the Humpback Whales, as they have been observed to do elsewhere (Pierotti 1988).

Humpback Whales that fed on Capelin at MSFAs terminated the foraging activities of the flock, and therefore may be described as "suppressors" (Hoffman *et al.* 1981). Whales can both drastically reduce prey with one feeding event and interfere with foraging by disrupting the configuration of the flock during surface lunge feeding. This is the converse of other situations in which Humpback Whales may aid in concentrating prey at the surface, making food more accessible to seabirds (Evans 1982). Considering the frequency with which Humpback Whales suppressed flocks, whales played an important role in the MSFA dynamics in the region. Generally, flocks did not reform after whales fed, although on occasions when they did, the whale returned and fed on the prey school a second time.

The importance of MSFAs in marine ecosystems has yet to be fully understood. MSFAs have been suggested to play a key role in structuring seabird communities (Ballance *et al.* 1997), and feeding in flocks can account for most feeding events in some areas (Hunt 1990). Furthermore, some species may be near-obligate commensals with sub-surface feeders (Au & Pitman 1986, Pitman & Ballance 1992). Other potential benefits of MSFA participation include information transfer opportunities for inexperienced foragers (Porter & Sealy 1982, Goodale *et al.* 2010) or other social functions. The diversity of species and the abundance of birds participating in MSFAs suggest that flocks play a key role in predator–prey dynamics in the inland waters of southeast Alaska, not just for seabirds, but also for other species. However, the costs and benefits of joining MSFAs remain unclear. Also, although functional roles of species, usually classified by feeding type, have been hypothesized, they have not been tested thoroughly, and the complex processes of MSFA initiation and persistence are not fully understood (Goodale & Beauchamp 2010). Future research should focus on quantifying the importance of MSFAs in marine ecosystems, further delineating the factors that cause flocks to form and persist, and factors promoting or deterring participation by individuals or species.

ACKNOWLEDGEMENTS

This project was funded by the Alaska Department of Fish and Game, Division of Wildlife Conservation, through a cooperative agreement (COOP 05-140) with Oregon State University. Thanks to Mary Rabe, Matthew Kirchhoff, David Thomson and Nancy Pierce (ADF&G). Field support was provided by many hardworking cooperators, crew and volunteers, including Sarah Thomsen and Spencer Plumb. We especially thank Blake Barbaree, Scott Newman, Darrell Whitworth, Harry Carter and Gus Van Vliet for their contributions to the overall project. This manuscript benefitted from insights and constructive comments from Kees Camphuysen.

REFERENCES

ANDERWALD, P., EVANS, P.G.H., GYGAX, L. & HOELZEL, A.R. 2011. Role of feeding strategies in seabird-Minke Whale associations. *Marine Ecology Progress Series* 424: 219-227.

ANTHONY, R.G., ESTES, J.A., RICCA, M.A., MILES, A.K. & FORSMAN, E.D. 2008. Bald Eagles and Sea Otters in the Aleutian Archipelago: indirect effects of trophic cascades. *Ecology* 89: 2725-2735.

AU, D.W.K. & PITMAN, R.L. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. *Condor* 88: 304-317.

BALLANCE, L.T., PITMAN, R.L. & REILLY, S.B. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology* 78: 1502-1518.

BAYER, R.D. 1983. Black-Legged Kittiwake feeding flocks in Alaska: selfish/reciprocal altruistic flocks? *Journal of Field Ornithology* 54: 196-199.

BRÄGER, S. 1998. Feeding associations between White-Fronted Terns and Hector's Dolphins in New Zealand. *Condor* 100: 560-562.

BROWN, E.D. 2002. Life history, distribution, and size structure of Pacific Capelin in Prince William Sound and northern Gulf of Alaska. *ICES Journal of Marine Science* 59: 983-996.

BUCHANAN, J.B. & WATSON, J.W. 2010. Group hunting by immature Bald Eagles directed at gulls. *Northwestern Naturalist* 91: 222-225.

CAIN, S.L. 1985. Nesting activity time budgets of Bald Eagles in southeast Alaska. M.S. thesis. Missoula: University of Montana.

CAMPHUYSEN, K. & WEBB, A. 1999. Multi-species feeding associations in North Sea seabirds: jointly exploiting a patchy environment. *Ardea* 87: 177-198.

CATRY, T., RAMOS, J.A., SAMPSON, E. & LE CORRE, M. 2009. Does interference competition explain why White Terns of Aride Island, Seychelles, breed predominantly when marine productivity is lower? *Ibis* 151: 265-273.

CHILTON, G. & SEALY, S.G. 1987. Species roles in mixed-species feeding flocks of seabirds. *Journal of Field Ornithology* 58: 456-463.

CLUA, É. & GROSVALET, F. 2001. Mixed-species feeding aggregation of dolphins, large tunas and seabirds in the Azores. *Aquatic Living Resources* 14: 11-18.

EVANS, P.G.H. 1982. Associations between seabirds and cetaceans: a review. *Mammal Review* 12: 187-206.

GENDE, S.M. 2008. Perspectives on the breeding biology of bald eagles in Southeast Alaska. In: Wright, B. & Schempf, P.F. (Eds.) Bald Eagles in Alaska. Juneau, AK: American Bald Eagle Institute. pp. 95-105.

GOODALE, E. & BEAUCHAMP, G. 2010. The relationship between leadership and gregariousness in mixed-species bird flocks. *Journal of Avian Biology* 41: 99-103.

GOODALE, E., BEAUCHAMP, G., MAGRATH, R.D., NIEH, J.C. & RUXTON, G.D. 2010. Interspecific information transfer influences animal community structure. *Trends in Ecology and Evolution* 64: 354-361.

GREBMEIER, J.M. & HARRISON, N.M. 1992. Seabird feeding on benthic amphipods facilitated by Gray Whale activity in the northern Bering Sea. *Marine Ecology Progress Series* 80: 125-133.

GROVER, J.J. & OLLA, B.L. 1983. The role of the Rhinoceros Auklet (*Cerorhinca monocerata*) in mixed-species feeding assemblages of seabirds in the Strait of Juan de Fuca, Washington. *Auk* 100: 979-982.

HARRISON, C.S. 1979. The association of marine birds and feeding Gray Whales. *Condor* 81: 93-95.

HARRISON, N.M., WHITEHOUSE, M.J., HEINEMANN, D., PRINCE, P.A., HUNT, G.L., JR. & VEIT, R.R. 1991. Observations of multispecies seabird flocks around South Georgia. *Auk* 108: 801-810.

HAWKE, D.J. 1994. Seabird association with Hector's Dolphins and trawlers at Lytelton Harbour mouth. *Notornis* 41: 206-209.

HAYNES, T.B., NELSON, S.K., POULSEN, F. & PADULA, V.M. 2008. At-sea habitat use and patterns in spatial distribution of Marbled Murrelets in Port Snettisham, SE Alaska [unpublished report]. Prepared for Alaska Department of Fish and Game. New York & Corvallis, OR: Wildlife Trust & Oregon State University. 57 pp.

HAYNES, T.B., NELSON, S.K., POULSEN, F. & PADULA, V.M. 2011. Spatial distribution and habitat use of Marbled Murrelets at sea in Port Snettisham, Alaska. *Marine Ornithology* 39: 151-162.

HENKEL, L.A. 2009. Co-occurrence and aggregation of marine birds and mammals in Monterey Bay, California, USA. *Marine Ecology Progress Series* 387: 295-303.

HERMAN, L.M. 1991. What the dolphin knows, or might know, in its natural world. In: Prior, K. & Norris, K.S. (Eds.) Dolphin societies: discoveries and puzzles. Los Angeles: University of California Press. pp. 340-364.

HOELZEL, A.R., DORSEY, E.M. & STERN, S.J. 1989. The foraging specializations of individual Minke Whales. *Animal Behaviour* 38: 786-794.

HOFFMAN, W., HEINEMANN, D. & WIENS, J.A. 1981. The ecology of seabird feeding flocks in Alaska. *Auk* 98: 437-456.

HUNT, G.L., JR.1990. The pelagic distribution of marine birds in a heterogeneous environment. *Polar Research* 8: 43-54.

HUNT, G.L., JR. 1995. Monospecific and mixed species foraging associations of Marbled Murrelets. In: Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G. & Piatt, J.F. (Eds.) Ecology and conservation of the Marbled Murrelet. Forest Service General Technical Report PSW-GTR-152. Albany, CA: US Department of Agriculture. pp. 255-256

HUNT, G.L., JR., HARRISON, N.M., HAMNER, W.M. & OBST, B.S. 1988. Observations of a mixed-species flock of birds foraging on euphausiids near St. Matthew Island, Bering Sea. *Auk* 105: 345-349.

IRONS, D.B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79: 647-655.

JULLIEN, M. & CLOBERT, J. 2000. The survival value of flocking in neotropical birds: reality or fiction? *Ecology* 81: 3416-3430.

MAHON, T.E., KAISER, G.W. & BURGER, A.E. 1992. The role of Marbled Murrelets in mixed-species feeding flocks in British Columbia. *Wilson Bulletin* 104: 738-743.

MANISCALCO, J.M., OSTRAND, W.D., SURYAN, R.M. & IRONS, D.B. 2001. Passive interference competition by Glaucous-Winged Gulls on Black-Legged Kittiwakes: a cost of feeding in flocks. *Condor* 103: 616-619.

MORSE, D.H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecological Monographs* 40: 119-168.

MORSE, D.H. 1977. Feeding behavior and predator avoidance in heterospecific groups. *BioScience* 27: 332-339.

MURIE, O.J. 1940. Food habits of the northern Bald Eagle in the Aleutian Islands, Alaska. *Condor* 42: 198-202.

OBST, B.S. & HUNT, G.L., JR. 1990. Marine birds feed at Gray Whale mud plumes in the Bering Sea. *Auk* 107: 678-688.

OFELT, C., H. 1975. Food habits of nesting Bald Eagles in southeast Alaska. *Condor* 77: 337-338.

OSTRAND, W.D. 1999. Marbled Murrelets as initiators of feeding flocks in Prince William Sound, Alaska. *Waterbirds* 22: 314-318.

PIEROTTI, R. 1988. Associations between marine birds and mammals in the Northwest Atlantic Ocean. In: Burger, J. (Ed.) Seabirds and other marine vertebrates: competition, predation and other interactions. New York: Columbia University Press. pp. 31-58.

PITMAN, R.L. & BALLANCE, L.T. 1992. Parkinson's Petrel distribution and foraging ecology in the eastern Pacific: aspects of an exclusive feeding relationship with dolphins. *Condor* 94: 825-835.

PORTER, J.M. & SEALY, S.G. 1981. Dynamics of seabird multispecies feeding flocks: chronology of flocking in Barkley Sound, British Columbia, in 1979. *Colonial Waterbirds* 4: 104-113.

PORTER, J.M. & SEALY, S.G. 1982. Dynamics of seabird multispecies feeding flocks: age-related feeding behaviour. *Behaviour* 81: 91-109.

POWELL, G.V.N. 1985. Sociobiology and adaptative significance of interspecific foraging flocks in the Neotropics. *Neotropic Ornithology* 36: 713-732.

RONCONI, R.A. & BURGER, A.E. 2011. Foraging space as a limited resource: inter- and intra-specific competition among sympatric pursuit-diving seabirds. *Canadian Journal of Zoology* 89: 356-368.

SEALY, S.G. 1973. Interspecific feeding assemblages of marine birds off British Columbia. *Auk* 90: 796-802.

TUBELIS, D.R.P., COWLING, A. & DONNELY, C. 2006. Role of mixed-species flocks in the use of adjacent savannas by forest birds in the central Cerrado, Brazil. *Austral Ecology* 31: 38-45.

VAUGHN, R.L., WÜRSIG, B., SHELTON, D.S., TIMM, L.L. & WATSON, L.A. 2008. Dusky Dolphins influence prey accessibility for seabirds in Admiralty Bay, New Zealand. *Journal of Mammalogy* 89: 1051-1058.