AN ABSTRACT OF THE THESIS OF

Adam G. Peck-Richardson for the degree of Master of Science in Wildlife Science presented on March 17, 2017

Title: Double-crested Cormorants (*Phalacrocorax auritus*) and Brandt's Cormorants (*P. penicillatus*) Breeding at East Sand Island in the Columbia River Estuary: Foraging Ecology, Colony Connectivity, and Overwinter Dispersal

Abstract approved:

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Double-crested cormorants (*Phalacrocorax auritus*) and Brandt's cormorants (*P. penicillatus*) nest sympatrically in a large mixed-species colony on East Sand Island (ESI) in the Columbia River estuary. Ecological theory predicts that such morphologically similar species will partition prey resources when faced with resource limitations. During the summer of 2014, I investigated local movements, foraging dive behavior, and foraging habitat selection by breeding adults of both cormorant species using GPS tags with integrated temperature and depth data-loggers (GPS-TDlog, Earth & Ocean Technologies). The overall foraging areas and core foraging areas (defined as the 95% and 50% kernel density estimates of dive locations, respectively) of double-crested cormorants were much larger and covered a broader range of estuarine habitats than those of Brandt's cormorants. Only 26% and 27% of the overall and core foraging areas, respectively, for double-crested cormorants overlapped with those of Brandt's cormorants. Most of the overall and core foraging areas of Brandt's cormorants (59% and 89%, respectively)

overlapped with those of double-crested cormorants, however. Within areas of overlap, Brandt's cormorants tended to dive deeper (median depth = 6.48 m) than double-crested cormorants (median depth = 2.67 m), and selected dive locations where the water was deeper. After accounting for local water depth, Brandt's cormorants utilized a deeper, more benthic portion of the water column than did double-crested cormorants. Our results indicate that species-specific patterns of foraging habitat utilization likely reflect past evolutionary divergence in foraging niche and evolved differences in behavioral and physiological adaptations, resulting in some partitioning of prey resources that would mitigate interspecific competition. Nevertheless, the substantial overlap in foraging habitat between the two cormorant species, particularly for Brandt's cormorants, suggests that superabundant prey resources allow these two large and productive cormorant colonies to coexist on a single island near the mouth of the Columbia River.

Annual consumption of millions of out-migrating juvenile salmonids (*Oncorhynchus* spp.), including smolts from populations listed under the U.S. Endangered Species Act, by double-crested cormorants nesting at ESI motivated natural resource managers to investigate potential management techniques to reduce cormorant predation by reducing the size of the breeding colony. To better understand potential dispersal of cormorants from the ESI colony due to management to reduce colony size, satellite transmitters were fitted on 83 double-crested cormorants captured on the ESI colony before egg-laying in 2013. Dispersal from ESI immediately following tagging was nearly ubiquitous, but temporary, and provided limited information on where cormorants might prospect for alternative nest sites if prevented from nesting on ESI. During this initial pre-nesting period, tagged cormorants were detected at colonies and roost sites as far from ESI as the Puget Sound region of coastal Washington; nevertheless, all but 4% of tagged cormorants returned to

ESI within 2 weeks of being tagged. Following the subsequent breeding season, tagged cormorants staged at several nearby estuaries before migrating both north and south from ESI to overwinter in areas from British Columbia to northwestern Mexico; only 3% overwintered in the Columbia River estuary. Tracking data revealed substantial connectivity between the ESI colony and other colonies and regions within the range of the western North America population, suggesting the potential for widespread dispersal throughout the population's breeding range if nesting habitat on ESI was reduced or eliminated. Dispersal did not extend across the Cascade-Sierra Divide, however; greater connectivity existed with estuary locations throughout the range and particularly with more proximate estuaries that served as post-breeding staging areas. Surprisingly low regional and colony connectivity was observed with the Oregon Coast, despite numerous active and historical colonies in that region, as well as proximity to the colony at ESI. The strong philopatry to ESI that nearly all tagged cormorants exhibited, however, suggests that few alternative nesting opportunities are as attractive for prospecting double-crested cormorants as the ESI colony site.

Double-crested Cormorants (*Phalacrocorax auritus*) and Brandt's Cormorants (*P. penicillatus*) Breeding at East Sand Island in the Columbia River Estuary: Foraging Ecology, Colony Connectivity, and Overwinter Dispersal

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I understand that my thesis will become part of the permanent collection of Oregon State University Libraries. My Signature below authorizes release of my thesis to any reader upon request.

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CONTRIBUTION OF AUTHORS

Dr. Daniel D. Roby acquired funding, assisted with study design and interpretation of results, and provided editorial comments for all chapters. Dr. Donald E. Lyons acquired funding for Chapter 2, provided assistance with field work, study design, data analysis, and interpretation for Chapters 2 and 3, and provided editorial comments for all chapters. Daniel C. Cushing assisted with data processing and analysis for Chapter 2. Dr. James A. Lerczak assisted with data acquisition and processing and provided editorial comments for Chapter 2.

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CHAPTER 1: GENERAL INTRODUCTION

Adam G. Peck-Richardson

Cormorants (Family: Phalacrocoracidae) are medium to large seabirds generally characterized by their long necks, slender bills, and monochromatic black and white plumage. The cormorant taxonomic group is represented by approximately 40 extant species with a nearly global distribution, and likely split off from the darter family (Anhingidae) more than 40 million years ago (Kennedy and Spencer 2014). Cormorants are generally coastal seabirds, as opposed to oceanic, but some species also inhabit inland lakes and waterways. Cormorants are mostly piscivorous, employ foot-propelled pursuit-diving, and utilize webbed totipalmate feet to aide in propulsion.

The double-crested cormorant (*Phalacrocorax auritus*) is a large piscivorous colonial waterbird found along seacoasts and at interior lakes and rivers throughout much of North America (Dorr et al. 2014). Distributed widely across the continent, but not beyond, double-crested cormorants are the most abundant of the six species of cormorants found in North America (Dorr et al. 2014). There are five putative subspecies, corresponding to fairly distinct geographic zones of North America, spanning from the Bahamas to Alaska (Wires et al. 2001, Dorr et al. 2014). The subspecies *P. a. albociliatus* is one of two subspecies found along the Pacific Coast, breeding from northwestern Mexico to southern British Columbia, Canada, and inland to the Continental Divide. The Alaska sub-species, *P. a. cincinatus*, also breeds along the Pacific coast, but its breeding range is limited to coastal Alaska (Dorr et al. 2014). A recent study by Mercer et al. (2013) determined that the three historically accepted subspecies in the conterminous United States are not genetically distinct and do not warrant classification as separate subspecies.

Brandt's cormorants (*P. penicillatus*) are specialized for foraging in marine environments and are endemic to the California Current system along the west coast of North America (Wallace and Wallace 1998). They nest primarily along exposed outer coasts, inhabiting mostly inshore coastal waters and estuaries, avoiding fresh or brackish water habitats, and their breeding range stretches from northwestern Mexico to Vancouver Island, British Columbia (Wallace and Wallace 1998). While few published data on dive depths exist, Brandt's cormorants are considered deep divers among the Phalacrocoracidae, with high tissue oxygen storage capacity and the ability to dive deeper than 100 m (Ainley 1984). They have been caught in fishing nets as deep as 70 m (Wallace and Wallace 1998). These characteristics suggest that Brandt's cormorants are better adapted for foraging in deeper nearshore marine habitats compared to double-crested cormorants, which typically forage in shallow waters less than 8 m deep (Dorr et al. 2014).

East Sand Island (ESI; 46º15'46"N, 123º59'15"W) is located in the lower Columbia River estuary (river kilometer 7), partially straddling the border between Clatsop County, Oregon, and Pacific County, Washington. ESI is a naturally occurring, low-lying island, about 20 km in area, comprised of mixed dune, forest, shrubland, and rocky habitat types, and surrounded by extensive intertidal sand and mudflats. The island has been heavily modified by the addition of dredged material and shoreline hardening. The surrounding Columbia River estuary comprises many habitat types and supports a wide variety and great abundance of forage fish species (Bottom and Jones 1990), which in turn support many piscivorous waterbirds. During this study, ESI was the site of the largest known breeding colonies of double-crested cormorants and Caspian terns (*Hydroprogne caspia*) in western North America (14,900 and 7,400 breeding pairs in 2013, respectively; BRNW 2014). The island is also home to smaller breeding colonies of Brandt's cormorants (1,550 pairs in 2013), glaucous-winged/western gulls (*Larus glaucescens* x *L. occidentalis*), and ring-billed gulls (*L. delawarensis*; BRNW 2014). Brandt's cormorants were first detected nesting at ESI on a pile dike off the west end of the island in 1997 (Couch and Lance 2004). In 2006 the Brandt's cormorant colony shifted to ESI itself, and the birds nested on the ground within the double-crested cormorant colony. The Brandt's cormorant colony grew from fewer than 50 breeding pairs to more than 1,600 pairs in 2012, making it one of the largest Brandt's cormorant colonies in Oregon (BRNW 2013). ESI is also a large post-breeding roost site for California brown pelicans (*Pelecanus occidentalis californicus*; Wright et al. 2007). The abundance of two congeneric cormorant species breeding on ESI, combined with the wide variety of available foraging habitat types, provides a unique opportunity to investigate interspecific niche partitioning in seabirds.

Miniaturization of remote-sensing technology has spurred the development of devices that are able to gather a wide array of data on the movements and behaviors of free-ranging animals. Tags that incorporate GPS devices with temperature and depth sensors have been used to describe the three-dimensional foraging behavior of seabirds at very high resolution (Gremillet et al. 1999, Daunt et al. 2003), and to compare foraging habitat use by sympatric seabird species (Kokubun et al. 2010). GPS tags with integrated environmental sensors are valuable tools that can provide insight into foraging habitat use and resource partitioning by Brandt's and double-crested cormorants nesting in the Columbia River estuary.

Double-crested cormorant populations in the conterminous U.S. and southern Canada have grown dramatically since the early 1970s (Wires et al. 2001); however, trends have not been as uniformly positive for the population along the Pacific Coast (Carter et al. 1995, Adkins et al. 2014). While the western North America population has rebounded from historical lows in the early 1900s, more recent declines have occurred in coastal regions of British Columbia, Washington, and southern California (Carter et al. 1995, Adkins et al. 2014). Adkins et al. (2014) estimated that in 2009 the western North America population, excluding colonies in northwestern Mexico, consisted of approximately 31,200 breeding pairs, and was growing at a rate of 3% per year. Nearly all of this growth, however, could be attributed to the colony on ESI in the Columbia River estuary. This one colony nearly tripled in size from 1997 (*ca*. 5,025 pairs) to 2013 (*ca*. 14,920 pairs), and accounted for more than 40% of the western North America population of double-crested cormorants (Adkins et al. 2014). Although the western North America population was at least an order of magnitude smaller than the population in central and eastern North America (> 300,000 breeding pairs; Hatch 1995), the breeding colony on ESI was the largest-known colony for the species in 2013. Nevertheless, the western North America population was still at least an order of magnitude smaller than it had been historically (Wright 1913, Wires and Cuthbert 2006).

The recovery and redistribution of double-crested cormorants in the conterminous U.S. have led to increased conflicts with humans relating to purported impacts on commercial fisheries, aquaculture, and game fish stocks, as well as damage to vegetation and competition with other colonial waterbirds (Wires et al. 2001, Collis et al. 2002, Duerr et al. 2007, Guillaumet et al. 2014, Wires 2014). Throughout much of their range in central and eastern North America, double-crested cormorants have been subjected to a wide array of management actions by USDA-Wildlife Services and state wildlife agencies, including systematic hazing and lethal control at breeding colonies (USFWS 2003, Wires 2014). Double-crested cormorants in the Columbia River system, and specifically those nesting on ESI in the Columbia River estuary, have been found to consume millions of out-migrating juvenile salmonids (*Oncorhynchus* spp.) annually (Collis et al. 2002, Evans et al. 2012), many of them listed as threatened or endangered under the U.S. Endangered

Species Act (ESA). The impact of predation by double-crested cormorants nesting at ESI on recovery of ESA-listed salmonids has become of increasing concern for fisheries managers since 2008 (PFC 2012). At the inception of this study, management options for the ESI cormorant colony were being considered and an environmental impact statement was being drafted to identify a preferred management option.

One potential management action to reduce predation by double-crested cormorants nesting at ESI on threatened and endangered juvenile salmonids was to reduce the size of the ESI colony. One technique to reduce the numbers of cormorants nesting on ESI would be a reduction in the area of cormorant nesting habitat in order to disperse a portion of those nesting on ESI away from the Columbia River estuary. This would be a similar approach to the current management strategy being implemented at the Caspian tern colony on ESI, which has also been implicated as a factor limiting recovery of ESA-listed salmonids in the Columbia River basin (USFWS 2005). Inter-colony movements of double-crested cormorants in the Pacific Northwest are poorly understood, however, and it is difficult to predict how emigration from the ESI colony might affect numbers of breeding pairs in other portions of their range. Courtot et al. (2012) examined colony and regional connectivity of ESI double-crested cormorants by placing Argos satellite tags on breeding birds and tracking their post-breeding season dispersal. Cormorants from ESI stayed west of the Cascade and Sierra Nevada mountain ranges, but dispersed widely from British Columbia to the Colorado River delta in northwestern Mexico. Direct connectivity was also demonstrated between the colony at ESI and numerous active and historical nesting sites throughout the coastal portion of the population's range during the non-breeding season (Courtot et al. 2012). If managed cormorant dispersal from ESI was implemented, however, prospecting and immigration rates would likely vary among regions and potential colony sites due to a number of factors, including distance from ESI and individual breeding history (Guillaumet et al. 2011, Courtot et al. 2012).

Habitat use away from the lower Columbia River estuary by cormorants currently nesting at the ESI colony could shed light on potential emigration destinations, if double-crested cormorants disperse from the ESI colony. Visits by cormorants to active or historical colony sites, including those of double-crested cormorants and other colonial waterbirds, or visits to locations with suitable nesting habitat, may represent prospecting behavior. Animals that breed colonially, including seabirds, often choose breeding locations where they have been successful in the past (Switzer 1993); however, stochastic environmental factors may cause nest failure at a colony site that is otherwise suitable for breeding. Therefore, complimentary cues, such as the reproductive success of neighbors or conspecifics at other colonies, may influence breeding site selection (Danchin et al. 1998, Hénaux et al. 2007). Prospecting for suitable nesting sites by visiting active colonies in the years prior to breeding, or possibly after a failed nesting attempt or during migration, has been shown to increase subsequent breeding success in great cormorants (*P. carbo*; Schjørring et al. 1999).

Studying movement patterns of cormorants nesting at ESI, across both fine and coarse regional and temporal scales, would contribute to a greater understanding of cormorant foraging ecology in a complex and dynamic estuarine environment, and also help to inform managers by predicting likely patterns of dispersal if cormorants were forced to leave ESI. A detailed study of cormorant foraging ecology bolsters our understanding of how these populations utilize important marine resources, while also addressing how resource partitioning may contribute to the coexistence of closely related species in a shared environment. The objectives of this thesis are to add to our understanding of the comparative foraging ecology of Brandt's and double-crested cormorants, as well as the migration patterns and inter-colony movements of double-crested cormorants nesting at ESI. Chapter 2 examines the foraging ecology and niche partitioning of the Brandt's and double-crested cormorants nesting sympatrically at ESI using GPS tags with integrated dive data recorders. Chapter 3 looks at broader patterns of inter-colony and inter-regional movements across the annual cycle for double-crested cormorants nesting at ESI utilizing data from Argos satellite tags.

LITERATURE CITED

Adkins, J. Y., D. D. Roby, D. E. Lyons, K. N. Courtot, K. Collis, H. R. Carter, W. D. Shuford, and P. J. Capitolo. 2014. Recent population size, trends, and limiting factors for the double-crested cormorant in western North America. Journal of Wildlife Management 78:1131–1142.

Ainley, D. G. 1984. Cormorants. Pages 92-101 *in* Seabirds of the eastern North Pacific and Arctic waters. (Haley, D., ed.) Pacific Search Press, Seattle, Washington, USA.

Bird Research Northwest [BRNW]. 2013. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River, Final 2012 Annual Report. Bonneville Power Administration, U.S. Army Corps of Engineers, and Grant County Public Utility District, Portland, Oregon, USA. <www.birdresearchnw.org>. Accessed 18 Jan 2017.

Bird Research Northwest [BRNW]. 2014. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River, Final 2013 Annual Report. Bonneville Power Administration, U.S. Army Corps of Engineers, and Grant County Public Utility District, Portland, Oregon, USA. <www.birdresearchnw.org>. Accessed 18 Jan 2017.

Bottom, D. L., and K. K. Jones. 1990. Species composition, distribution, and invertebrate prey of fish assemblages in the Columbia River estuary. Progress in Oceanography 25:243–270.

Carter, H. R., A. L. Sowls, M. S. Rodway, U. W. Wilson, R. W. Lowe, G. J. McChesney, F. Gress, and D. W. Anderson. 1995. Population size, trends, and conservation problems of the double-crested cormorant on the Pacific coast of North America. Colonial Waterbirds 18:189–215.

Collis, K., D. D. Roby, D. P. Craig, S. Adamany, J. Y. Adkins, and D. E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: Implications for losses of juvenile salmonids to avian predation. Transactions of the American Fisheries Society 131:537–550.

Couch, S. L. L., and M. M. Lance. 2004. Diet composition and breeding success of Brandt's cormorants in the Columbia River estuary. Northwestern Naturalist 85:62–66.

Courtot, K. N., D. D. Roby, J. Y. Adkins, D. E. Lyons, D. T. King, and R. S. Larsen. 2012. Colony connectivity of Pacific Coast double-crested cormorants based on post-breeding dispersal from the region's largest colony. Journal of Wildlife Management 76:1462–1471.

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79:2415–2428.

Daunt, F., G. Peters, B. Scott, D. Gremillet, and S. Wanless. 2003. Rapid-response recorders reveal interplay between marine physics and seabird behaviour. Marine Ecology Progress Series 255:283–288.

Dorr, B. S., J. J. Hatch, and D. V. Weseloh. 2014. Double-crested cormorant (*Phalacrocorax auritus*). The Birds of North America. *Cornell Lab of Ornithology, Ithaca, New York, USA. <https://birdsna.org/Species-Account/bna/species/doccor>. Accessed 18 Jan 2017.*

Duerr, A. E., T. M. Donovan, and D. E. Capen. 2007. Management-induced reproductive failure and breeding dispersal in double-crested cormorants on Lake Champlain. Journal of Wildlife Management 71:2565–2574.

Evans, A. F., N. J. Hostetter, D. D. Roby, K. Collis, D. E. Lyons, B. P. Sandford, R. D. Ledgerwood, and S. Sebring. 2012. Systemwide evaluation of avian predation on juvenile salmonids from the Columbia River based on recoveries of passive integrated transponder tags. Transactions of the American Fisheries Society 141:975-989.

Gremillet, D., R. P. Wilson, S. Storch, and Y. Gary. 1999. Three-dimensional space utilization by a marine predator. Marine Ecology Progress Series 183:263–273.

Guillaumet, A., B. Dorr, G. Wang, J. D. Taylor, R. B. Chipman, H. Scherr, J. Bowman, K. F. Abraham, T. J. Doyle, and E. Cranker. 2011. Determinants of local and migratory movements of Great Lakes double-crested cormorants. Behavioral Ecology 22:1096–1103.

Hatch, J. J. 1995. Changing populations of double-crested cormorants. Colonial Waterbirds 18:8–24.

Hénaux, V., T. Bregnaballe, and J. D. Lebreton. 2007. Dispersal and recruitment during population growth in a colonial bird, the great cormorant (*Phalacrocorax carbo sinensis*). Journal of Avian Biology 38:44–57.

Kennedy, M., and H. G. Spencer. 2014. Classification of the cormorants of the world. Molecular Phylogenetics and Evolution 79:249-257.

Kokubun, N., A. Takahashi, Y. Mori, S. Watanabe, and H.-C. Shin. 2010. Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. Marine Biology 157:811–825.

Mercer, D. M., S. M. Haig, and D. D. Roby. 2013. Phylogeography and population genetic structure of double-crested cormorants (*Phalacrocorax auritus*). Conservation Genetics 14:823–836.

Pacific Flyway Council [PFC]. 2012. Pacific flyway plan: a framework for the management of double-crested cormorant depredation on fish resources in the Pacific flyway. Pacific Flyway Council, U.S. Fish and Wildlife Service, Portland, Oregon, USA.

Schjørring, S., J. Gregersen, and T. Bregnaballe. 1999. Prospecting enhances breeding success of first-time breeders in the great cormorant (*Phalacrocorax carbo sinensis*). Animal Behaviour 57:647–654.

Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7:533–555.

U.S. Fish and Wildlife Service [USFWS]. 2003. Final environment impact statement: double-crested cormorant management in the United States. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, Virginia, USA.

U.S. Fish and Wildlife Service [USFWS]. 2005. Record of decision: Caspian tern management to reduce predation of juvenile salmonids in the Columbia River estuary, final environmental impact statement. U.S. Fish and Wildlife Service, Migratory Birds and Habitat Programs, Portland, Oregon, USA.

Wallace, E. A. H., and G. E. Wallace. 1998. Brandt's cormorant (*Phalacrocorax penicillatus*). The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://birdsna.org/Species-Account/bna/species/doccor>. Accessed 18 Jan 2017.

Wires, L. R. 2014. The double-crested cormorant: plight of a feathered pariah. Yale University Press, New Haven, Connecticut, USA.

Wires, L. R., and F. J. Cuthbert. 2006. Historic populations of the double-crested cormorant (*Phalacrocorax auritus*): implications for conservation and management in the 21st century. Waterbirds 29:9–37.

Wires, L. R., F. J. Cuthbert, D. R. Trexel, and A. R. Joshi. 2001. Status of the double-crested cormorant (*Phalocrocorax auritus*) in North America. Final Report to U.S. Fish and Wildlife Service. University of Minnesota, St. Paul, USA.

Wright, H. W. 1913. The birds of San Martin Island, lower California. Condor 15:207–210.

Wright, S. K., D. D. Roby, and R. G. Anthony. 2007. Responses of California brown pelicans to disturbances at a large Oregon roost. Waterbirds 30:479-487.

CHAPTER 2: FORAGING ECOLOGY OF DOUBLE-CRESTED AND BRANDT'S CORMORANTS NESTING AT EAST SAND ISLAND IN THE COLUMBIA RIVER ESTUARY, OREGON

Adam G. Peck-Richardson, Donald E. Lyons, Daniel D. Roby, Daniel A. Cushing,
and James A. Lerczak

ABSTRACT

Ecological theory predicts that co-existing, morphologically similar species will partition prey resources when faced with resource limitations. During the summer of 2014, we investigated local movements, foraging dive behavior, and foraging habitat selection by breeding adults of two closely related cormorant species, double-crested cormorants (*Phalacrocorax auritus*) and Brandt's cormorants (*P. penicillatus*). These species nest sympatrically at East Sand Island in the Columbia River estuary at the border of Oregon and Washington states, USA. Breeding individuals of each species were tracked using GPS tags with integrated temperature and depth data-loggers (GPS-TDlog, Earth & Ocean Technologies). The overall foraging areas and core foraging areas (defined as the 95% and 50% kernel density estimates of dive locations, respectively) of double-crested cormorants were much larger and covered a broader range of estuarine habitats than those of Brandt's cormorants. Only 26% and 27% of the overall and core foraging areas, respectively, for double-crested cormorants overlapped with those of Brandt's cormorants. Most of the overall and core foraging areas of Brandt's cormorants (59% and 89%, respectively) overlapped with those of double-crested cormorants, however. Within areas of overlap, Brandt's cormorants tended to dive deeper (median depth = 6.48 m) than double-crested cormorants (median depth = 2.67 m), and selected dive locations where the water was deeper. After accounting for local water depth, Brandt's cormorants utilized a deeper, more benthic portion of the water column than did double-crested cormorants. Our results indicate that species-specific patterns of foraging habitat utilization likely reflect past evolutionary divergence in foraging niche and evolved differences in behavioral and physiological adaptations, resulting in some partitioning of prey resources that would mitigate interspecific competition. Nevertheless, the substantial overlap in foraging habitat between the two

cormorant species in the Columbia River estuary, particularly for Brandt’s cormorants, suggests that superabundant prey resources allow these two large and productive cormorant colonies to coexist on a single island near the mouth of the Columbia River.

INTRODUCTION

Ecological theory predicts that morphologically similar, co-occurring species of predators will partition prey resources, through either dietary, spatial, or temporal segregation, when those resources are limited (Schoener 1971, Holbrook and Schmitt 1989). Double-crested cormorants (*Phalacrocorax auritus*) and Brandt's cormorants (*P. penicillatus*) are two closely-related, sympatric species that co-occur throughout much of their breeding range in the California Current system along the Pacific Coast of North America (Wallace and Wallace 1998, Dorr et al. 2014). These two species are both pursuit-diving piscivores that consume a wide variety of forage fishes and often nest in close proximity in mixed-species breeding colonies.

Both Double-crested and Brandt's cormorants are large colonial waterbirds that are endemic to North America. Double-crested cormorants are widely distributed across much of the continent and they nest and forage in a variety of habitats, including marine coastlines, interior lakes and rivers, and are considered aquatic ecosystem *generalists* (Dorr et al. 2014). At large lake systems in the northeastern U.S., double-crested cormorants preferentially select shallower foraging habitats (Coleman et al. 2005, Dorr et al. 2014), and along the Pacific Coast of the U.S. they are more likely to forage in estuaries than the other two congeneric and sympatric cormorant species, Brandt's cormorant and pelagic cormorant (*P. pelagicus*; Ainley et al. 1981). Brandt's cormorants, in contrast, are marine ecosystem *specialists* and endemic to the California Current system (Wallace and Wallace 1998). They nest primarily along exposed outer coasts, inhabiting mostly inshore coastal waters, and their breeding range stretches from northwestern Mexico to Vancouver Island, British Columbia, Canada (Wallace and Wallace 1998). While few published dive data exist, Brandt's cormorants are considered deep divers, with high tissue oxygen storage capacity and the ability to dive deeper than 100 m (Ainley 1984). They have been caught in fishing nets as deep as 70 m (Wallace and Wallace 1998). These observations suggest that Brandt's cormorants are better adapted for foraging in deeper nearshore marine habitats compared to double-crested cormorants, which typically forage in shallower waters less than 8 m deep (Dorr et al. 2014).

The Columbia River estuary, located where the Columbia River enters the Pacific Ocean, straddles the border of Oregon and Washington. This large system comprises many habitat types and supports a wide variety and abundance of forage fish species (Bottom and Jones 1990). In turn, prey resources in the estuary support many piscivorous waterbirds, including large breeding colonies of double-crested cormorants, Brandt's cormorants, Caspian terns (*Hydroprogne caspia*), glaucous-winged/western gulls (*Larus glaucescens* × *L. occidentalis*), and ring-billed gulls (*L. delawarensis*). ESI is also a large post-breeding roost site for California brown pelicans (*Pelecanus occidentalis californicus*; Wright et al. 2007). The west end of East Sand Island, located near the mouth of the estuary, is home to a large mixed-species colony of double-crested and Brandt's cormorants. The abundance of these congeneric species breeding on East Sand Island, combined with the wide variety of available foraging habitat types with marine, estuarine, and freshwater forage fish species, provides a unique opportunity to investigate interspecific niche partitioning.

Out-migrating juvenile salmonids (*Oncorhynchus* spp.) are abundant in the Columbia River estuary early in the cormorant nesting season and serve as an important prey resource, particularly in the freshwater portions of the estuary (Collis et al. 2002, Lyons et al. 2007). The productivity of marine habitats near the mouth of the Columbia River is enhanced by circulation patterns within the Columbia River plume and bolstered by dynamic patterns of coastal upwelling

(Huyer 1983, Kudela et al. 2010). Upwelling along the Oregon and Washington coasts, part of the California Current system, is highly seasonal and generally develops during the cormorant nesting season (Brodeur et al. 2005). These coastal marine systems are extremely productive and have the potential to support superabundant forage fish resources, which in turn support large aggregations of piscivorous seabirds (Kudela et al. 2010, Adams et al. 2012, Zamon et al. 2014). The location of East Sand Island, near the mouth of the estuary, provides excellent access to forage fish resources for colonial seabirds nesting on the island, including both double-crested cormorants (Dorr et al. 2014) and Brandt's cormorants (Wallace and Wallace 1998).

Double-crested cormorants were first detected nesting on East Sand Island in 1989, and the colony grew rapidly over the following decade and a half before leveling off around 2004. In 2014, the colony was estimated at 13,626 nesting pairs, making it the largest known breeding colony for the species at that time. Brandt's cormorants were first detected nesting at East Sand Island on a pile dike off the west end of the island in 1997 (Couch and Lance 2004). In 2006 the Brandt's cormorant colony shifted to East Sand Island itself and pairs began nesting on the ground within the double-crested cormorant colony. The Brandt's cormorant colony grew from fewer than 50 breeding pairs in 2006 to more than 1,600 pairs in 2014, making it one of the largest Brandt's cormorant colonies in Oregon (Naughton et al. 2007, BRNW 2015).

Double-crested cormorants nesting at East Sand Island have previously been documented to forage predominantly in the freshwater and marine mixing zones within the Columbia River estuary (Anderson et al. 2004). Couch and Lance (2004) found that Brandt's cormorants nesting at East Sand Island were opportunistic foragers and that their diet composition was similar to that of double-crested cormorants nesting in the Columbia River estuary. More recent studies, using recoveries of passive integrated transponder (PIT) tags implanted in juvenile salmonids, have found that Brandt's cormorants nesting on East Sand Island consume roughly an order of magnitude fewer salmonids per capita than do double-crested cormorants nesting in the same colony (BRNW 2014). This suggests that Brandt's cormorants are either targeting other forage fish species throughout the estuary, or are foraging predominantly in marine habitats, where a greater diversity of marine forage fish species is available.

Miniaturization of remote-sensing technology has spurred the development of devices that are able to gather a wide array of data on the movements and behaviors of free-ranging animals. Tags that incorporate GPS devices with temperature and depth sensors have been used to describe the three-dimensional foraging behavior of seabirds at very high resolution (Gremillet et al. 1999, Daunt et al. 2003), and to compare foraging habitat use by sympatric seabird species (Kokubun et al. 2010). GPS tags with integrated environmental sensors are valuable tools that can provide insight into foraging habitat use and resource partitioning by cormorant species nesting sympatrically in the Columbia River estuary.

The objective of this study was to determine how, and to what degree, double-crested and Brandt's cormorants nesting at East Sand Island segregate their foraging environments and thereby partition their food resources. We investigated the foraging behavior of breeding adult cormorants by deploying GPS data loggers with integrated temperature and depth sensors. This approach allowed us to examine foraging patterns and habitat selection across the horizontal plane. It also provided the opportunity to examine how these two cormorant species utilize the vertical spatial dimension in order to evaluate how dive behavior or environmental variables within the water column might contribute to resource partitioning. In meeting this objective, we also present the first high-resolution GPS tracking and diving data for either of these two cormorant species.

METHODS

Study Area

East Sand Island (ESI; 46º15’46”N, 123º59’15”W) is located in the lower Columbia River estuary (river kilometer 7), partially straddling the border between Clatsop County, Oregon, and Pacific County, Washington. ESI is a semi-natural low-lying island, about 20 ha in area, that is comprised of mixed dune, forest, shrubland, and rocky habitat types and surrounded by extensive intertidal sand and mudflats. In 2014, an estimated 13,626 pairs of double-crested cormorants and 1,629 pairs of Brandt’s cormorants nested in a large mixed-species colony on the west end of the island (BRNW 2015). ESI is owned and managed by the U.S. Army Corps of Engineers and has been designated as an internationally recognized Important Bird Area by the National Audubon Society and the American Bird Conservancy (NAS 2013).

GPS Tracking and Environmental Data Logging

Brandt’s and double-crested cormorants were captured by hand on their nests at night through removable panels on the sides of above-ground tunnel-blinds (Courtot et al. 2016). Capture was conducted at night to limit disturbance to nearby nesting cormorants and reduce the potential for predation on cormorant eggs or chicks by nest predators (e.g., glaucous-winged/western gulls). Captures were conducted during the late incubation period or midway through the chick-rearing period. This timing increased our chances of capturing adult cormorants that were highly committed to their nesting attempts and reduced the chance of nest abandonment by tagged individuals. We avoided capturing breeding adults with young chicks, which have a limited ability to thermoregulate independent of their parents. Cormorant nests of both species were initiated asynchronously at the East Sand Island colony; thus, there were adults at appropriate stages of the nesting cycle available for capture across much of the breeding season. Capture and tagging began in late May and continued through July. All individuals were weighed (± 50 g) using Pesola® spring scales (5-kg capacity) and breast feather samples were collected for DNA sexing (Avian Biotech International, Tallahassee, Florida). Interspecific and sexual differences in body mass were investigated with nonparametric 2-sample Wilcoxon rank-sum tests due to small sample sizes and potential lack of normality using program R (R Version 3.1.2, www.r-project.org, accessed 18 Jan 2015).

GPS data loggers (GPS-TDlog, Earth & Ocean Technologies, Kiel, Germany) with integrated temperature and pressure sensors were affixed to 24 double-crested cormorants and 18 Brandt's cormorants. Loggers were mounted to baseplates using fabric Tesa® 4651 tape and urethane adhesive (Aquaseal® with Cotol-240™). Baseplates served as attachment platforms for PTFE ribbon harnesses, as described by King et al. (2000). Logger mass was approximately 41 g, including the baseplate and harness, which ranged from 1.5% to 2.3% of the body mass of captured cormorants. Each logger was encased in a streamlined composite housing measuring 55 mm x 31 mm x 20 mm, with a 2-mm diameter flexible external thermistor extending 48 mm posteriorly. Each cormorant was also marked with a field readable alphanumeric plastic leg band, which identified the individual and the species, and a numbered USGS metal leg band. In addition, a small 1-g VHF radio tag (Advanced Telemetry Systems, Isanti, MN) was attached to the central rectrices of each tagged cormorant to aid in relocation and recapture efforts. Finally, the fabric Tesa® tape used to secure tags to the mounting plates was color-coded to aid identification of individuals in the field. Several individuals received an additional 21-g CTD data logger (DST-CTD, Star-Oddi, Gardabaer, Iceland) to collect data for a concurrent study. The combined weight of the GPS and CTD data loggers, attachment materials, VHF tag, and bands was less than 3% of the body mass of every transmitter-equipped cormorant. All animal handling and tagging procedures were approved by the Institutional Animal Care and Use Committee at Oregon State University.

GPS-TDlog tags were programmed to collect GPS data in two phases, normal and active. During normal phase, locations were obtained once every four minutes. The active phase was triggered when a tag detected diving activity (based on pressure; dive deeper than approximately .5 m) and each active phase continued until dive activity had ceased for two minutes. During an active phase, tags were programmed to collect GPS locations either continuously, which resulted in approximately one location per second, or at a 2-second interval, which resulted in approximately one location per five seconds. To conserve battery life, tags were programed to skip obtaining GPS location fixes during dives and to turn off for 15 min when unable to obtain a fix after 5 min of attempts. Temperature and depth sensors (TDRs) sampled either once every second or once every 2 seconds for the duration of the deployment. The tags were reprogrammable, rechargeable, and could be redeployed multiple times. Data were archived during deployments and later downloaded directly from the tag through a PC-cable interface, necessitating recapture of the tagged cormorant in order to retrieve the tag and download the data.

Logger Data Processing

Data collected by TDRs at 1-second intervals were subsampled to match the temporal resolution of the TDR data sampled at 2-second intervals. Pressure data were converted from bars to depth in meters using a conversion factor of 10.06 m per bar. This conversion factor represents a simple compromise between the standard conversion factors for freshwater (10.20 m/bar; Sea-Bird 2002) and saltwater (9.92 m/bar; Saunders 1981), and limited the potential conversion error for depth to less than 1.5% for dives in completely fresh or completely marine water. Depth data were calibrated using zero-offset correction with the package diveMove in program R (diveMove version 1.3.9., github.com/spluque/diveMove, accessed 18 Jan 2016). This process followed the methods of Luque and Fried (2011) for identifying the surface signal and for removing artifacts arising from sensor hysteresis and temporal drift.

Temperature measurements were calibrated to correct for effects of thermal inertia within the temperature sensor. Inspection of depth plots with over-plotted temperature values indicated that observed temperature values at a particular depth consistently differed between descent and ascent phases of a dive. Plots of depth against temperature generally showed two offset depth-temperature relationships, one recorded during the descent, and the other recorded during the ascent. Therefore, calibration was required to remove the error associated with thermal inertia. Following an exploratory analysis of calibration methods, we performed a 0.85-second offset for temperature data, with the value at the offset point computed via monotonic Hermite interpolation (Fritsch and Carlson 1980), at a frequency of 20Hz, within the subsurface portion of each dive. In order to avoid interpolating beyond the range of the data, 0.85 seconds of temperature data were lost at the end of each dive. Hermite interpolation was performed using the function “splinefun” in program R.

We detected unexpected temporal deviations between GPS and sensor data, resulting in a loss of synchrony between GPS locations and corresponding environmental measurements. GPS data appeared to “drift” ahead of environmental sensor data systematically, but at a non-constant rate. This issue was detected by comparison of dive activity with GPS signatures created by normal versus active GPS data acquisition rates. Consequently, all data files were manually synchronized by visually inspecting dive activity, line by line, and adjusting GPS data to match corresponding dive and surface intervals.

GPS loggers cannot obtain location fixes while underwater; therefore, we used simple linear interpolation to estimate dive locations from a single previous and a single subsequent GPS location per dive. Interpolation used the previous and subsequent locations and times, as well as the point in time midway between the dive start and dive end, to geolocate dives. Potential error associated with rapidly moving, or possibly flying, birds was reduced by excluding dives when the previous GPS location was obtained more than 5 minutes before the dive began and the subsequent GPS location was obtained more than 1 minute after the dive ended. Dives were also excluded if the dive location was on land, as defined by a high-water shoreline map based on ESRI satellite imagery from 2013 and 2014. All mapping and geographic analyses were conducted after converting location data to Universal Transverse Mercator (UTM) Zone 10 North projection. To reduce the likelihood of including non-foraging dives, an *a priori* decision was made to exclude from analysis all dives less than 0.5 m deep or lasting 6 seconds or less (Kokubun et al. 2016).

Water depths at foraging dive locations were estimated using a digital elevation model (DEM) with 5-m resolution, compiled from 8 digital bathymetric survey datasets collected between 2004 and 2014 (A. W. Stevens, U.S. Geological Survey, personal communication, January 6, 2016). Source bathymetry data were converted to the land-based North American Vertical Datum of 1988 (NAVD88) and projected in UTM Zone 10 North. Apparent water depths at dive locations, defined as water column depths, were estimated by correcting DEM data to account for tide height and stage by dive location. Tidal corrections were based on the nearest NOAA tide gauges, located at Astoria, OR, Skamokawa, WA, or Toke Point, WA (A. W. Stevens, U.S. Geological Survey, personal communication, January 6, 2016).

Dives were defined as benthic if they traversed at least 90% of the water column, or if the maximum dive depth was within 1 m of water column depth. We then calculated the percentage of dives that were classified as benthic for each individual cormorant. An additional parameter, percentage of the water column traversed during a dive, was defined as the maximum depth of a dive expressed as a percentage of water column depth. For any dive with a maximum dive depth that exceeded the estimated water column depth (possible in areas of high benthic slope, due to imprecision in location estimation), the percentage of the water column traversed was defined as 100%.

Foraging Areas

Estimates of foraging area utilization were generated for each cormorant species from geolocated dive records. Kernel density estimates (KDE) were generated in ArcMap 10.2.2 using methods developed by Macleod (2014). These methods utilized the “Kernel Interpolation with

Barriers” tool in the Spatial Analyst toolbox to generate a kernel density estimate while incorporating complex boundaries. This methodology allowed us to estimate utilization of foraging areas within a complex estuarine environment, while excluding unsuitable foraging habitat, such as islands, jetties, and other landmasses. Dive density was estimated at a grid size of 100 m × 100 m, which provided ample resolution to account for narrow water channels within the study area. The kernel function used a Gaussian distribution with the polynomial order set to zero. We used a fixed bandwidth that was selected ad hoc, following methods of Macleod (2014), with subsequent visual inspection (Wand and Jones 1994). Overall foraging areas and core foraging areas for each species were estimated using the 95% and 50% kernel contour lines, respectively (Wood et al. 2000, Hamer et al. 2007, Kokubun et al. 2010). Contours were determined using the genmcp tool in the program Geospatial Modeling Environment (Version 0.7.3.0 www.spatialecology.com/gme, accessed 15 Jan 2016). To evaluate foraging habitat diversity we compared overall and core foraging areas to broad scale (static) salinity zones adapted from Simenstad et al. (1990) and Anderson et al. (2004) (Figure 2.1).

Dive Parameter Comparisons

Cormorant dive data were analyzed using generalized linear models (GLMs) or generalized linear mixed models (GLMMs) to determine the effect of species on habitat use. Our modeling approach was closely based on the methods of Kokubun et al. (2010, 2016). GLMs accommodate non-normally distributed data and were used to compare parameters that were measured once per individual, such as the proportion of benthic dives (Venables and Dichmont 2004, Kokubun et al. 2010). We used a binomial distribution for all GLMs and used a Wald test to estimate significance.

GLMMs are related to GLMs, but allow for the additional incorporation and analysis of parameters that form natural groups or hierarchical datasets (Venables and Dichmont 2004). We used GLMMs to examine the effect of species on parameters that were measured multiple times per individual through repeated sampling, such as dive depth, water depth, or water temperature. We used a gamma distribution for all GLMMs to account for skewedness, and individual bird identity was defined as a random effect. Significance of the fixed effect, species, on dependent variables, such as dive depth or temperature, were tested by comparing models with and without the species term. Comparisons were made using likelihood ratio tests (LRTs; Faraway 2006, Kokubun et al. 2010). All models were fit using the “lme4” package (Bates et al. 2015) and LRTs were performed using the “anova” function, both in program R.

RESULTS

Capture, Recapture, and Data Recovery

We recaptured and retrieved GPS-TDlog data loggers from 21 of 24 double-crested cormorants (88%) and 18 of 20 Brandt’s cormorants (90%) on which data loggers had been deployed. We were unable to relocate or recapture five tagged individuals, two data loggers failed to collect or record any data, and five data loggers failed to record environmental sensor data. Individual cormorants were tracked for between three and five days, and the median tracking period was slightly more than four days. We chose to analyze data only from loggers that successfully recorded both GPS and environmental data (n = 17 double-crested cormorants, n = 15 Brandt’s cormorants). Our final sample included 9 males and 8 females for double-crested cormorants, and 10 males and 4 females for Brandt's cormorants, plus one Brandt's cormorant whose gender was undetermined.

The body mass of double-crested cormorants ranged from 1,850 g to 2,550 g, with a mean of 2,272 g (n = 17), while that of Brandt's cormorants ranged from 1,850 g to 2,700 g, with a mean of 2,347 g (n = 15; Table 2.1). The body mass of female double-crested cormorants ranged from 1,850 g to 2,350 g, with a mean of 2,164 g (n = 8), and the body mass of male double-crested cormorants ranged from 2,200 g to 2,550 g, with a mean of 2,356 g (n = 9; Table 2.1). The body mass of female Brandt's cormorants ranged from 1,850 g to 2,050 g, with a mean of 1,944 g (n = 4), and the body mass of male Brandt's cormorants ranged from 2,350 g to 2,700 g, with a mean of 2,498 g (n = 10; Table 2.1). Mean body mass of male Brandt's cormorants was significantly greater than that of female Brandt's cormorants (Wilcoxon rank-sum test, *P*-value = 0.006). Also, body mass of male double-crested cormorants was significantly greater than that of female double-crested cormorants (Wilcoxon rank-sum test, *P*-value = 0.01).

Logger Data Processing

We identified a total of 25,794 dives by double-crested cormorants and a total of 11,536 dives by Brandt's cormorants in the retrieved logger data (Figure 2.2). Loggers from 17 double-crested cormorants recorded data from between 435 and 2,267 dives per individual, with a median of 1,627 dives. Loggers from 15 Brandt's cormorants recorded data from 511 to 1,040 dives per individual, with a median of 761 dives. The maximum recorded dive depths for individual double-crested cormorants ranged from as little as 5.7 m to as much as 20.6 m, with a median maximum dive depth per individual of 13.9 m. The maximum recorded dive depths for individual Brandt's cormorants ranged from as little as 18.5 m to as much as 50.8 m, with a median maximum dive depth per individual of 29.7 m.

Foraging Area Comparisons

Double-crested cormorants foraged across a broader area and utilized a wider range of marine and estuarine habitat types compared to Brandt's cormorants. Double-crested cormorants commuted up to 40 km from their nest site to the north, south, and east to forage in freshwater rivers and sloughs, mixed-water estuaries in the Columbia River and Willapa Bay, marine waters close to the mouth of the Columbia River, and nearshore marine habitats north and south of the Columbia River mouth (Figure 2.3a; Table 2.2). Brandt's cormorants, in contrast, generally utilized foraging habitats closer to the breeding colony and foraged predominantly in marine waters close to the Columbia River mouth. Three individuals, however, commuted nearly 40 km to the south of the colony to forage near Tillamook Head, matching the maximum foraging distance from the breeding colony observed for double-crested cormorants. Additionally, the core foraging area for Brandt's cormorants was locally clustered around three prominent roost sites at the mouth of the Columbia River: the tip of the south jetty, South Head at Cape Disappointment, and the pile dike at Sand Island (west of ESI). The foraging range of Brandt's cormorants from their nest site extended slightly farther offshore than that of double-crested cormorants (Figure 2.3b).

The overall area used for foraging by the tagged sample of double-crested cormorants nesting on East Sand Island (the area within the 95% kernel density contour) was 451 km^2, more than four times greater than that of the tagged sample of Brandt's cormorants (108 km^2). Similarly, the core foraging area used by the sample of double-crested cormorants (the area within the 50%

kernel density contour) was 197 km^2, compared to 32 km^2 for the sample of Brandt's cormorants. Most of the overall foraging area and core foraging area used by the sample of Brandt's cormorants, 59.1% and 89.2%, respectively, overlapped with those of the sample of double-crested cormorants. In contrast, the overall foraging area and core foraging area of the sample of double-crested cormorants only overlapped with those of the sample of Brandt's cormorants by 25.8% and 26.5%, respectively (Table 2.3; Figure 2.5). Overall, double-crested cormorants foraged across a much greater areal extent than Brandt's cormorants.

Double-crested cormorants were tracked commuting directly to and from Willapa Bay, approximately 10 km north of East Sand Island, by crossing the approximately 5 km-wide strip of land separating Willapa Bay from the Columbia River estuary. Without crossing land, Willapa Bay is greater than 50 km from East Sand Island. Double-crested cormorants were also observed crossing the Long Beach Peninsula between Willapa Bay and coastal marine habitat north of the Columbia River mouth, and crossing Clatsop Spit between the Columbia River estuary and coastal marine habitat south of the Columbia River mouth. These crossings significantly shortened the commuting distances between these habitats, relative to a strictly over-water route (discounting jetties). In contrast, we did not track any tagged Brandt's cormorants commuting over land.

Dive Parameter Comparisons

Brandt's cormorants dove significantly deeper, dove in deeper locations, and made longer dives than double-crested cormorants (Table 2.4). The maximum recorded dive depth for a Brandt's cormorant was more than twice that of a double-crested cormorant, and the median maximum dive depth per individual Brandt's cormorant was also more than twice that of double-crested cormorants. Double-crested cormorants dove into significantly warmer water than did Brandt's cormorants (dive bottom temperature, Table 2.4). Warmer water temperatures correlate with lower salinity in Columbia River estuary system during the summer. We did not detect differences between the two cormorant species in the percentage of benthic dives or the percentage of the water column traversed during a foraging dive (Table 2.4).

For dives occurring within the area of overlap between the 95% kernel density estimates of the two cormorant species, we still found that Brandt's cormorants dove significantly deeper, selected deeper dive locations, and made longer dives compared to double-crested cormorants (Table 2.4). There was, however, no interspecific difference in temperature at the bottom of the dive in areas of overlap between the 95% kernel density estimates. Also, Brandt's cormorants traversed a greater proportion of the water column than did double-crested cormorants in areas of overlap, suggesting that in areas where both species foraged, Brandt's cormorants were diving closer to the bottom (Table 2.4).

DISCUSSION

Segregation in foraging habitat

This is the first study to use a combination of GPS and temperature-depth data loggers to describe high resolution foraging distributions and habitat of sympatrically breeding double-crested and Brandt's cormorants. This robust data set allowed us to not only describe and compare species-specific foraging areas across the geographic plane, it also allowed us to detect subtle interspecific differences in vertical habitat use within the water column. Our results revealed that double-crested cormorants and Brandt’s cormorants, breeding at a mixed-species colony on East Sand Island, selected and exploited foraging habitat differently. While the overall and core foraging areas of both species overlapped substantially double-crested cormorants foraged over a much larger area and utilized a much wider variety of habitat types than did Brandt’s cormorants, which foraged almost exclusively in marine habitat. Double-crested cormorants also dove into significantly warmer water than Brandt’s cormorants (Table 2.4), which reflects the greater use of freshwater habitats by double-crested cormorants. Moreover, in areas where the two species overlapped, they selected different microhabitats for foraging.

Previous studies of sympatric seabirds have identified several behavioral mechanisms for partitioning of forage resources, including geographic segregation of foraging areas and interspecific differences in dive behavior and water column use (Kokubun et al. 2010, Miller et al. 2010, Navarro et al. 2013, Kokubun et al. 2016). Such horizontal and vertical segregation is often attributed to interspecific competition, reflecting the hypothesis that competition drives divergence in species’ foraging ecology and prey preferences (Trivelpiece et al. 1987, Kokubun et al. 2010). While avoidance of direct competition for food resources may partially explain the interspecific differences in foraging patterns that we observed, we also observed a substantial amount of overlap in foraging habitat, both in the horizontal and vertical planes. The foraging habitat overlap was not associated with any apparent competition-induced reproductive penalty, however; annual productivity for both species at ESI was often well above the average reported for each species, with the primary limiting factor being top-down effects (BRNW 2014, 2015). This suggests that forage fish resources near the mouth of the Columbia River were sufficiently abundant so that large populations of both cormorant species could utilize largely overlapping foraging habitats.

Our observations are consistent with the alternative hypothesis that interspecific differences in foraging behavior are primarily due to previously evolved foraging strategies and physiological adaptations for diving in these two cormorant species.

Species-specific foraging patterns: double-crested cormorants

Our results demonstrated that double-crested cormorants nesting at East Sand Island utilized more freshwater and mixed estuarine habitats and selected shallower locations to dive relative to Brandt's cormorants. This is consistent with prior studies that found double-crested cormorants preferentially select shallower foraging habitat (Coleman et al. 2005, Dorr et al. 2014) and are more likely to forage in estuaries than other cormorant species along the West Coast of the U.S. (Ainley et al. 1981). Across their range, double-crested cormorants exploit many shallow water habitats where the capacity for deep dives may confer little or no advantage while foraging for fish (Dorr et al. 2014). Consequently, behavioral and physiological traits that support deep diving may not be subject to strong selection pressure in double-crested cormorants throughout much of their range.

Previous studies of the foraging patterns of double-crested cormorants nesting at East Sand Island reported that they disproportionately utilized freshwater habitats early in the nesting season, and then shifted more to marine habitats later in the nesting season (Anderson et al. 2004, Lyons et al. 2007). This mid-nesting season shift in foraging distribution corresponds with the seasonal decline in abundance of out-migrating juvenile salmonids in the Columbia River estuary (Lyons et al. 2007, Weitkamp et al. 2012), and also corresponds with the seasonal decline in juvenile salmonids in the diet of double-crested cormorants nesting on East Sand Island (Lyons 2010).

Marine forage fish comprise the majority of the diet of East Sand Island double-crested cormorants during the latter part of the nesting season (Collis et al. 2002, Lyons 2010). The freshwater foraging distribution of double-crested cormorants observed in our study is consistent with previous studies in the Columbia River estuary, and suggests that double-crested cormorants nesting at this colony exploit seasonally abundant out-migrating juvenile salmonids as they pass through the estuary (Anderson et al. 2004, Lyons et al. 2007).

Some double-crested cormorants that nest on East Sand Island visit interior rivers and lakes during the non-breeding season, and follow inland migration routes to reach wintering areas (Courtot et al. 2012, Chapter 3). Therefore, at least a portion of the double-crested cormorants nesting on East Sand Island are accustomed to travelling over land. This may explain our observations of some of the tagged sample of double-crested cormorants commuting over land to more directly access foraging habitat, such as Willapa Bay, or to shorten commuting routes between estuarine and marine areas. In contrast, the strictly marine Brandt’s cormorant was not detected crossing land masses, indicating consistency between movement patterns across the annual cycle and the utilization patterns of foraging habitats near East Sand Island.

Species-specific foraging patterns: Brandt’s cormorants

Previous research on the feeding ecology of Brandt’s and double-crested cormorants nesting in a marine setting along the Pacific Coast found almost no dietary overlap between the two species (Ainley et al. 1981). Couch and Lance (2004), however, found that forage species present in the diet of Brandt’s cormorants nesting on East Sand Island almost completely overlapped with those present in the diet of double-crested cormorants (relative proportions of prey in the diet of each species could not be directly compared due to methodological differences, however). These prior diet results from East Sand Island are consistent with the foraging patterns observed in this study, where the foraging area of Brandt's cormorants mostly overlapped with that of double-crested cormorants. Subsequent research using juvenile salmonid PIT tags recovered from the East Sand Island cormorant colony indicated that Brandt's cormorants consumed approximately an order of magnitude fewer salmonids per individual compared to double-crested cormorants (BRNW 2014). This is consistent with our findings that Brandt's cormorants did not forage in freshwater estuarine habitats where they would be more likely to encounter juvenile salmonids relative to other potential prey types. Instead, they foraged overwhelmingly in marine habitats, tended to select deeper dive locations, and utilized a deeper portion of the water column compared with double-crested cormorants, all behavioral traits that would be expected to result in relatively fewer encounters with juvenile salmonids.

Our tracking data suggest that the location of suitable roost sites may play an important role in use of foraging habitats by Brandt's cormorants. Brandt's cormorants usually roost on rocky islets or coastal headlands (Wallace and Wallace 1998). Three tagged Brandt's cormorants made foraging trips to Tillamook Head, a prominent headland 35 km south of East Sand Island with several surrounding rocky islets. In addition to foraging, all of the Brandt's cormorants that visited this area spent time roosting on at least one of three roost sites. This area was an exclave of their overall foraging area, with the coastal marine habitat between the mouth of the Columbia River and Tillamook Head not utilized for foraging. The coastal habitat adjacent to the mouth of the Columbia River, both to the north and south, is characterized by wide sandy beaches with minimal structure or vertical relief. To the north, the closest coastal rocky feature is the jetty at Grays

Harbor, Washington, about 80 km from East Sand Island, and the closest feature to the south is Tillamook Head. Adaptations that facilitate deep diving by Brandt's cormorants, such as wettable plumage and high wing-loading, represent physiological trade-offs that favor diving efficiency over flight efficiency. Brandt's cormorants may select foraging habitats adjacent to roost sites to facilitate drying, preening, and resting during or after foraging bouts, and prior to the return commute to the breeding colony. This is supported by our findings that the core foraging areas of Brandt's cormorants were clustered around prominent roost sites near the mouth of the Columbia River, and when Brandt's cormorants did venture away from the mouth of the Columbia River, they skipped over foraging habitat adjacent to wide sand beaches to forage near and roost at Tillamook Head.

Conclusions

Segregation among sympatric species may not be solely a function of proximate competition for limiting resources, but instead a product of historical evolutionary divergence. Species-specific evolutionary constraints were likely a causal mechanism for the partitioning of foraging habitat observed in this study. Furthermore, there may be little overlap in diet when there is an abundant prey resource that one species is better adapted to exploit, as appeared to be the case for double-crested cormorants preying on juvenile salmonids in the Columbia River estuary. It is also likely that superabundant forage fish resources at the mouth of the Columbia River have allowed a large colony of Brandt's cormorants to form on an island where they share the majority of their foraging habitat with a similar-sized and far more numerous congener.

Our interspecific comparison of the foraging ecology of double-crested cormorants and Brandt's cormorants leads to the following conclusions: (1) Brandt's cormorants foraged almost exclusively in marine habitats near the mouth of the Columbia River, while double-crested cormorants foraged over a much larger area with a much broader array of aquatic habitats, including extensive use of freshwater and mixed estuarine habitats; (2) in areas of interspecific overlap in foraging habitat, Brandt's cormorants utilized deeper locations and a more benthic portion of the water column than did double-crested cormorants; (3) species-specific patterns of habitat utilization and foraging behavior likely reflect past evolutionary divergence and resultant interspecific differences in behavioral and physiological adaptations, rather than partitioning of limited prey resources to avoid interspecific competition within commuting distance of the breeding colony; and (4) the degree of interspecific overlap in foraging areas, particularly for Brandt's cormorants, suggests that superabundant prey resources allow these two large and productive cormorant colonies to coexist on a single island near the mouth of the Columbia River.

LITERATURE CITED

Adams, J., C. MacLeod, R. M. Suryan, K. D. Hyrenbach, and J. T. Harvey. 2012. Summer-time use of west coast US national marine sanctuaries by migrating sooty shearwaters (*Puffinus griseus*). Biological Conservation: Seabirds and Marine Protected Areas Planning 156:105–116.

Ainley, D. G., D. W. Anderson, and P. R. Kelly. 1981. Feeding ecology of marine cormorants in southwestern North America. Condor 83:120–131.

Ainley, D. G. 1984. Cormorants. Pages 92-101 *in* Seabirds of the eastern North Pacific and Arctic waters. (Haley, D., ed.) Pacific Search Press, Seattle, Washington, USA.

Anderson, C. D., D. D. Roby, and K. Collis. 2004. Foraging patterns of male and female double-crested cormorants nesting in the Columbia River estuary. Canadian Journal of Zoology 82:541–554.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-48.

Bottom, D. L., and K. K. Jones. 1990. Species composition, distribution, and invertebrate prey of fish assemblages in the Columbia River estuary. Progress in Oceanography 25:243–270.

Bird Research Northwest [BRNW]. 2014. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River, Final 2013 Annual Report. Bonneville Power Administration, U.S. Army Corps of Engineers, and Grant County Public Utility District, Portland, Oregon, USA. <www.birdresearchnw.org>. Accessed 18 Jan 2017.

Bird Research Northwest [BRNW]. 2015. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River, Final 2014 Annual Report. Bonneville Power Administration, U.S. Army Corps of Engineers, and Grant County Public Utility District, Portland, Oregon, USA. <www.birdresearchnw.org>. Accessed 18 Jan 2017.

Brodeur, R. D., J. P. Fisher, R. L. Emmett, C. A. Morgan, and E. Casillas. 2005. Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. Marine Ecology Progress Series 298:41-57.

Coleman, J. T. H., M. E. Richmond, L. G. Rudstam, and P. M. Mattison. 2005. Foraging location and site fidelity of the Double-Crested Cormorant on Oneida Lake, New York. Waterbirds 28:498–510.

Collis, K., D. D. Roby, D. P. Craig, S. Adamany, J. Y. Adkins, and D. E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: Implications for losses of juvenile salmonids to avian predation. Transactions of the American Fisheries Society 131:537–550.

Couch, S. L. L., and M. M. Lance. 2004. Diet composition and breeding success of Brandt's cormorants in the Columbia River estuary. Northwestern Naturalist 85:62–66.

Courtot, K. N., D. D. Roby, J. Y. Adkins, D. E. Lyons, D. T. King, and R. S. Larsen. 2012. Colony connectivity of Pacific Coast double-crested cormorants based on post-breeding dispersal from the region's largest colony. Journal of Wildlife Management 76:1462–1471.

Courtot, K. N., D. D. Roby, L. H. Kerr, D. E. Lyons, and J. Y. Adkins. 2016. A low-disturbance capture technique for ground-nesting double-crested cormorants (*Phalacrocorax auritus*). Waterbirds 3:193–198.

Daunt, F., G. Peters, B. Scott, D. Gremillet, and S. Wanless. 2003. Rapid-response recorders reveal interplay between marine physics and seabird behaviour. Marine Ecology Progress Series 255:283–288.

Dorr, B. S., J. J. Hatch, and D. V. Weseloh. 2014. Double-crested cormorant (*Phalacrocorax auritus*). The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://birdsna.org/Species-Account/bna/species/doccor>. Accessed 18 Jan 2017.

Faraway, J. J. 2006. Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Chapman & Hall/CRC Press, Boca Raton, Florida, USA.

Fritsch, F. N., and R. E. Carlson. 1980. Monotone piecewise cubic interpolation. SIAM Journal on Numerical Analysis 17:238–246.

Gremillet, D., R. P. Wilson, S. Storch, and Y. Gary. 1999. Three-dimensional space utilization by a marine predator. Marine Ecology Progress Series 183:263–273.

Hamer, K. C., E. M. Humphreys, S. Garthe, J. Hennicke, G. Peters, D. Gremillet, R. A. Phillips, M. P. Harris, and S. Wanless. 2007. Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. Marine Ecology Progress Series 338:295–305.

Holbrook, S. J., and R. J. Schmitt. 1989. Resource overlap, prey dynamics, and the strength of competition. Ecology 70:1943–1953.

Huyer, A. 1983. Coastal upwelling in the California Current System. Progress in Oceanography 12:259–284.

King, D. T., M. E. Tobin, and M. Bur. 2000. Capture and telemetry techniques for double-crested cormorants (*Phalocrocorax auritus*). Pages 54-57 *in* Proceedings of the 19th Vertebrate Pest Conference, University of California, Davis, USA.

Kokubun, N., A. Takahashi, Y. Mori, S. Watanabe, and H.-C. Shin. 2010. Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. Marine Biology 157:811–825.

Kokubun, N., T. Yamamoto, N. Sato, Y. Watanuki, A. Will, A. S. Kitaysky, and A. Takahashi. 2016. Foraging segregation of two congeneric diving seabird species breeding on St. George Island, Bering Sea. Biogeosciences 13:2579–2591.

Kudela, R. M., A. R. Horner-Devine, N. S. Banas, B. M. Hickey, T. D. Peterson, R. M. McCabe, E. J. Lessard, et al. 2010. Multiple trophic levels fueled by recirculation in the Columbia River plume. Geophysical Research Letters 37:L18607.

Luque, S. P., and R. Fried. 2011. Recursive filtering for zero offset correction of diving depth time series with GNU R Package diveMove. PLoS ONE 6:e15850.

Lyons, D. E. 2010. Bioenergetics-based predator-prey relationships between piscivorous birds and juvenile salmonids in the Columbia River estuary. Dissertation, Oregon State University, Corvallis, Oregon, USA.

Lyons, D. E., D. D. Roby, and K. Collis. 2007. Foraging patterns of Caspian terns and double-crested cormorants in the Columbia River estuary. Northwest Science 81:91–103.

MacLeod, C. D. 2014. An introduction to using GIS in marine biology: supplementary workbook four: Investigating home ranges of individual animals. Pictish Beast Publications, Glasgow, U.K.

Miller, A. K., M. A. Kappes, S. G. Trivelpiece, and W. Z. Trivelpiece. 2010. Foraging-niche separation of breeding gentoo and chinstrap penguins, South Shetland Islands, Antarctica. Condor 112:683–695.

National Audubon Society [NAS]. 2013. Important Bird Areas in the U.S., East Sand Island. National Audubon Society, Manhattan, New York, USA. <netapp.audubon.org/IBA/Reports/3604/>. Accessed 18 Jan 2017.

Naughton, M., D. S. Pitkin, R. W. Lowe, K. J. So, and C. S. Strong. 2007. Catalog of Oregon Seabird Colonies. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Washington, D.C., USA. <http://www.fws.gov/uploadedFiles/Catalog_of_Oregon_Seabird_Colonies_1-TOC.pdf>. Accessed 18 Jan 2017.

Navarro, J., S. C. Votier, J. Aguzzi, J. J. Chiesa, M. G. Forero, and R. A. Phillips. 2013. Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. PLoS ONE 8:e62897.

Saunders, P. M. 1981. Practical conversion of pressure to depth. Journal of Physical Oceanography 11:573–574.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369–404.

Sea-Bird Electronics, Inc [Sea-Bird]. 2002. Application note no. 69, conversion of pressure to depth. Sea-Bird Electronics Inc., Bellevue, Washington, USA. <http://www.seabird.com/sites/default/files/documents/appnote69.pdf.>. Accessed 18 Jan 2017.

Simenstad, C. A., L. F. Small, C. D. McIntire, D. A. Jay, and C. Sherwood. 1990. Columbia River estuary studies: an introduction to the estuary, a brief history, and prior studies. Progress in Oceanography 25:1-13.

Trivelpiece, W. Z., S. G. Trivelpiece, and N. J. Volkman. 1987. Ecological segregation of Adelie, gentoo, and chinstrap penguins at King George Island, Antarctica. Ecology 68:351–361.

Venables, W. N., and C. M. Dichmont. 2004. GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fisheries Research 70:319–337.

Wallace, E. A. H., and G. E. Wallace. 1998. Brandt’s cormorant (*Phalacrocorax penicillatus*). The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://birdsna.org/Species-Account/bna/species/doccor>. Accessed 18 Jan 2017.

Wand, M. P., and M. C. Jones. 1994. Kernel smoothing. Chapman & Hall/CRC Press, Boca Raton, Florida, USA.

Weitkamp, L. A., P. J. Bentley, and M. N. C. Litz. 2012. Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. Fishery Bulletin 110:426–450.

Wood, A. G., B. Naef-Daenzer, P. A. Prince, and J. P. Croxall. 2000. Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. Journal of Avian Biology 31:278–286.

Wright, S. K., D. D. Roby, and R. G. Anthony. 2007. Responses of California brown pelicans to disturbances at a large Oregon roost. Waterbirds 30:479-487.

Zamon, J. E., E. M. Phillips, and T. J. Guy. 2014. Marine bird aggregations associated with the tidally-driven plume and plume fronts of the Columbia River. Deep Sea Research II: Topical Studies in Oceanography, Fronts, Fish and Top Predators 107:85–95.

Table 2.1. Body mass (grams) of double-crested cormorants and Brandt's cormorants nesting on East Sand Island in the Columbia River estuary and used in this study of foraging behavior.

	Double-crested cormorants			Brandt's cormorants			
	All	Female	Male	All	Female	Male	Unknown
Maximum	2550	2350	2550	2700	2050	2700	2450
Minimum	1850	1850	2200	1850	1850	2350	2450
Mean	2272	2164	2356	2347	1944	2498	2450
St. Dev.	164	163	113	278	83	138	2450
n	17	8	9	15	4	10	1

Table 2.2. Estimates of foraging areas used by double-crested cormorants (n = 17) and Brandt's cormorants (n = 15) nesting on East Sand Island in the Columbia river estuary and overlap with broad habitat types, as determined by fixed kernel density (KDE) interpolation of dive locations.

		Double-crested cormorants		Brandt's cormorants	
	Habitat (salinity zone)	Area (km^2)	% Overlap	Area (km^2)	% Overlap
Overall foraging area (95% KDE)	Coastal marine	99.9	22%	125.4	63.6%
	Estuarine marine	89.1	20%	71.3	36.2%
	Estuarine mixing	86.0	19%	0.4	0.2%
	Estuarine freshwater	117.6	26%	0.0	0%
	Willapa Bay	58.8	13%	0.0	0%
Core foraging area (50% KDE)	Coastal marine	17.6	16.3%	7.7	24.0%
	Estuarine marine	55.4	51.3%	24.4	76.0%
	Estuarine mixing	12.6	11.6%	0.0	0%
	Estuarine freshwater	19.1	17.7%	0.0	0%
	Willapa Bay	3.3	3.1%	0.0	0%

Table 2.3. Area of foraging habitat used by double-crested and Brandt's cormorants and area of overlap between species in foraging habitat, as determined by fixed kernel density interpolation of dive locations.

		Double-crested cormorants		Brandt's cormorants	
Foraging Area	Overlap Area (km^2)	Area (km^2)	% Overlap	Area (km^2)	% Overlap
95% KDE	116.5	451.3	26%	197.1	59%
50% KDE	28.7	108.1	27%	32.1	89%

Table 2.4. Comparison of diving parameters between double-crested cormorants and Brandt's cormorants (means ± SD). Model results for all dives and for dives within the area of 95% overlap in foraging areas for the two species are presented separately. Abbreviations for statistical models are GLM (generalized linear model) and GLMM (generalized linear mixed model) and for significance tests are LRT (likelihood ratio test) and W (Wald test). Model distributions are abbreviated (G) for gamma and (B) for binomial. Asterisks are used to denote significant interspecific differences.

	Double-crested	Brandt's	Model used	Statistic	*P*-value
All Dives					
n	17 birds	15 birds			
Dive depth (m)	3.11 ± 2.60	7.94 ± 5.97	GLMM (G) & LRT	$\chi^2 = 39.6$	<0.001*
Dive duration (s)	17.10 ± 7.97	28.72 ± 17.02	GLMM (G) & LRT	$\chi^2 = 36.08$	<0.001*
Dive bottom temp	15.52 ± 3.70	11.95 ± 2.68	GLMM (G) & LRT	$\chi^2 = 18.54$	<0.001*
Water column depth (m)	6.44 ± 5.54	12.57 ± 7.11	GLMM (G) & LRT	$\chi^2 = 22.81$	<0.001*
Percent of water column traversed (%)	70.06 ± 28.17	71.90 ± 29.04	GLMM (G) & LRT	$\chi^2 = 0.83$	0.361
Percent of benthic dives (%)	52.46 ± 18.13	47.42 ± 13.53	GLM (B) & W	$z = 0.29$	0.776
Dives in area of 95% KDE overlap					
n	17 birds	15 birds			
Dive depth (m)	3.68 ± 2.79	7.26 ± 4.72	GLMM (G) & LRT	$\chi^2 = 33.3$	<0.001*
Dive duration (s)	17.17 ± 8.12	26.98 ± 13.70	GLMM (G) & LRT	$\chi^2 = 29.6$	<0.001*
Dive bottom temp	12.97 ± 2.80	12.21 ± 2.64	GLMM (G) & LRT	$\chi^2 = 1.2$	0.272
Water column depth (m)	9.43 ± 6.62	11.86 ± 6.36	GLMM (G) & LRT	$\chi^2 = 13.07$	<0.001*
Percent of water column traversed (%)	58.67 ± 31.12	70.95 ± 28.33	GLMM (G) & LRT	$\chi^2 = 4.36$	0.037*
Percent of benthic dives (%)	39.16 ± 19.69	43.34 ± 14.48	GLM (B) & W	$z = 0.24$	0.810

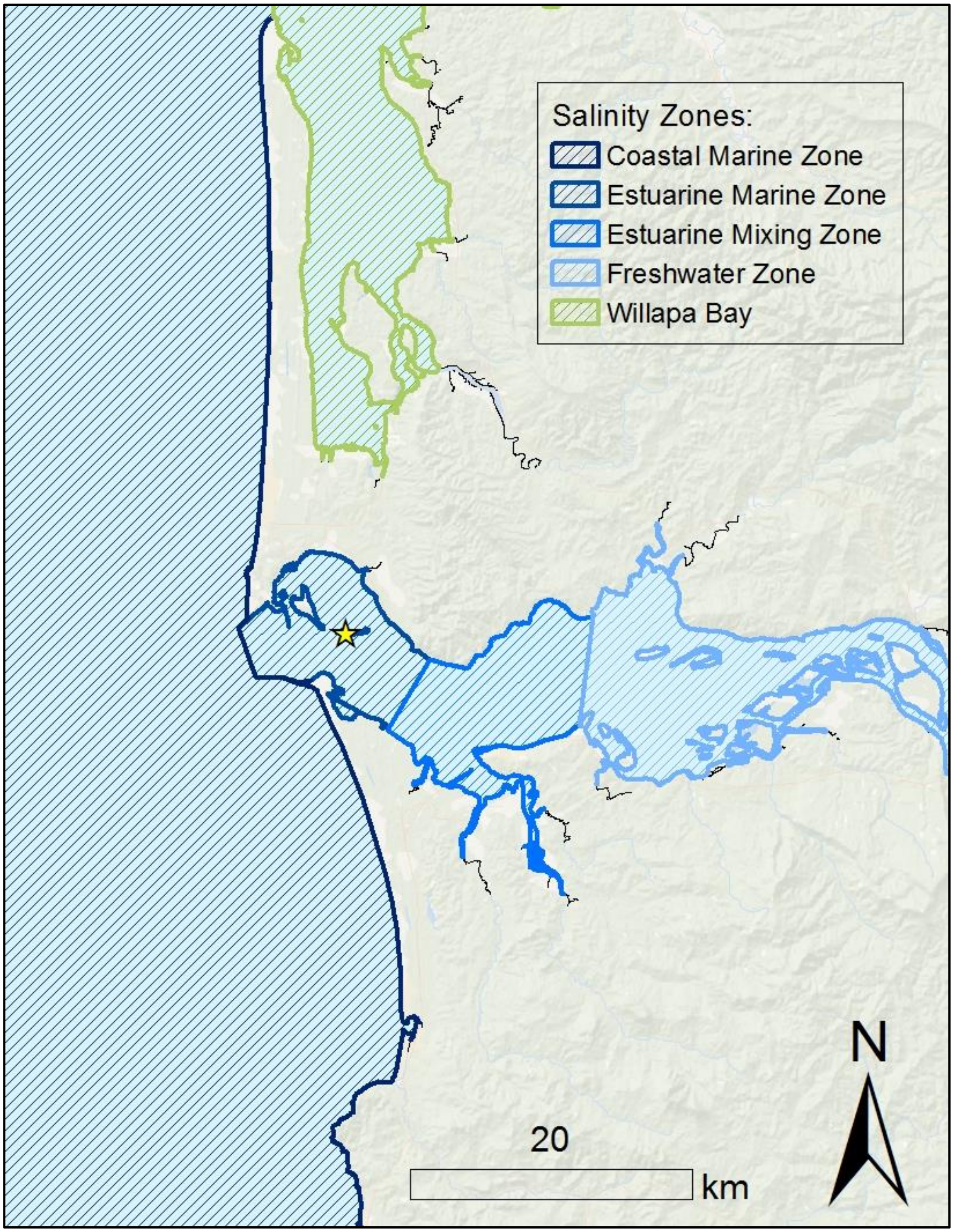

Figure 2.1. Map of the study area showing major foraging habitats for cormorants nesting on East Sand Island in the Columbia River estuary, based on salinity zones and adapted from Simenstad et al. (1990) as modified by Anderson et al. (2004). The location of East Sand Island is depicted with the star.

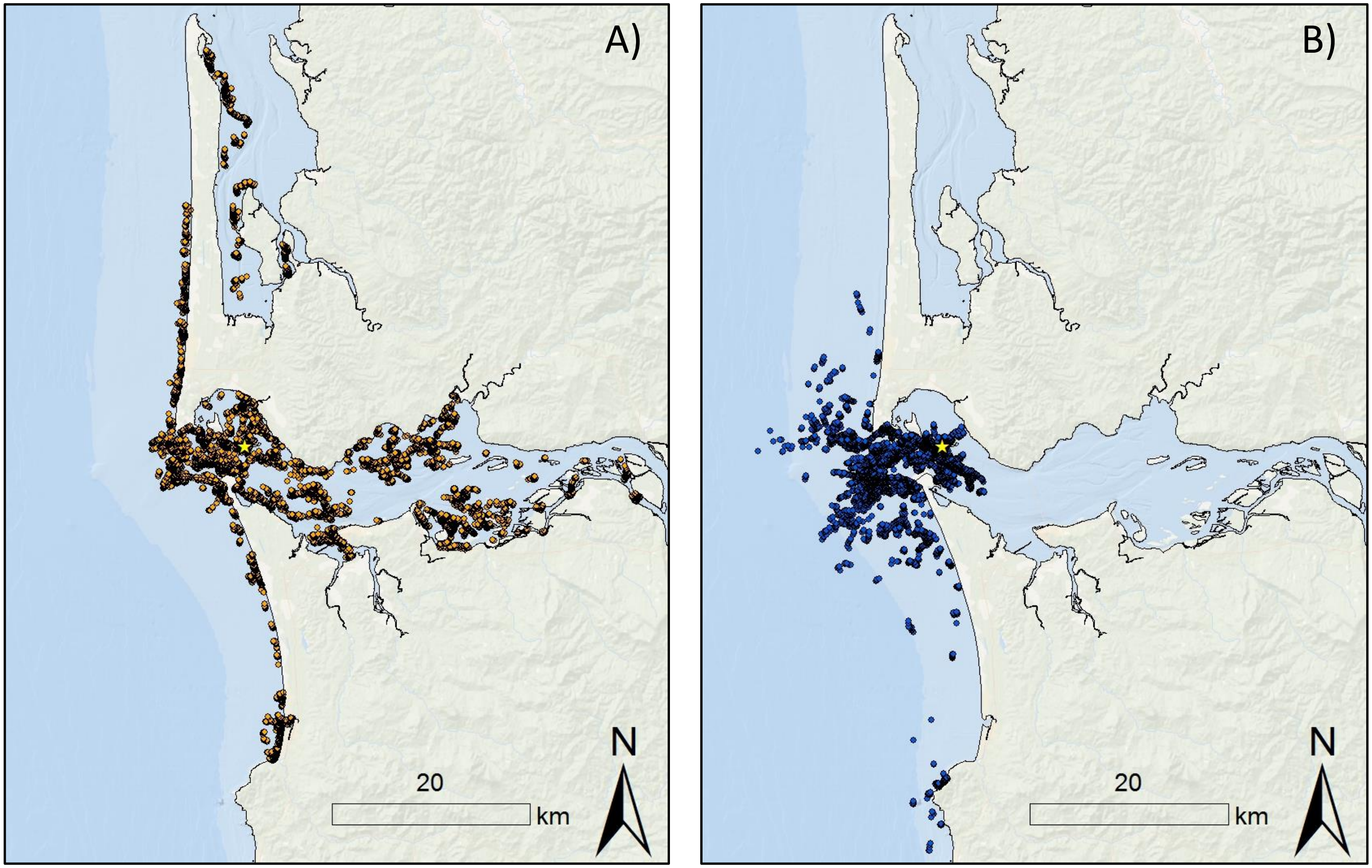

Figure 2.2. All dive locations recorded for double-crested cormorants (A; n = 17 individuals) and Brandt's cormorants (B; n = 15 individuals) that were GPS-tagged at the breeding colony on East Sand Island (indicated by the star) in the Columbia River estuary.

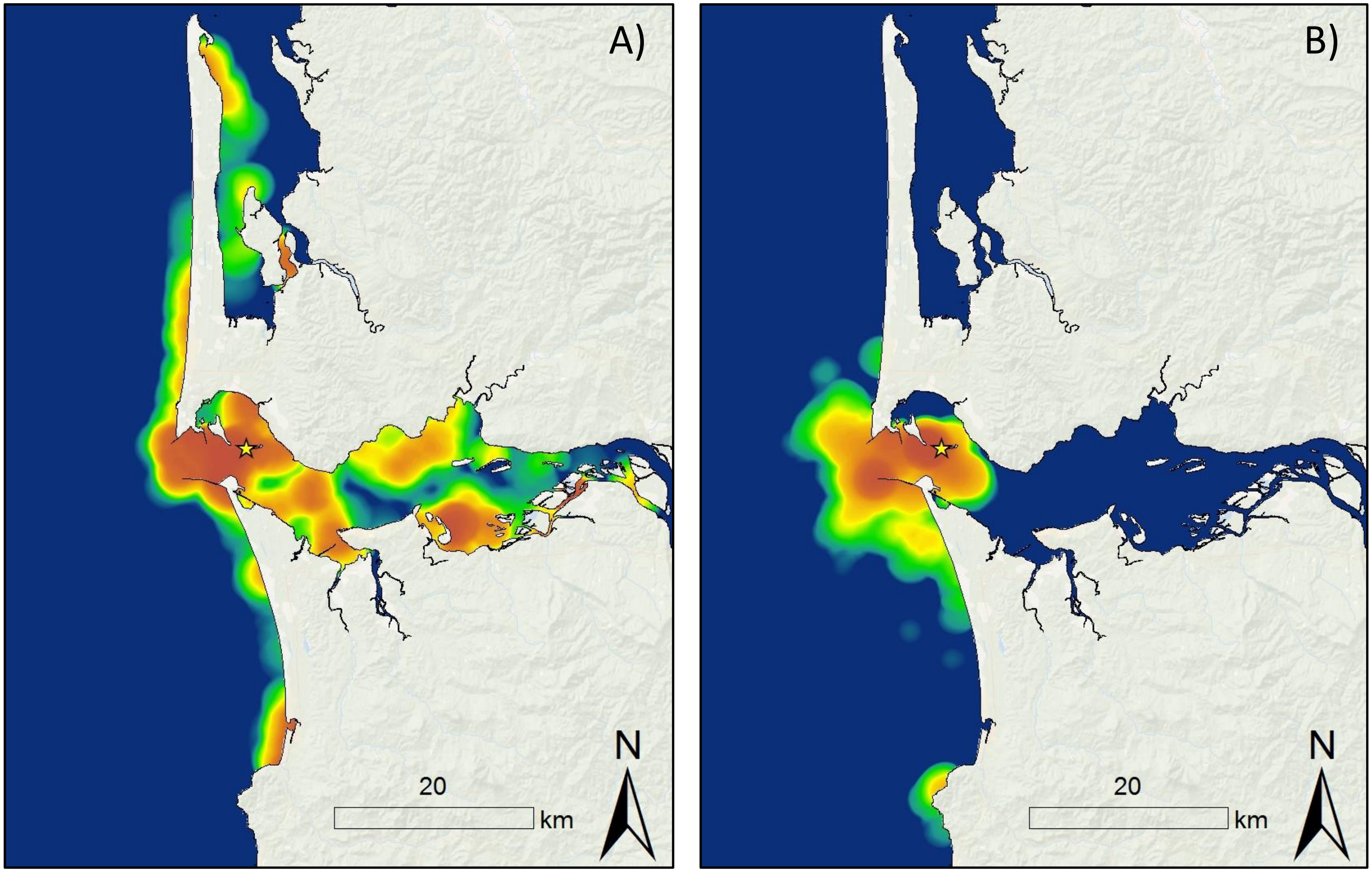

Figure 2.3. Foraging areas used by double-crested cormorants (A; n = 17 individuals) and Brandt's cormorants (B; n = 15 individuals) nesting on East Sand Island in the Columbia River estuary. Foraging areas were estimated using a kernel density interpolation approach, which accounted for hard boundaries to foraging activities, such as islands, jetties, and other landmasses. The range of relative densities, from low to high, is represented by a color ramp, from dark blue representing the lowest density to red representing the highest density. The location of the cormorant breeding colony on East Sand Island is indicated by the star.

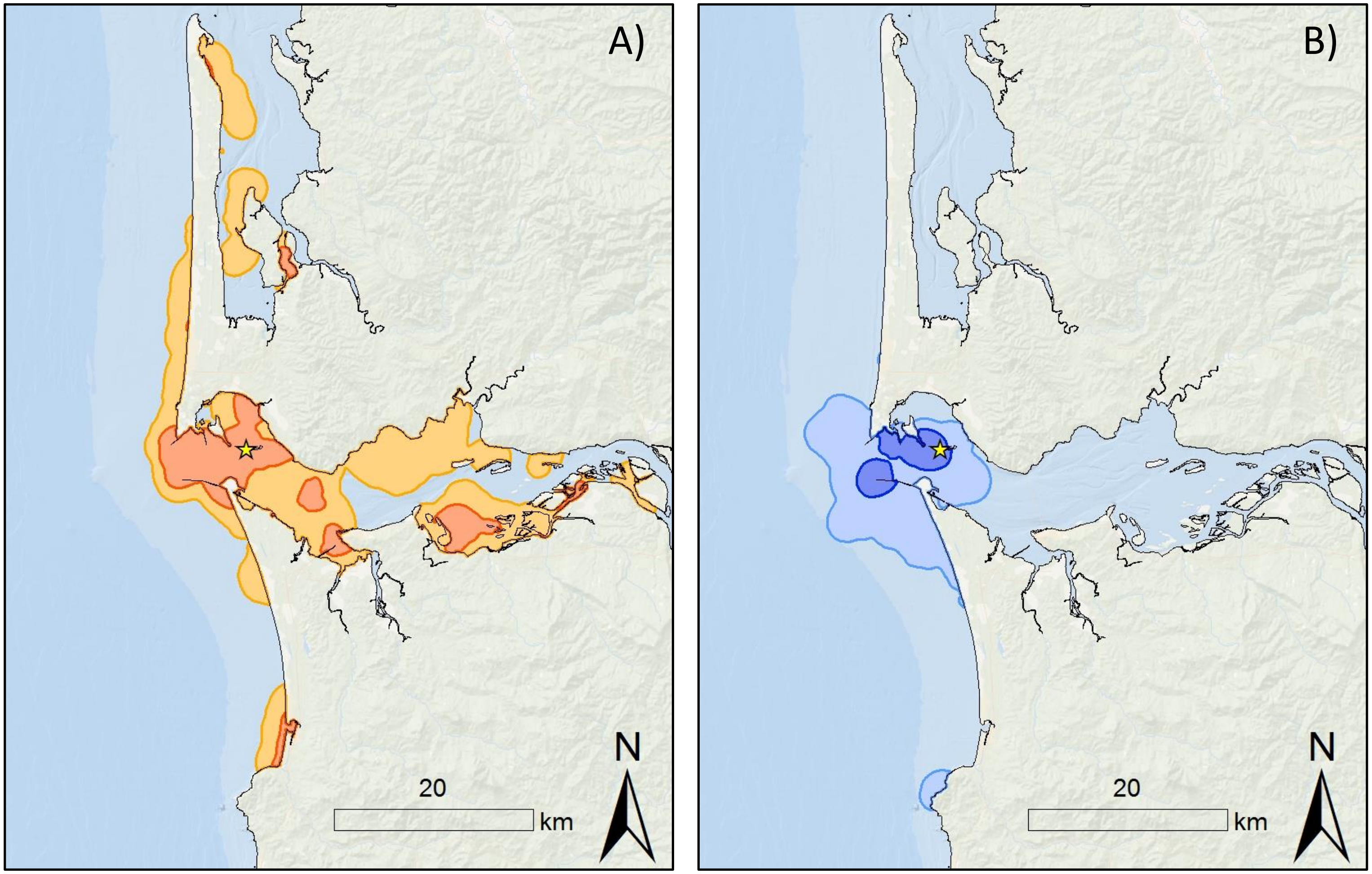

Figure 2.4. Foraging areas used by double-crested cormorants (A; n = 17 individuals) and Brandt's cormorants (B; n = 15 individuals) nesting on East Sand Island in the Columbia River estuary. Overall foraging area estimates (95% KDE) are indicated by lighter shaded areas and core foraging area estimates (50% KDE) are indicated by darker shaded areas. The location of the cormorant breeding colony on East Sand Island is indicated by the star.

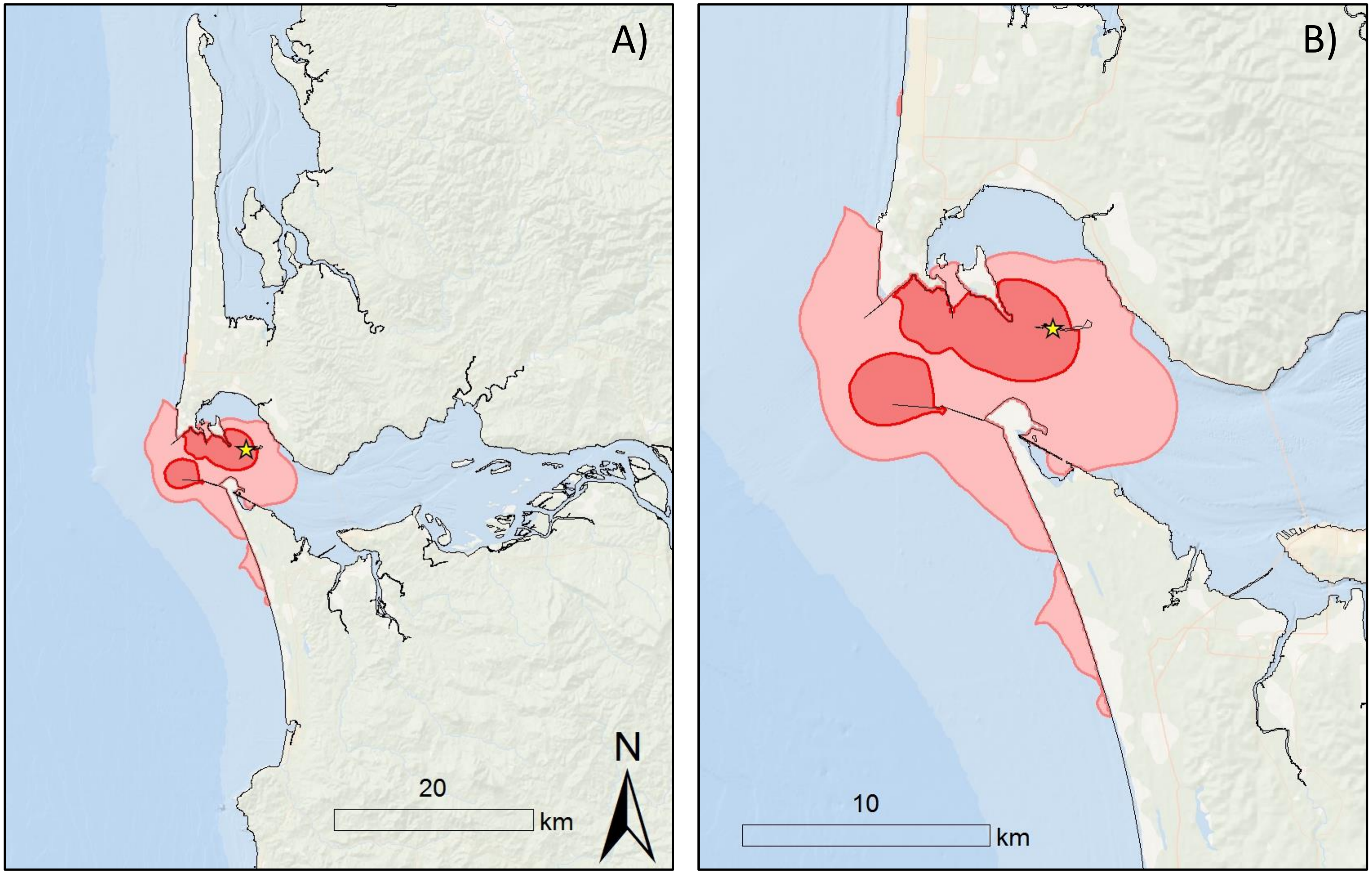

Figure 2.5. Overlap in foraging areas used by double-crested cormorants (n = 17 individuals) and Brandt's cormorants (n = 15 individuals) nesting on East Sand Island in the Columbia River estuary. Overlap in overall foraging area estimates (95% KDE) are indicated by lighter shaded areas and overlap in core foraging area estimates (50% KDE) are indicated by darker shaded areas at a regional scale (A) and at a detailed scale (B). The location of the cormorant breeding colony on East Sand Island is indicated by the star.

CHAPTER 3: DISPERSAL FROM THE LARGEST COLONY OF DOUBLE-CRESTED CORMORANTS IN WESTERN NORTH AMERICA

Adam G. Peck-Richardson, Donald E. Lyons, and Daniel D. Roby

ABSTRACT

East Sand Island (ESI) in the Columbia River estuary was recently home to the largest breeding colony of double-crested cormorants (*Phalacrocorax auritus*) in western North America (an average of 12,981 breeding pairs during 2010-2012), supporting *ca*. 40% of the Pacific Flyway population. Annual consumption of millions of out-migrating juvenile salmonids (*Oncorhynchus* spp.), including smolts from populations listed under the U.S. Endangered Species Act, motivated managers to test methods to reduce cormorant predation by using habitat management to reduce or constrain colony size. One uncertainty regarding habitat management to reduce colony size is the possible dispersal of individuals to areas where they may still consume fish of conservation concern. In 2012 and 2013, in conjunction with experiments to investigate possible habitat restriction techniques at this colony, satellite transmitters were fitted on 94 cormorants during the pre-breeding period to identify possible dispersal patterns if cormorant habitat was managed to reduce colony size in the future. Dispersal from ESI immediately following tagging was temporary, but nearly ubiquitous, and tagged cormorants were detected at colonies and roost sites as far from ESI as a site in Puget Sound, Washington, 210 km away; nevertheless, all but 4% returned to ESI within 2 weeks. During the subsequent breeding and non-breeding seasons, tagged cormorants staged at several nearby estuaries before migrating either north or south from ESI to overwinter in areas from British Columbia to northwestern Mexico; only 2 individuals overwintered in the Columbia River estuary. Tracking data revealed substantial connectivity between the ESI colony and other colonies and regions within nearly the entire latitudinal range of the Pacific Flyway population, suggesting the capacity for widespread dispersal if nesting habitat on ESI was reduced or eliminated. Dispersal did not extend across the Cascade-Sierra Divide, however; greater connectivity existed with estuary locations throughout the range and

particularly with more proximate estuaries that served as post-breeding staging areas. The strong philopatry to ESI that nearly all tagged cormorants exhibited, however, suggests that few alternative nesting opportunities are currently as attractive for prospecting cormorants as the ESI colony site.

INTRODUCTION

Double-crested cormorant (*Phalacrocorax auritus*) populations increased across North America following protection under the Migratory Bird Treaty Act and the banning of DDT, both of which occurred in 1972 (Wires et al. 2001). The recovery and redistribution of the species has led to increased conflicts with humans relating to purported impacts on commercial fisheries, aquaculture, and game fish stocks, as well as damage to vegetation and competition with other colonial waterbirds (Wires et al. 2001, Collis et al. 2002, Duerr et al. 2007, Guillaumet et al. 2014, Wires 2014). Throughout much of their range in central and eastern North America, double-crested cormorants have been subjected to a wide array of management actions by USDA-Wildlife Services and state wildlife agencies, including systematic hazing and lethal control at breeding colonies (USFWS 2003, Wires 2014).

Double-crested cormorants in the Columbia River system, and specifically those nesting on East Sand Island (ESI) in the Columbia River estuary, have been found to consume millions of out-migrating juvenile salmonids (*Oncorhynchus* spp.) annually (Collis et al. 2002, Lyons 2010, Evans et al. 2012), many of them listed as threatened or endangered under the U.S. Endangered Species Act (ESA). The impact of predation by double-crested cormorants nesting at ESI on recovery of ESA-listed salmonids has become of increasing concern for fisheries managers since

2008 (PFC 2012). At the inception of this study, management options for the ESI cormorant colony were being considered and a Draft Environmental Impact Statement (EIS) was being drafted to identify a preferred management option.

One potential management action to reduce predation by double-crested cormorants nesting at ESI on threatened and endangered juvenile salmonids was to reduce the size of the ESI colony. One technique to reduce the numbers of cormorants nesting on ESI would be a reduction in the area of cormorant nesting habitat in order to disperse a portion of those nesting on ESI away from the Columbia River estuary. This would be a similar approach to the current management strategy being implemented at the Caspian tern (*Hydroprogne caspia*) colony on ESI, which has also been implicated as a factor limiting recovery of ESA-listed salmonids in the Columbia River basin (USFWS 2005). Inter-colony movements of double-crested cormorants in the Pacific Northwest are poorly understood, however, and it is difficult to predict how emigration from the ESI colony might affect the distribution of breeding cormorants across other portions of their range. Courtot et al. (2012) examined colony and regional connectivity of ESI double-crested cormorants dispersing during the post-breeding season by placing Argos satellite tags on breeding birds. Cormorants from ESI stayed west of the Cascade and Sierra Nevada mountain ranges, but dispersed widely from British Columbia, Canada, to the Colorado River delta in northwestern Mexico. Direct connectivity was also demonstrated between the colony on ESI and numerous active and historical nesting sites throughout the population’s range during the non-breeding season (Courtot et al. 2012). If managed cormorant dispersal from ESI is implemented, however, prospecting and immigration rates will likely vary among regions and potential colony sites due to a number of factors, including distance from ESI and individual breeding history (Guillaumet et al. 2011, Courtot et al. 2012).

Habitat use away from the lower Columbia River estuary by cormorants currently nesting at the ESI colony could shed light on potential emigration destinations, if double-crested cormorants are actively dispersed from the ESI colony. Visits to active or historical colony sites, including those of double-crested cormorants and other colonial waterbirds, or visits to locations with suitable nesting habitat, may represent prospecting behavior. Animals that breed colonially, including seabirds, often choose breeding locations where they have been successful in the past (Switzer 1993); however, stochastic factors may cause nest failure at a colony site that is otherwise suitable for breeding. Therefore, complimentary cues, such as the reproductive success of neighbors or conspecifics at other colonies, may influence breeding site selection (Danchin et al. 1998, Hénaux et al. 2007). Prospecting for suitable nesting sites by visiting active colonies in the years prior to breeding, or possibly after a failed nest attempt or during migration, has been shown to increase subsequent breeding success in great cormorants (*P. carbo*; Schjørring et al. 1999).

Staging areas and stopover sites can play critical roles in energy acquisition for migratory birds (Hedenström and Alerstam 1997). Staging areas can represent sites with predictable and abundant food resources for birds facing energetic hurdles, such as migration or nest initiation (Weber et al. 1998). Scherr et al. (2010) used satellite telemetry to determine the migration routes, staging areas, and wintering home ranges of double-crested cormorants nesting on Lake Huron, Ontario, Canada. Twenty-one of 26 tagged cormorants (81%) visited two staging areas for multiple days or weeks after departing the breeding colonies and before migrating to wintering areas. Courtot et al. (2012) also identified post-breeding season staging areas for cormorants nesting at ESI, in two large estuaries 45 km and 75 km north of ESI. Pre-breeding staging areas are less well studied and understood, but may differ from post-breeding staging areas due to seasonally shifting prey resources (Lyons et al. 2007, Dorr et al. 2014).

To gain insight into dispersal behavior and potential emigrant destinations for double-crested cormorants nesting at the colony on ESI, we used satellite telemetry to track individual cormorants throughout the annual cycle, following experimental capture and tagging at the ESI colony during the pre-nesting period. The objectives of this study included: (1) investigating potential dispersal and redistribution of double-crested cormorants following capture and tagging at ESI early in the nesting season; (2) understanding connectivity between the ESI colony and other active, historical, and prospective colonies within the breeding range of double-crested cormorants in western North America; and (3) describing post-breeding staging areas, winter dispersal patterns, and regional connectivity for double-crested cormorants nesting at the largest colony for the species in western North America.

METHODS

Study Area

East Sand Island (ESI; 46º15’46”N, 123º59’15”W) is located in the lower Columbia River estuary (river kilometer 7), partially straddling the border between Clatsop County, Oregon, and Pacific County, Washington. ESI is a semi-natural, low-lying island, about 20 ha in area, that is comprised of mixed dune, forest, shrubland, and rocky habitat types and surrounded by extensive intertidal sand and mudflats. The island has been heavily modified by the addition of dredged material and shoreline hardening. During this study, ESI was the site of the largest known breeding colonies of double-crested cormorants and Caspian terns in western North America (averages of 12,981 breeding pairs and 7,204 breeding pairs, respectively, during 2010-2012; BRNW 2014). The island is also home to smaller breeding colonies of Brandt’s cormorants (*P. penicillatus*; 1,550 pairs in 2013), glaucous-winged/western gulls (*Larus glaucescens* x *L. occidentalis*), and ring-billed gulls (*L. delawarensis*; BRNW 2014).

Habitat Restriction

Previous research at ESI has focused partly on developing non-lethal management options to reduce available nesting habitat for cormorants in order to potentially reduce the size of the ESI colony (BRNW 2014). One option that has shown promise during feasibility studies is the use of visual barriers and limited human disturbance (hazing) on a portion of the existing cormorant colony. By subdividing the colony with visual barrier fences (privacy fencing), cormorants can be hazed and excluded from pre-defined areas, while nesting birds behind the fences remain undisturbed. A series of feasibility studies were conducted from 2011 through 2013, which incrementally reduced the area of available nesting habitat for cormorants on ESI. During the 2013 breeding season, two privacy fences were placed across the cormorant nesting area at the west end of ESI. The roughly 1.6 ha (4 acres) of cormorant nesting habitat between the two fences were left undisturbed, while cormorants that attempted to nest outside the two fences, in areas where cormorants had nested in previous years, were hazed. During 2012, all cormorants had nested west of the western privacy fence, because areas east of that fence were actively hazed. The 1.6 ha of undisturbed habitat in 2013 was sufficient area for the number of cormorants present in any previous year to nest in, but also precluded the use of the entire area used by nesting cormorants on ESI in 2012. Thus, in 2013, all double-crested cormorants nesting on ESI were forced to either establish their nests in a different area on the island or prospect for nesting opportunities elsewhere. Progressively greater habitat manipulations during 2011 – 2013 allowed for (1) the demonstration of suitable visual barriers (privacy fencing), (2) the development of effective hazing protocols, and

(3) the investigation of colony site philopatry by ESI cormorants under moderate and potentially reversible habitat restriction.

PTT Satellite Tracking

Adult double-crested cormorants were captured during the pre-breeding stage of the nesting cycle, shortly after their arrival at the colony on ESI. Our capture efforts focused solely on areas where cormorants were to be excluded from nesting using hazing techniques throughout the breeding season. We captured cormorants just after some nest-building had commenced, but before eggs were laid. Capture sessions were conducted solely at night using spotlights, dip nets, and hands. In 2012 and 2013 a combined total of 96 double-crested cormorants were tagged with one of two types of satellite tag (Platform Terminal Transmitter; PTT) using polytetrafluoroethylene (Teflon®) ribbon harnesses, as described by King et al. (2000). In 2012 we deployed 12 modified Kiwisat 202 PTTs (Sirtrack Ltd., Havelock North, New Zealand). In 2013, we deployed an additional 65 modified Kiwisat 202 PTTs and 18 modified Kiwisat 303 PTTs (Sirtrack Ltd.). The Kiwisat 202 PTTs were modified to include reinforced antennae and the Kiwisat 303 PTTs were potted in epoxy to replicate the proven physical design of the Kiwisat 202 PTTs for use on double-crested cormorants (Courtot et al. 2012). All PTTs weighed approximately 50 g, and tags and harnesses were less than 3% of cormorant body mass in all cases.

All individual cormorants were weighed (± 50 g) using Pesola® spring scales (5 kg capacity), and breast feather samples were collected for DNA sexing (Avian Biotech International, Tallahassee, Florida). Each satellite-tagged cormorant was marked with a USGS stainless steel, numbered leg band on one leg and a unique, field-readable engraved plastic (Darvic) leg band on the other. All animal handling and tagging procedures were approved by the Institutional Animal Care and Use Committee at Oregon State University.

Kiwisat 202 PTTs were programmed to transmit using a 7-hours on/41-hours off duty-cycle from 1 March to 31 July. The Kiwisat 303 PTTs were programmed to transmit using a 7-h on/17-h off duty-cycle during the same period. All PTT tags switched to a 7-h on/137-h off duty-cycle from 1 August through 28 February, before reverting to the higher frequency duty-cycle on 1 March. The "on" periods were programmed to coincide with nighttime hours (0500-1159 UTC), when birds were most likely at a colony or a roost location, rather than commuting or foraging. Based on these duty cycles, the battery lifespan for the PTTs was initially estimated by the manufacturer to be approximately 16 months.

PTT Data Processing

Position data for satellite-tagged cormorants were received via the Argos satellite system and delivered by e-mail (CLS America, Inc., Lanham, Maryland, USA). Argos assigned preliminary location classes (LCs; 3, 2, 1, 0, A, B, and Z, in descending order of accuracy), based on estimated accuracy of the location data. We filtered the location data using the Douglas Argos-Filter Algorithm version 7.03 (USGS, Alaska Science Center, https://alaska.usgs.gov/science/biology/spatial/douglas.html, accessed 20 Jan 2013), utilizing SAS software version 9.3 (© 2011, SAS Institute, Cary, North Carolina, USA). Following the methods of Courtot et al. (2012), we retained all LC3 locations and locations within 2 km of the previous location. Consecutive locations requiring flying speeds greater than 70 km/hr were excluded. The best single location per "on" period was then selected based on the LC and the most messages received during a satellite overpass. The resulting roost location positions were estimated by Argos to have location error of less than 1.5 km (LCs 3, 2, or 1: Argos 2007).

We manually checked the filtered PTT data for each individual cormorant to identify improbable locations. Aberrant locations, such as locations greater than 20 km out to sea or locations likely associated with a motionless PTT or dead bird, were removed. If a PTT was recovered from a dead bird, final locations were removed accordingly. If more than five consecutive locations from the end of a deployment were located at the same site, only the first five locations were retained. Two PTTs either did not transmit, or only transmitted for less than one week, and consequently were removed from the analysis completely.

Classification of Cormorant Location Data

We classified all retained location data into one of three distinct study periods corresponding with (1) the initial two-week period following the 2013 captures and tag deployments, (2) the 2012 – 2014 breeding seasons (excluding the 2013 pre-breeding period defined above), and (3) the 2012 – 2014 non-breeding seasons. The 2013 pre-breeding dispersal period began on 14 April 2013, corresponding with the onset of cormorant capture and tagging, and extended through 30 April 2013, a period of time that reasonably covered the tracked cormorants' initial response to capture and tagging. The nominal breeding season was then defined as 16 April through 15 September, and was selected to cover the period of time when active reproductive behaviors (nest-building, incubation, or chick-rearing) were observed at ESI. The non-breeding period was defined as 16 September through 15 April. Location data collected in 2012 from individuals tagged in 2012 were classified using these same dates; data from these individuals during 14 April 2013 – 30 April 2013 were excluded from the pre-breeding period analysis to more clearly document dispersal behavior of individuals tagged in 2013.

Roosting sites of satellite-tagged cormorants were described relative to regions, active cormorant colonies, and historical cormorant colony sites. Regional delineations were adapted from Adkins and Roby (2010) and Courtot et al. (2012) and revised to more clearly follow natural watersheds, estuaries, inland seas, as well as political boundaries. For example, portions of the Coastal Washington and Coastal British Columbia regions were combined into the Salish Sea region, while the remaining portions were renamed the Outer Washington Coast region and Outer Vancouver Island region. The Columbia River estuary region was modified to include just the Columbia River watershed downstream of Puget Island (river kilometer 61), and did not include portions of Willapa Bay. A sub-region within the Columbia River estuary region was delineated around ESI to allow for the exclusion from the analysis of roost locations associated with the ESI cormorant colony.

Colony locations and status were obtained from two sources, the double-crested cormorant status assessment for the western population by Adkins and Roby (2010) and the Pacific Flyway Council Management Framework for double-crested cormorants (PFC 2012). Individual colony locations in Grays Harbor and the Columbia River estuary were added to more accurately reflect the locations of small, individual cormorant colonies located on channel markers or navigational aids. Colony locations were also included for the mid-river power transmission towers near Troutdale, Oregon, and the Lewis and Clark Bridge (Lower Columbia River; AGP, pers. obs.). A reported cormorant colony at Woodard Bay, southern Puget Sound, was removed from the analysis because it was likely reported in error (B. Troutman, Washington Department of Fish and Wildlife, pers. comm., Jan. 2014). Colony locations were buffered with 2-km radius circles to account for potential error in Argos locations and imprecision of colony locations (Courtot et al. 2012). Roost locations that fell within the 2-km buffer were included as visits to the colony. If buffer circles were close enough to overlap, they were bisected so that no single roosting location could be counted at more than one colony site.

Three primary post-breeding staging areas were identified by *post hoc* analysis of PTT tracking data from this study, and informed by the findings of Courtot et al. (2012). Staging area sub-regions in the upper Columbia River estuary, Willapa Bay, and Grays Harbor were delineated with 15-km radius circles. The staging period was defined to begin on 1 July so as to include the earliest juvenile cormorants that fledged from the ESI colony, based on historical data from ESI (BRNW 2014), and continued through November when Courtot et al. (2012) found > 95% of tagged adult cormorants had departed the Columbia River estuary region. PTT locations from July through November were then classified as being at ESI (within the ESI sub-region of the Columbia River estuary), at a staging area (within one of the three staging area sub-regions), or as departed (all other locations). Tagged cormorants were only included in the staging area analysis if they nested at ESI and PTTs provided sufficient data to evaluate winter dispersal patterns. Two tagged individuals that remained resident in the Columbia River estuary throughout the non-breeding season were also excluded from this analysis.

Analysis

We used ArcGIS version 10.2.2 (Environmental Systems Research Institute, Inc., Redlands, CA) to plot roost and colony locations, to delineate buffers around each colony, to delineate regions, and to enumerate cormorant detections at each colony and within each region.

We quantified connectivity at the level of colony or region based on three statistics: (1) the number of tagged individuals that visited a colony or region, (2) the total number of detection days for tagged individuals at each colony or region, and (3) an index to connectivity, which used both the number of individuals and the total number of detection days to estimate the relative magnitude of use by tagged individuals among all locations (colonies or regions) where tagged individuals were detected. To estimate the number of detection days for a particular location, we used a simple correction based on the sampling rate programmed in the PTT tag. PTT tags were programmed to collect locations every day, every other day, or once a week, depending on the tag model and duty-cycle; accordingly, the number of detections at a particular location was multiplied by 1, 2, or 7, respectively, to correct for the differences in sampling rate.

The connectivity index statistic utilized a standardized anomaly index to combine both the number of individuals that visited a location and the total number of cormorant detection days at that location to estimate the relative utilization by tagged cormorants of a particular location (colony site or region; Wilks 2011). This statistic was calculated by first finding the mean number of individuals that visited each location, separately for colonies or regions, during a given study period (i.e. pre-breeding immediately post-tagging, breeding season, or non-breeding season). We then calculated the difference between the mean number of individuals visiting the sample of locations and the number of individuals visiting each location, in units of standard deviation. This process was then repeated for the number of detection days at particular locations, and the two resulting values for each colony site or region were summed to yield the connectivity index statistic. The resulting value is dimensionless and may be positive or negative, with zero indicating average connectivity within the sample group of colony sites or regions. The connectivity index statistic is useful for comparing relative connectivity among colonies or regions within a particular study period, but should not be used to compare connectivity across different periods of the study or to compare connectivity between colonies and regions.

RESULTS

Habitat Restriction

All cormorants that nested at ESI in 2013 did so in the 1.6 ha of undisturbed habitat between the two privacy fences. An estimated 14,900 breeding pairs of double-crested cormorants attempted to nest on ESI in 2013, the greatest number ever recorded at that colony. The colony produced an average of approximately 2.4 fledglings per breeding pair, the third highest estimate of annual productivity for the ESI colony recorded during 1997 – 2013 (BRNW 2014).

PTT Satellite Tracking

We obtained tracking data from 11 of 12 PTTs deployed on double-crested cormorants in 2012, and from all 83 PTTs deployed on cormorants in 2013; however, four tags deployed in 2013 transmitted data for less than 2 weeks and were only included in the analysis of the 2-week pre-breeding study period following capture and tagging in 2013. Two PTTs deployed on double-crested cormorants in 2013 were recovered from dead birds during the first half of the 2013 nesting season and were redeployed on breeding adult double-crested cormorants that were captured on their nests at ESI. Therefore, our final sample of location fixes for satellite-tagged cormorants included data from 94 PTTs deployed on 96 individuals. Cormorants were satellite-tracked between seven and 615 days, with a mean tracking period of 284 days (sd = 145.3, n = 96) and a median tracking period of 298 days. Our sample included tracking data from 49 females, 46 males, and one individual whose gender was undetermined.

2013 Pre-breeding Season

Initially, 96% of cormorants tagged on ESI during the 2013 pre-breeding season (80 of 83) were detected at cormorant roost sites away from ESI. This dispersal was temporary, however, and by 30 April, two weeks later, 96% of these tagged dispersers (73 of 76; four tags ceased transmitting) were detected back at East Sand Island. The timing of the return of most tagged cormorants to ESI coincided with a large increase in the numbers of cormorants initiating nests in the portion of the ESI cormorant colony that was not being managed.

During this two-week period immediately after pre-breeding season satellite-tagging at ESI in 2013, tagged cormorants were tracked away from ESI and had the greatest regional connectivity with the Columbia River estuary, the region that includes ESI. Eighty-six percent of all tracked individuals (n = 68) and 58% of weighted detections away from ESI (n = 565) were located at sites within the estuary (Table 3.1). Satellite-tagged cormorants were also detected at cormorant roost locations outside the Columbia River estuary but within the Columbia River basin (n = 29), along the Outer Washington Coast (n = 18; mostly in Grays Harbor and Willapa Bay), and in the Salish Sea region of Washington (n = 1; Figure 3.1A).

Tracked cormorants demonstrated the greatest inter-colony connectivity with the mixed colony of double-crested and pelagic cormorants (*P. pelagicus*) on the Astoria-Megler Bridge over the Columbia River (river kilometer 23); 80% of tracked individuals were detected roosting at this one colony and it accounted for 50% of all weighted detections (n = 482) during this initial two-week period following tagging (Table 3.1). The Astoria-Megler Bridge is about 12 km from the cormorant colony on ESI and the site of one of the closest double-crested cormorant colonies to ESI. Tagged cormorants were also detected at other active colony sites in the Columbia River estuary, in the Columbia River basin above the estuary, and on the Outer Washington Coast (Figure 3.1B). Three tagged cormorants did not return to nest at ESI during the 2013 nesting season, and likely nested at alternative colony sites in 2013. Two of these three tagged cormorants were regularly detected at the colony on the Astoria-Megler Bridge and one remained at the colony on the Troutdale Power Tower (on the lower Columbia River near Troutdale, Oregon, river kilometer 186) throughout the 2013 nesting season.

Breeding Season

We collected tracking data from 84 satellite-tagged cormorants during the breeding season, which included location fixes collected between 16 April and 15 September during the summers of 2012, 2013, and 2014. Tracking data collected during the 2013 pre-breeding period were excluded from this portion of the analysis. The data set of location fixes during the breeding season included data from all tagged individuals tracked during this period, regardless of where they eventually nested. This included tagged individuals that visited or emigrated to other colonies after visiting ESI early in the breeding season, as well as tagged individuals that spent time at other colonies early in the breeding season, before arriving at ESI to nest, or late in the breeding season after departing ESI.

During the breeding season, tagged cormorants that were tracked away from ESI had the greatest regional connectivity with the Outer Washington Coast and the Columbia River estuary. Sixty-four percent of all tracked cormorants (n = 54) were detected along the Outer Washington Coast (mostly in Grays Harbor and Willapa Bay) and accounted for 45% of all weighted locations away from ESI (n = 1,947; Table 3.2). Eighty percent of all tracked individuals (n = 67) and 33% of weighted detections away from ESI (n = 1,425) were located elsewhere in the Columbia River estuary (Table 3.2). Satellite-tagged cormorants were also detected at cormorant roosts or colonies outside the Columbia River estuary, but within the Columbia River basin (n = 17; 20%), in the Salish Sea (n = 16; 19%), on Outer Vancouver Island (N = 3; 4%), along the Oregon Coast (n = 3; 4%), along the northern California Coast (n = 3; 4%), in the Central Valley of California (n = 3; 4%), in the Salton Trough of southern California (n = 2; 2%), and in San Francisco Bay (n = 1; 1%; Figure 3.2A).

Tracked cormorants demonstrated the greatest inter-colony connectivity during the breeding season with former cormorant colony sites at an unnamed sandy island in central Grays Harbor, Washington, and at Rice Island in the upper Columbia River estuary, as well as the extant cormorant colony site on the Astoria-Megler Bridge in the lower Columbia River estuary (connectivity index values of 5.2, 4.8, and 4.4, respectively; Table 2.2). Thirty-seven percent of tagged individuals tracked during the breeding season (n = 31; 23% of weighted detections) were detected roosting at the former colony site in Grays Harbor. Forty-nine percent of tagged individuals (n = 41; 16% of weighted detections) were detected roosting at the former colony site on Rice Island, and 51% of tagged individuals (n = 43; 12% of weighted detections) were detected at the active mixed-species cormorant colony on the Astoria-Megler Bridge. Tagged cormorants were also detected roosting at active and former colony sites across most of the latitudinal extent of the breeding range of the western North America population of double-crested cormorants, including one individual at the colony on the Second Narrows Bridge in Vancouver, B.C., and one individual at the “Salton Sea – North” colony in the Salton Trough of southern California (Table 3.2; Figure 3.1B).

Non-breeding Season

We collected tracking data from 80 satellite-tagged cormorants during the non-breeding season, which included location data collected between 16 September and 15 April, 2012-2013 and 2013-2014. Satellite-tracked cormorants overwintered in regions to the north and south of the Columbia River estuary, and in the Willamette River valley of western Oregon, the closest large sub-basin within the Columbia River basin (Figure 3.3A). Seventy-two of the 80 PTTs that were operational during the non-breeding season provided sufficient location data to evaluate dispersal patterns following post-breeding migration. Thirty-one individuals (43%) overwintered to the north in Washington or British Columbia, with a maximum dispersal distance of 504 km from ESI and a mean maximum dispersal distance of 262 km (sd = 99). An additional 28 cormorants (39%) overwintered in California, with a maximum dispersal distance of 1,636 km and a mean maximum dispersal distance of 1,082 km (sd = 386). Eleven individuals (15%) spent the winter in the vicinity of the Willamette River valley, with a maximum dispersal distance of 234 km from ESI and a mean dispersal distance of 145 km (sd = 45). Only two tracked individuals tagged at ESI (3%) overwintered in the Columbia River estuary.

During the non-breeding study period, cormorants tagged at ESI had the greatest regional connectivity with the Salish Sea, followed by the Outer Washington Coast, and then the Columbia River estuary (Figure 2.3A). Thirty-one percent of all tracked cormorants (n = 25) were detected in the Salish Sea and accounted for 33% of all weighted detections away from ESI (n = 4,479; Table 3.3). An even greater proportion of tagged individuals (59%; n = 47) were tracked to the Outer Washington Coast (mostly in Grays Harbor and Willapa Bay), but accounted for only 12% of all weighted detections away from ESI (n = 1,476; Table 3.3). Similarly, 59% of all tagged individuals (n = 47) were detected at roost sites away from ESI in the Columbia River estuary, but accounted for only 7% of weighted detections (n = 944; Table 3.3). Satellite-tagged cormorants were also detected at cormorant roost locations outside the Columbia River estuary, but within the Columbia River basin (n = 19; 24%), in the Central Valley of California (n = 14; 18%), along the northern California Coast (n = 14; 18%), in San Francisco Bay (n = 13; 16%), along the Oregon Coast (n = 8; 10%), in the Salton Trough of California (n = 5; 6%), on Outer Vancouver Island (n = 4; 5%), in the southern California Bight (n = 4; 5%), and in the interior of northern California (n = 1; 1%; Figure 3.2A).

During the non-breeding season, tagged cormorants demonstrated the greatest inter-colony connectivity with the colony at the Astoria-Megler Bridge in the lower Columbia River estuary and with the unnamed sandy island in Grays Harbor, Washington (connectivity index values of 8.8 and 6.7, respectively; Table 3.3). Forty-nine percent of tagged individuals tracked during the non-breeding season (n = 39; 5% of weighted detections) were detected roosting at the Astoria-Megler Bridge colony. Thirty-five percent of tagged individuals tracked during the non-breeding season (n = 28; 4% of weighted detections) were detected roosting at the Grays Harbor colony. Tagged cormorants also had high connectivity during the non-breeding season with active and former colonies at the San Francisco – Oakland Bay Bridge (n = 6 individuals; connectivity index = 3.3), Rice Island in the Columbia River estuary (n = 14 individuals; connectivity index = 3.3), the Arcata Bay sand islands on the northern California Coast (n = 8 individuals; connectivity index = 1.1), and the Snohomish River Mouth in the Salish Sea (n = 3 individuals; connectivity index = 1.0). Tagged cormorants were also detected roosting at active and historical colony sites across most of the latitudinal extent of the breeding range of the western North America population, including one individual tracked to the colony on Mandarte Island in the Gulf Islands, B.C., and one individual tracked to Ramer Lake south of the Salton Sea in southern California (Table 3.3; Figure 3.2B).

Staging Area Use

We identified three major staging areas utilized by tagged cormorants after departing ESI, but before moving to overwintering areas. From July through the first half of November, tagged cormorants frequently roosted at Rice Island and the Astoria-Megler Bridge, located in the Columbia River estuary 12 km and 20 km upriver from ESI, respectively. Tagged cormorants also utilized the low-lying sandy islands located in Willapa Bay and Grays Harbor, two large estuaries located approximately 40 km and 75 km north of the Columbia River estuary, respectively. During this transition period, 81% of all tagged individuals (n = 65) that nested at ESI in 2012 or 2013 roosted in at least one of these staging areas for at least one night. Tagged cormorants eventually departed staging areas to spend the winter to the north or south of the Columbia River estuary (Figure 3.4), with the exception of two individuals that overwintered in the estuary.

DISCUSSION

Our results support the hypothesis that double-crested cormorants nesting at ESI have high connectivity with regions and colonies across the full latitudinal extent of the range of the western North America population of the species. Furthermore, ESI cormorants visited regions and colonies throughout this range during both the breeding and non-breeding seasons. Visits to regions and colonies during the breeding period could provide a cormorant with information on breeding activity and nesting success, information that could inform decisions about where to attempt to nest if the cormorant lost its current nesting site. Overall, ESI cormorants demonstrated the greatest connectivity with the Salish Sea, the outer Washington coast, and the lower Columbia River basin, but also visited regions throughout California. Cormorant detections away from ESI also clustered around major coastal estuary systems. Despite this pattern of broad regional connectivity, no cormorants tagged on ESI were detected east of the Cascade or Sierra Nevada mountain ranges, supporting previous evidence of limited connectivity between the coastal and Great Basin subpopulations within the western North America population (Courtot et al. 2012, Mercer et al. 2013). Furthermore, cormorants tagged in the present study had surprisingly low regional and colony connectivity with the Oregon Coast, despite numerous active and historical colonies in that region, and close proximity to the colony at ESI.

Results of this study were generally consistent with a previous tracking study by Courtot et al. (2012), which found that the great majority of double-crested cormorants nesting at ESI moved either north or south from the Columbia River estuary to overwinter, after departing fall staging areas either on the outer Washington coast or in the Columbia River estuary; however, very few remained in the Columbia River estuary overwinter. Also, northward and southward dispersing individuals did not mix after departing the staging areas; southward migrating individuals did not visit regions to the north during winter, and northward migrating individuals did not visit regions to the south.

Staging area use was a major driver of regional and colony connectivity during both the breeding and non-breeding periods. Cormorant detections at staging areas in the upper Columbia River estuary, Willapa Bay, and Grays Harbor peaked from late August through early October (Figure 3.4), spanning both the breeding and non-breeding periods. High connectivity index values with the outer Washington coast and the Columbia River estuary during the non-breeding period were due to the high proportion of tagged individuals that staged in these two regions during fall (59% for each region; Table 3.3), before moving to regions where they overwintered. The proportion of weighted detections in these two regions during the non-breeding period was low, however; only 12% of detections during the non-breeding period were from the outer Washington coast and only 7% of detections were from the Columbia River estuary. Tagged cormorants eventually departed these fall staging areas and overwintered elsewhere to the north or south. No tagged cormorants overwintered along the outer Washington coast and only two tagged individuals overwintered in the Columbia River estuary.

Although the aggregation of post-breeding cormorants at fall staging areas may have inflated the connectivity values between the ESI colony and the Columbia River estuary and outer Washington coast regions during the non-breeding period, fall staging and prospecting for breeding sites are not necessarily mutually exclusive. Staging areas fundamentally satisfy most of the requirements for colony sites, including proximity to high-quality foraging habitat, protection from ground-based predators, and isolation from anthropogenic disturbance (Wires and Cuthbert 2010). Furthermore, there are several active and former colony sites in Grays Harbor and in the Columbia River estuary, and several of these sites might provide suitable nesting substrate and allow for potential future immigration of ESI cormorants. Nevertheless, several factors may negatively affect the potential for future growth or revival of these colonies, and therefore their prospects for recruiting cormorants emigrating from ESI.

During our study, active cormorant colonies in the upper Columbia River estuary were limited to several anthropogenic structures: the Astoria-Megler Bridge and a series of navigational channel markers upstream of the bridge. The channel markers were generally saturated with nesting cormorants and provided very little potential for colony expansion. Similarly, expansion of the cormorant colony on the Astoria-Megler Bridge would likely be restricted by disturbance from shipping traffic and recreational boating, as well as limited additional prospective nest-sites on the substructure of the bridge. The former cormorant colony sites on Rice Island and Miller

Sands Spit, two dredged material disposal islands in the upper estuary, are actively monitored and managed to prevent the formation of Caspian tern nesting colonies (BRNW 2015), which would also prevent the formation of a cormorant colony. The former cormorant colony site on the Desdemona Sands pilings, which previously supported the Desdemona Sands Lighthouse, has degraded into the river and no longer provides suitable nesting substrate. Therefore, despite substantial connectivity between ESI and the rest of the Columbia River estuary, opportunities for major colony expansion at sites in the Columbia River estuary away from ESI are apparently quite limited.

Along the outer Washington coast, connectivity and staging area use were focused on the Grays Harbor and Willapa Bay estuaries; however, these coastal estuaries also present limited opportunities for future cormorant colony formation or expansion. Active cormorant colonies in Grays Harbor are located on channel markers, similar to those in the Columbia River estuary, which provide limited space for colony expansion. Roosting cormorants were detected at both Sand Island and a nearby un-named sandy island in central Grays Harbor. These islands offer potentially suitable nesting habitat (Courtot et al. 2012); however, cormorants have not successfully nested at Sand Island since 1999 (Adkins and Roby 2010), likely because of frequent disturbance by bald eagles (*Haliaeetus leucocephalus*; Courtot et al. 2012; AGP, pers. obs.). Increasing bald eagle populations have resulted in greater predation pressure and increased disturbance frequency for several colonial seabird species in the Pacific Northwest, including double-crested cormorants (Parrish et al. 2001, Adkins et al. 2014). Willapa Bay's low-lying sandy islands have also been used by staging cormorants; however, these islands are apparently susceptible to tidal inundation and have no known history of cormorant nesting (Adkins et al. 2014).

During the non-breeding season, the distribution of tagged cormorants was clustered in major estuarine systems throughout their winter range, including the Salish Sea, the outer Washington coastal estuaries, the Columbia River estuary, Arcata Bay, San Francisco Bay, and the Salton Sea. Estuaries are among the most biologically productive systems in the world and provide enhanced foraging opportunities for both marine and freshwater predators (Day, Jr. et al. 2013). Our findings are consistent with prior research that has found that double-crested cormorants are more likely to forage in estuaries than other cormorant species along the West Coast of the U.S. (Ainley et al. 1981). Double-crested cormorants are also unique among cormorant species of the eastern North Pacific because they regularly exploit prey resources in both freshwater and marine systems (Dorr et al. 2014). Double-crested cormorants have been shown to shift foraging effort between freshwater and marine zones within estuaries, apparently to more efficiently exploit seasonally abundant prey (Anderson et al. 2004, Lyons et al. 2007). Furthermore, estuaries are often structurally complex and may provide a variety of roosting habitats and ample shelter from severe weather.

Pre-breeding Dispersal

Our cormorant tracking results during the pre-breeding period in 2013 suggest that double-crested cormorants nesting at the ESI colony are highly motivated to continue nesting at this colony. Despite being captured and tagged at ESI early in the 2013 nesting season, 96% of satellite-tagged cormorants returned to ESI within two weeks and attempted to nest. Consistent with the tracking results, the large colony also remained at ESI in 2013, individuals readily shifted their nesting area from the location in the previous year to the space provided between the two privacy fences, and the colony actually grew in size. Although our tracking results demonstrate that cormorants nesting at ESI are aware of other potential breeding colonies, outside of the two-week pre-breeding period we did not detect any permanent emigration of tagged cormorants from ESI to other nesting colonies during either the 2012, 2013, or 2014 breeding seasons.

Several factors likely contribute to the attractiveness of ESI as a nesting site for double-crested cormorants, and the persistence of this colony as the largest for the species in western North America. ESI provides suitable nesting substrate, without land-based predators, and in close proximity to superabundant prey resources at the mouth of the Columbia River estuary (Weitkamp et al. 2012, Zamon et al. 2014, Weitkamp et al. 2016). Individuals with a history of nesting at ESI have demonstrated high fidelity and nesting persistence when faced with temporary disturbances from humans or avian predators (e.g., bald eagles) at this colony. Furthermore, the large size of the ESI cormorant colony is likely a highly attractive social stimulus at a site where double-crested cormorants can nest among a large number of conspecifics. Many seabird colonies along the West Coast have experienced increased pressure from bald eagle disturbance and predation as eagle numbers have rebounded following the banning of the pesticide DDT (Horton 2014), and it is likely that the large size of the cormorant colony at ESI provides security in numbers and mitigates the impact from such disturbances. It remains unclear, however, how tolerant cormorants nesting at ESI would be to a large reduction in available nesting habitat or a sustained, intensive disturbance event.

Regional shifts in the breeding population of double-crested cormorants in western North America, plus changes in relative colony sizes, can provide additional insight on the potential suitability of alternative nesting sites away from ESI. Between 1992 and 2009, numbers of double-crested cormorants breeding throughout coastal British Columbia and Washington declined by

66% (Adkins et al. 2014). This decline was attributed to bald eagle and human disturbances (Henny et al. 1989, Moul and Gebauer 2002), and may still limit the emigration of cormorants from ESI to colonies in the Salish Sea region. At several inland colony sites, changing water levels have led to large fluctuations in colony sizes. The two largest colonies in western North America after ESI, one at Upper Klamath Lake in interior Oregon and the other on Mullet Island in the Salton Sea of southern California, have experienced dramatic declines in recent years, changes that highlight the impact of increasing water demands from irrigation-based agriculture and growing urban populations, as well as reduced overall water availability due to drought in the western U.S. Colonies with connectivity to ESI, such as those in the Salton Sea, may not be able to support breeding cormorants in any given year.

Management Considerations

ESI has supported the largest breeding colony of double-crested cormorants in western North American and is likely the only site in this region that provides the necessary combination of abundant forage fish resources and ample nesting habitat secure from human disturbance and mammalian predators to support such a large colony. Furthermore, the large size of the ESI cormorant colony likely serves to dilute the impact of disturbance and predation from bald eagles and secondary nest predators, such as gulls (*Larus* spp.) and corvids (Family: Corvidae).

This study demonstrated that double-crested cormorants were highly motivated to continue nesting at ESI and, in 2013, tagged individuals returned despite being captured, handled, tagged, and forced to relocate to a new nesting area on ESI. The habitat restriction experiment conducted in conjunction with the tracking study did not restrict nesting habitat sufficiently to preclude even a small proportion of the cormorant colony from nesting on the ESI colony in 2013, and a record number of double-crested cormorants nested on ESI that year. In order to substantially reduce the size of the cormorant colony at ESI, nesting habitat would need to be restricted to a much smaller area, and managers would need to be prepared to dissuade cormorants from colonizing previously unused habitats on ESI. Furthermore, it is possible that a much smaller colony will be more vulnerable to bald eagle disturbance, and more susceptible to reproductive failure or abandonment.

If management actions or other disturbances do result in the dispersal of nesting double-crested cormorants from ESI, our results suggest numerous locations where these individuals may prospect for future nesting opportunities. This study has demonstrated high connectivity between ESI and potential breeding sites elsewhere in the Columbia River estuary, as well as the nearby Grays Harbor estuary on the outer Washington coast. However, these regions apparently do not have sufficient unoccupied suitable nesting habitat (i.e. habitat without land-based predators, human disturbance, or high rates of bald eagle depredation) to support large increases in double-crested cormorant nesting populations. We also demonstrated high connectivity of the ESI cormorant colony with coastal regions throughout the range of the western North America population, with the highest connectivity to major estuary systems. We did not detect strong connectivity with the Oregon Coast, however, or with interior regions east of the Cascade-Sierra Nevada mountain divide. Finally, in our study cormorant capture and satellite-tagging occurred very early in the nesting season and it is entirely possible that dispersal patterns would be different if double-crested cormorants had experienced this disturbance at ESI later in the nesting season. To fully understand the potential dispersal and redistribution of ESI cormorants in response to future disturbances, either management-related or natural, we recommend regular comprehensive region-wide breeding population censuses, as well as research on cormorant movements following reduction of nesting habitat on ESI to levels that will not accommodate the current number of breeding pairs.

Regional natural resource managers have established a goal of reducing the number of double-crested cormorant nesting pairs at the ESI colony by ca. 60% in order to limit the colony's impact on survival of ESA-listed juvenile salmonids out-migrating to the North Pacific (NOAA 2014). To accomplish this goal, in 2015 management agencies began to implement a four-year plan to cull ca. 11,000 adult double-crested cormorants in the lower Columbia River estuary, as well as oil or otherwise destroy 72.5% of ESI's cormorant nests during the first three years (USACE 2015). Culling was viewed as a preferable option to that of habitat reduction intended to encourage dispersal due to the possible need for management efforts to prevent the growth or establishment of colonies in areas where dispersing cormorants might still consume fish of conservation concern. During the 2016 nesting season, as lethal management actions were underway, the entire ESI cormorant colony abandoned nesting from mid-May through mid-June, after which some cormorants returned and attempted to re-nest (USACE 2017). The precise cause of this colony abandonment remains undetermined, but this unexpected event illustrates the possibility of large-scale dispersal under any management approach to reducing the size of the ESI colony. The dispersal patterns observed in this study indicate that cormorants have the capacity to disperse long distances to the north or south if necessary, but most individuals would likely choose more proximate estuary locations, if appropriate habitat were available and suitably secure from predators and human disturbance.

LITERATURE CITED

Adkins, J. Y., and D. D. Roby. 2010. A status assessment of the double-crested cormorant (*Phalacrocorax auritus*) in western North America: 1998-2009. Unpublished Report to the U.S. Army Corps of Engineers. U.S. Geological Survey, Corvallis, Oregon, USA.

Adkins, J. Y., D. D. Roby, D. E. Lyons, K. N. Courtot, K. Collis, H. R. Carter, W. D. Shuford, and P. J. Capitolo. 2014. Recent population size, trends, and limiting factors for the double-crested cormorant in western North America. Journal of Wildlife Management 78:1131–1142.

Ainley, D. G., D. W. Anderson, and P. R. Kelly. 1981. Feeding ecology of marine cormorants in southwestern North America. Condor 83:120–131.

Anderson, C. D., D. D. Roby, and K. Collis. 2004. Foraging patterns of male and female double-crested cormorants nesting in the Columbia River estuary. Canadian Journal of Zoology 82:541–554.

Argos. 2007. Argos user's manual. Collecte Localisation Satellites. Ramonville Saint-Agne, France. <http://www.argos-system.org/manual>. Accessed 18 Jan 2017.

Bird Research Northwest [BRNW]. 2014. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River, Final 2013 Annual Report. Bonneville Power Administration, U.S. Army Corps of Engineers, and Grant County Public Utility District, Portland, Oregon, USA. <www.birdresearchnw.org>. Accessed 18 Jan 2017.

Bird Research Northwest [BRNW]. 2015. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River, Final 2014 Annual Report. Bonneville Power Administration, U.S. Army Corps of Engineers, and Grant County Public Utility District, Portland, Oregon, USA. <www.birdresearchnw.org>. Accessed 18 Jan 2017.

Carter, H. R., A. L. Sowls, M. S. Rodway, U. W. Wilson, R. W. Lowe, G. J. McChesney, F. Gress, and D. W. Anderson. 1995. Population size, trends, and conservation problems of the double-crested cormorant on the Pacific coast of North America. Colonial Waterbirds 18:189–215.

Collis, K., D. D. Roby, D. P. Craig, S. Adamany, J. Y. Adkins, and D. E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: implications for losses of juvenile salmonids to avian predation. Transactions of the American Fisheries Society 131:537–550.

Courtot, K. N., D. D. Roby, J. Y. Adkins, D. E. Lyons, D. T. King, and R. S. Larsen. 2012. Colony connectivity of Pacific coast double-crested cormorants based on post-breeding dispersal from the region's largest colony. Journal of Wildlife Management 76:1462–1471.

Courtot, K. N., D. D. Roby, L. H. Kerr, D. E. Lyons, and J. Y. Adkins. 2016. A low-disturbance capture technique for ground-nesting double-crested cormorants (*Phalacrocorax auritus*). Waterbirds 3:193–198.

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79:2415–2428.

Day, J. W., Jr., B .C. Crump, W. M. Kemp, and A. Yanez-Arancibia, editors. 2013. Estuarine Ecology. Second Edition. Wiley-Blackwell, Hoboken, New Jersey, USA.

Dorr, B. S., J. J. Hatch, and D. V. Weseloh. 2014. Double-crested cormorant (*Phalacrocorax auritus*). The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://birdsna.org/Species-Account/bna/species/doccor>. Accessed 18 Jan 2017.

Duerr, A. E., T. M. Donovan, and D. E. Capen. 2007. Management-induced reproductive failure and breeding dispersal in double-crested cormorants on Lake Champlain. Journal of Wildlife Management 71:2565–2574.

Evans, A. F., N. J. Hostetter, D. D. Roby, K. Collis, D. E. Lyons, B. P. Sandford, R. D. Ledgerwood, and S. Sebring. 2012. Systemwide evaluation of avian predation on juvenile salmonids from the Columbia River based on recoveries of passive integrated transponder tags. Transactions of the American Fisheries Society 141:975-989.

Guillaumet, A., B. S. Dorr, G. Wang, and T. J. Doyle. 2014. The cumulative effects of management on the population dynamics of the double-crested cormorant (*Phalacrocorax auritus*) in the Great Lakes. Ibis 156:141–152.

Guillaumet, A., B. Dorr, G. Wang, J. D. Taylor, R. B. Chipman, H. Scherr, J. Bowman, K. F. Abraham, T. J. Doyle, and E. Cranker. 2011. Determinants of local and migratory movements of Great Lakes double-crested cormorants. Behavioral Ecology 22:1096–1103.

Hatch, J. J. 1995. Changing populations of double-crested cormorants. Colonial Waterbirds 18:8–24.

Hedenström, A., and T. Alerstam. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227–234.

Hénaux, V., T. Bregnaballe, and J. D. Lebreton. 2007. Dispersal and recruitment during population growth in a colonial bird, the great cormorant (*Phalacrocorax carbo sinensis*). Journal of Avian Biology 38:44–57.

Henny, C. J., L. J. Blus, S. P. Thompson, and U. W. Wilson. 1989. Environmental contaminants, human disturbance and nesting of double-crested cormorants in northwest Washington. Colonial Waterbirds 12:198-206.

Horton, C. A. 2014. Top-down influences of bald eagles on common murre populations in Oregon. Thesis, Oregon State University, Corvallis, Oregon, USA.

King, D. T., M. E. Tobin, and M. Bur. 2000. Capture and telemetry techniques for double-crested cormorants (*Phalocrocorax auritus*). Pages 54-57 *in* Proceedings of the 19th Vertebrate Pest Conference, University of California, Davis, USA.

Lyons, D. E. 2010. Bioenergetics-based predator-prey relationships between piscivorous birds and juvenile salmonids in the Columbia River estuary. Dissertation, Oregon State University, Corvallis, Oregon, USA.

Lyons, D. E., D. D. Roby, and K. Collis. 2007. Foraging patterns of Caspian terns and double-crested cormorants in the Columbia River estuary. Northwest Science 81:91–103.

Mercer, D. M., S. M. Haig, and D. D. Roby. 2013. Phylogeography and population genetic structure of double-crested cormorants (*Phalacrocorax auritus*). Conservation Genetics 14:823–836.

Moul, I. E., and M. B. Gebauer. 2002. Status of the double-crested cormorant in British Columbia. British Columbia Ministry of Water, Land and Air Protection, Biodiversity Branch, Victoria, British Columbia, Canada.

National Oceanic and Atmospheric Administration [NOAA]. 2014. Federal Columbia River power system 2014 supplemental biological opinion. National Marine Fisheries Service, Northwest Region, Seattle, Washington, USA.

Pacific Flyway Council [PFC]. 2012. Pacific flyway plan: a framework for the management of double-crested cormorant depredation on fish resources in the Pacific flyway. Pacific Flyway Council, U.S. Fish and Wildlife Service, Portland, Oregon, USA.

Parrish, J. K., M. Marvier, and R. T. Paine. 2001. Direct and indirect effects: interactions between bald eagles and common murres. Ecological Applications 11:1858-1869.

Scherr, H., J. Bowman, and K. F. Abraham. 2010. Migration and winter movements of double-crested cormorants breeding in Georgian Bay, Ontario. Waterbirds 33:451–460.

Schjørring, S., J. Gregersen, and T. Bregnaballe. 1999. Prospecting enhances breeding success of first-time breeders in the great cormorant (*Phalacrocorax carbo sinensis*). Animal Behaviour 57:647–654.

Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7:533–555.

U.S. Army Corps of Engineers [USACE]. 2015. Final environmental impact statement: double-crested cormorant management plan to reduce predation of juvenile salmonids in the Columbia River estuary. U.S. Army Corps of Engineers, Portland District, Portland, Oregon, USA.

U.S. Army Corps of Engineers [USACE]. 2017. Double-crested cormorant monitoring report, avian predation program monitoring, draft report. U.S. Army Corps of Engineers, Portland District, Portland, Oregon, USA.

U.S. Fish and Wildlife Service [USFWS]. 2003. Final environment impact statement: double-crested cormorant management in the United States. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, Virginia, USA.

U.S. Fish and Wildlife Service [USFWS]. 2005. Record of decision: Caspian tern management to reduce predation of juvenile salmonids in the Columbia River estuary, final environmental impact statement. U.S. Fish and Wildlife Service, Migratory Birds and Habitat Programs, Portland, Oregon, USA.

Weber, T. P., B. J. Ens, and A. I. Houston. 1998. Optimal avian migration: a dynamic model of fuel stores and site use. Evolutionary Ecology 12:377–401.

Weitkamp, L. A., P. J. Bentley, and M. N. C. Litz. 2012. Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. Fishery Bulletin 110:426–450.

Weitkamp, L. A., T. P. Good, D. E. Lyons, and D. D. Roby. 2016. The influence of environmental variation on the Columbia River estuarine fish community: implications for predation on juvenile salmonids. North Pacific Anadromous Fish Commission Bulletin 6:33-44.

Wilks, D. S. 2011. Statistical methods in the atmospheric sciences. Academic Press, Cambridge, Massachusetts, USA.

Wires, L. R. 2014. The double-crested cormorant: plight of a feathered pariah. Yale University Press, New Haven, Connecticut, USA.

Wires, L. R., and F. J. Cuthbert. 2006. Historic populations of the double-crested cormorant (*Phalacrocorax auritus*): implications for conservation and management in the 21st century. Waterbirds 29:9–37.

Wires, L. R., and F. J. Cuthbert. 2010. Characteristics of double-crested cormorant colonies in the U.S. Great Lakes island landscape. Journal of Great Lakes Research 36:232–241.

Wires, L. R., F. J. Cuthbert, D. R. Trexel, and A. R. Joshi. 2001. Status of the double-crested cormorant (*Phalocrocorax auritus*) in North America. Final Report to U.S. Fish and Wildlife Service. University of Minnesota, St. Paul, USA.

Wright, H. W. 1913. The birds of San Martin Island, lower California. Condor 15:207–210.

Zamon, J. E., E. M. Phillips, and T. J. Guy. 2014. Marine bird aggregations associated with the tidally-driven plume and plume fronts of the Columbia River. Deep Sea Research II: Topical Studies in Oceanography, Fronts, Fish and Top Predators 107:85–95.

Table 3.1. Connectivity of double-crested cormorants (n = 80) satellite-tagged on East Sand Island (ESI) during the pre-breeding period with other regions and colonies (indented) away from ESI during the 2-week period (April 14-30) immediately following capture and tagging early in the 2013 nesting season. Weighted distributions were adjusted to account for different satellite tag (PTT) sampling rates. The connectivity index is a measure of relative magnitude of use of locations where tagged cormorants were detected; the higher the value, the greater the apparent connectivity. Connectivity indices are comparable among regions or among colonies, but not between regions and colonies. Each colony was assigned a classification of either "A" for active or "H" for historical (formerly active).

Region Colony (status)	**Individuals** Count (percentage)	**Weighted detections** Count (percentage)	**Connectivity Index**
Salish Sea	**1 (1)**	**16 (2)**	**-1.9**
Outer Washington Coast	**18 (23)**	**80 (8)**	**-1.0**
Grays Harbor Channel Markers (A)	2 (3)	20 (2)	-0.8
Columbia River Basin[a]	**29 (37)**	**299 (31)**	**0.2**
Lewis & Clark Bridge - Longview (A)	10 (13)	88 (9)	0.1
McGuire Island (H)	1 (1)	2 (<1)	-1.0
Troutdale Power Towers (A)	3 (4)	30 (3)	-0.7
Columbia River Estuary[b]	**68 (86)**	**565 (58)**	**2.7**
Astoria-Megler Bridge (A)	63 (80)	482 (50)	5.3
Desdemona Sands Pilings (H)	9 (11)	17 (2)	-0.5
Rice Island (H)	1 (1)	2 (<1)	-1.0
Trestle Bay (H)	1 (1)	1 (<1)	-1.0
Upper Estuary Channel Markers (A)	6 (8)	28 (3)	-0.5

[a] Not including the Columbia River estuary, below Puget Island

[b] Not including East Sand Island

Table 3.2. Connectivity of double-crested cormorants (n = 84) satellite-tagged on East Sand Island (ESI) during the pre-breeding period with other regions and colony sites (indented) away from ESI during the breeding season (May 1 – September 15). Weighted distributions were adjusted to account for different satellite tag (PTT) sampling rates. The connectivity index is a measure of relative magnitude of use of locations where cormorants were detected; the higher the value, the greater the apparent connectivity. Connectivity indices are comparable among regions or among colonies, but not between regions and colonies. Each colony was assigned a classification of either "A" for active or "H" for historical (formerly active).

Region Colony (status)	**Individuals** Count (percentage)	**Weighted detections** Count (percentage)	**Connectivity Index**
Outer Vancouver Island	**3 (4)**	**131 (3)**	**-1.0**
Salish Sea	**16 (19)**	**389 (9)**	**-0.1**
Second Narrows Bridge (A)	1 (1)	8 (<1)	-1.0
Snohomish River Mouth (A)	1 (1)	50 (1)	-0.8
Outer Washington Coast	**54 (64)**	**1947 (45)**	**3.8**
Goose Island (H)	12 (14)	80 (2)	0.2
Grays Harbor Channel Markers (A)	7 (8)	76 (2)	-0.2
Tunnel Islands (A)	1 (<1)	2 (<1)	-1.0
Unnamed Sand Island (A)	31 (37)	981 (23)	5.2
Willoughby Rock (A)	1 (1)	2 (<1)	-1.0
Columbia River Basin[a]	**17 (20)**	**382 (9)**	**-0.1**
Lewis & Clark Bridge - Longview (A)	7 (8)	60 (1)	-0.3
McGuire Island (H)	1 (1)	10 (<1)	-1.0
Tri-Club Island (H)	1 (1)	2 (<1)	-1.0
Troutdale Power Towers (A)	1 (1)	179 (4)	-0.3
Columbia River Estuary[b]	**67 (80)**	**1425 (33)**	**3.5**
Astoria-Megler Bridge (A)	43 (51)	532 (12)	4.4
Desdemona Sands Pilings (H)	8 (10)	17 (<1)	-0.4
Rice Island (H)	41 (49)	698 (16)	4.8
Trestle Bay (H)	1 (1)	1 (<1)	-1.0
Upper Estuary Channel Markers (A)	13 (15)	28 (1)	0.0
Oregon Coast	**3 (4)**	**33 (1)**	**-1.2**
Three Arches Rock - Finley Rock (A)	1 (1)	7 (<1)	-1.0
Three Arches Rock - Middle Rock (A)	1 (1)	1 (<1)	-1.0
Three Arches Rock - Shag Rock (H)	1 (1)	1 (<1)	-1.0
Unnamed - Southern Coast 3 (A)	1 (1)	2 (<1)	-1.0
Northern California Coast	**3 (4)**	**13 (<1)**	**-1.2**
Prince Island (A)	4 (7)	2 (<1)	-0.8
White Rock - Del Norte (A)	2 (3)	2 (<1)	-0.9
San Francisco Bay	**1 (1)**	**4 (<1)**	**-1.3**
Central Valley	**3 (4)**	**24 (1)**	**-1.2**
Salton Trough	**2 (2)**	**9 (<1)**	**-1.2**
Salton Sea - North (A)	1 (1)	1 (<1)	-1.0

[a] Not including the Columbia River estuary, below Puget Island

[b] Not including East Sand Island

Table 3.3. Connectivity of double-crested cormorants (n = 80) satellite-tagged on East Sand Island (ESI) during the pre-breeding season with other regions and colony sites (indented) away from ESI during the non-breeding season (September 16 - April 15). Weighted distributions were adjusted to account for different satellite tag (PTT) sampling rates. The connectivity index is a measure of relative magnitude of use of locations where cormorants were detected; the higher the value, the greater the apparent connectivity. Connectivity indices are comparable among regions or among colonies, but not between regions and colonies. Each colony was assigned a classification of either "A" for active or "H" for historical (formerly active).

Region Colony (status)	**Individuals** Count (percentage)	**Weighted detections** Count (percentage)	**Connectivity Index**
Outer Vancouver Island	**4 (5)**	**656 (5)**	**-1.2**
Salish Sea	**25 (31)**	**4479 (33)**	**3.3**
Bird Rocks (A)	1 (1)	49 (<1)	-0.6
Mandarte Island (A)	1 (1)	14 (<1)	-0.8
Minor Island (A)	1 (1)	21 (<1)	-0.8
Snohomish River Mouth (A)	3 (4)	243 (2)	1.0
Outer Washington Coast	**47 (59)**	**1576 (12)**	**2.3**
Goose Island - Grays Harbor (H)	6 (8)	63 (<1)	0.2
Grays Harbor Channel Markers (A)	1 (1)	7 (<1)	-0.9
Unnamed Sand Island (A)	28 (35)	553 (4)	6.7
Columbia River Basin[a]	**19 (24)**	**2097 (15)**	**0.9**
Lewis and Clark Bridge - Longview (A)	6 (8)	48 (<1)	0.1
Smith and Bybee (H)	1 (1)	7 (<1)	-0.9
Troutdale Power Towers (A)	1 (1)	9 (<1)	-0.9
Columbia River Estuary[b]	**47 (59)**	**944 (7)**	**1.8**
Astoria-Megler Bridge (A)	39 (49)	631 (5)	8.8
Desdemona Sands Pilings (H)	3 (4)	27 (<1)	-0.5
Rice Island (H)	14 (18)	210 (2)	2.3
Upper Estuary Channel Markers (A)	4 (5)	9 (<1)	-0.4
Oregon Coast	**8 (10)**	**107 (1)**	**-1.4**
Table Rock (A)	1 (1)	2 (<1)	-0.9
Unnamed - Cape Lookout N. Rock (H)	1 (1)	7 (<1)	-0.9
Unnamed - Central Coast (A)	1 (1)	2 (<1)	-0.9
Unnamed - Southern Coast 1 (A)	1 (1)	7 (<1)	-0.9
Unnamed - Southern Coast 3 (A)	1 (1)	7 (<1)	-0.9
Northern California Coast	**14 (18)**	**657 (5)**	**-0.6**
Arcata Bay Sand Islands (A)	8 (10)	149 (1)	1.1
Castle Rock (A)	1 (1)	2 (<1)	-0.9
Hog Island (A)	2 (3)	90(1)	-0.2
Little River Rock (A)	1 (1)	1 (<1)	-0.9
Old Arcata Wharf (A)	1 (1)	30 (<1)	-0.7
Tolowa Rocks (H)	1 (1)	1 (<1)	-0.9
Northern California Interior	**1 (1)**	**21 (<1)**	**-1.9**

Table 3.3. (continued).

Region Colony (status)	**Individuals** Count (percentage)	**Weighted detections** Count (percentage)	**Connectivity Index**
San Francisco Bay	**13 (16)**	**1449 (11)**	**0.0**
Cut off Slough - Bohannon (A)	2 (3)	117 (1)	0.0
Eucalyptus Island (A)	3 (4)	77 (<1)	-0.1
Greco Island Power Towers (A)	1 (1)	35 (<1)	-0.7
Lake Merritt (A)	2 (3)	14 (<1)	-0.7
Moffett B2 (A)	1 (1)	7 (<1)	-0.9
Moffett Power Towers (A)	1 (1)	7 (<1)	-0.9
Richmond - San Rafael Bridge (A)	5 (6)	116 (1)	0.4
San Fran. - Oakland Bay Bridge (A)	6 (8)	511 (4)	3.3
San Mateo Bridge & PG&E Towers (A)	2 (3)	23 (<1)	-0.6
Wheeler Island (A)	1 (1)	2 (<1)	-0.9
Central Valley	**14 (18)**	**658 (5)**	**-0.6**
Buena Vista Lake (H)	1 (1)	14 (<1)	-0.8
Gardner's Cove - San Joaquin River (A)	1 (1)	7 (<1)	-0.9
Kern County Water Agency (A)	1 (1)	85 (1)	-0.3
Milburn - San Juaquin River (A)	1 (1)	7 (<1)	-0.9
Southern California Bight	**4 (5)**	**235 (2)**	**-1.5**
Sepulveda Dam Rec. Area (A)	1 (1)	2 (<1)	-0.9
Salton Trough	**5 (6)**	**695 (5)**	**-1.1**
76th Avenue (H)	1 (1)	1 (<1)	-0.9
Mallard Rd. Gun Club (H)	3 (4)	58 (<1)	-0.2
Ramer Lake (A)	3 (4)	90 (1)	0.0
Salton Sea - North (A)	3 (4)	45 (<1)	-0.3

[a] Not including the Columbia River estuary, below Puget Island

[b] Not including East Sand Island

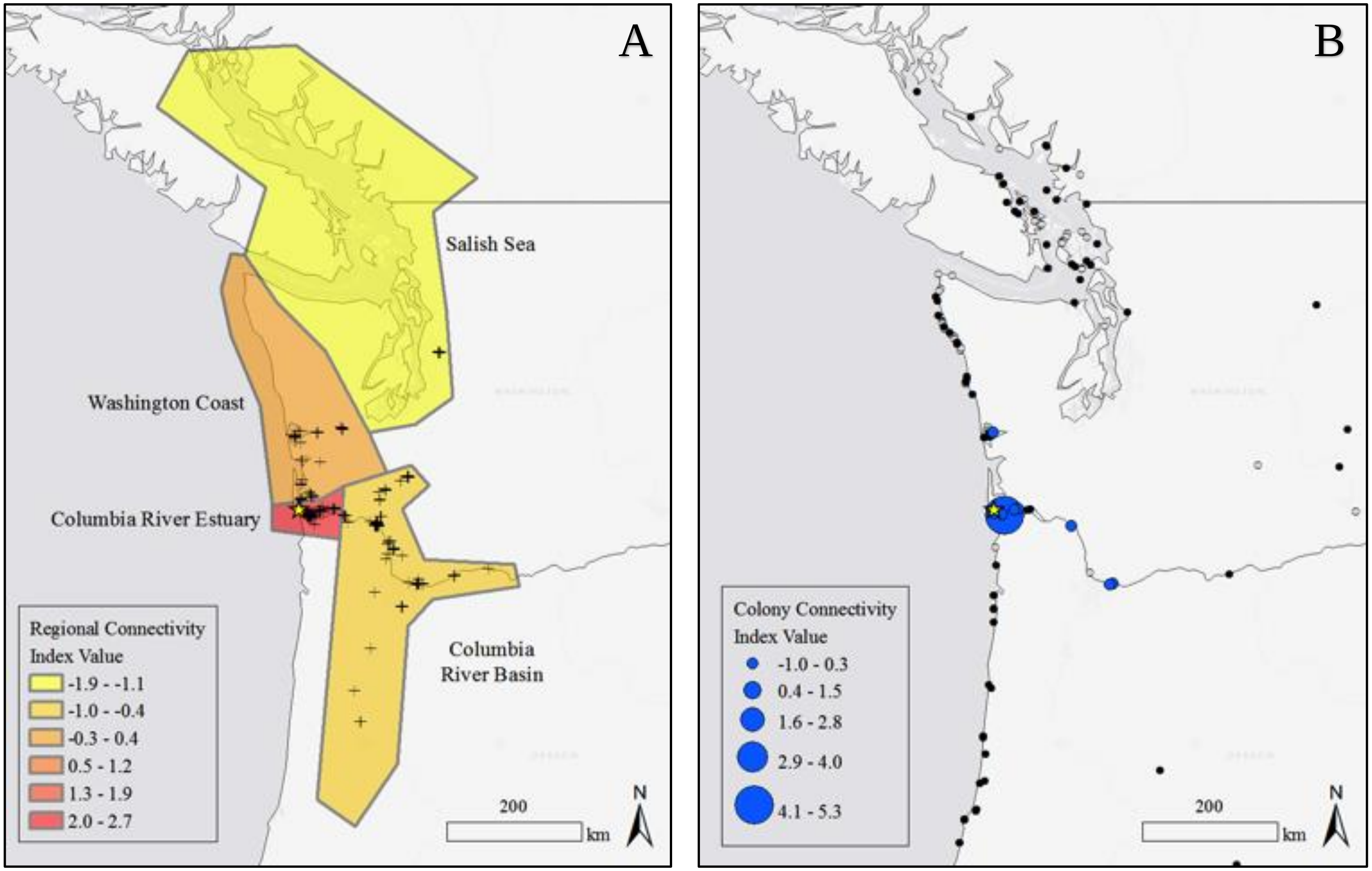

Figure 3.1. Relative regional connectivity (A) based on roost locations (+) during the two-week pre-breeding period for double-crested cormorants satellite-tagged at East Sand Island (n = 80) in 2013, represented by shaded regions. Colony connectivity (B) during the same period is depicted by graduated blue circles. Distributions of active (●) and historical (○) colony locations for the western North America breeding population that were not visited by satellite-tagged cormorants from East Sand Island during this period are also shown.

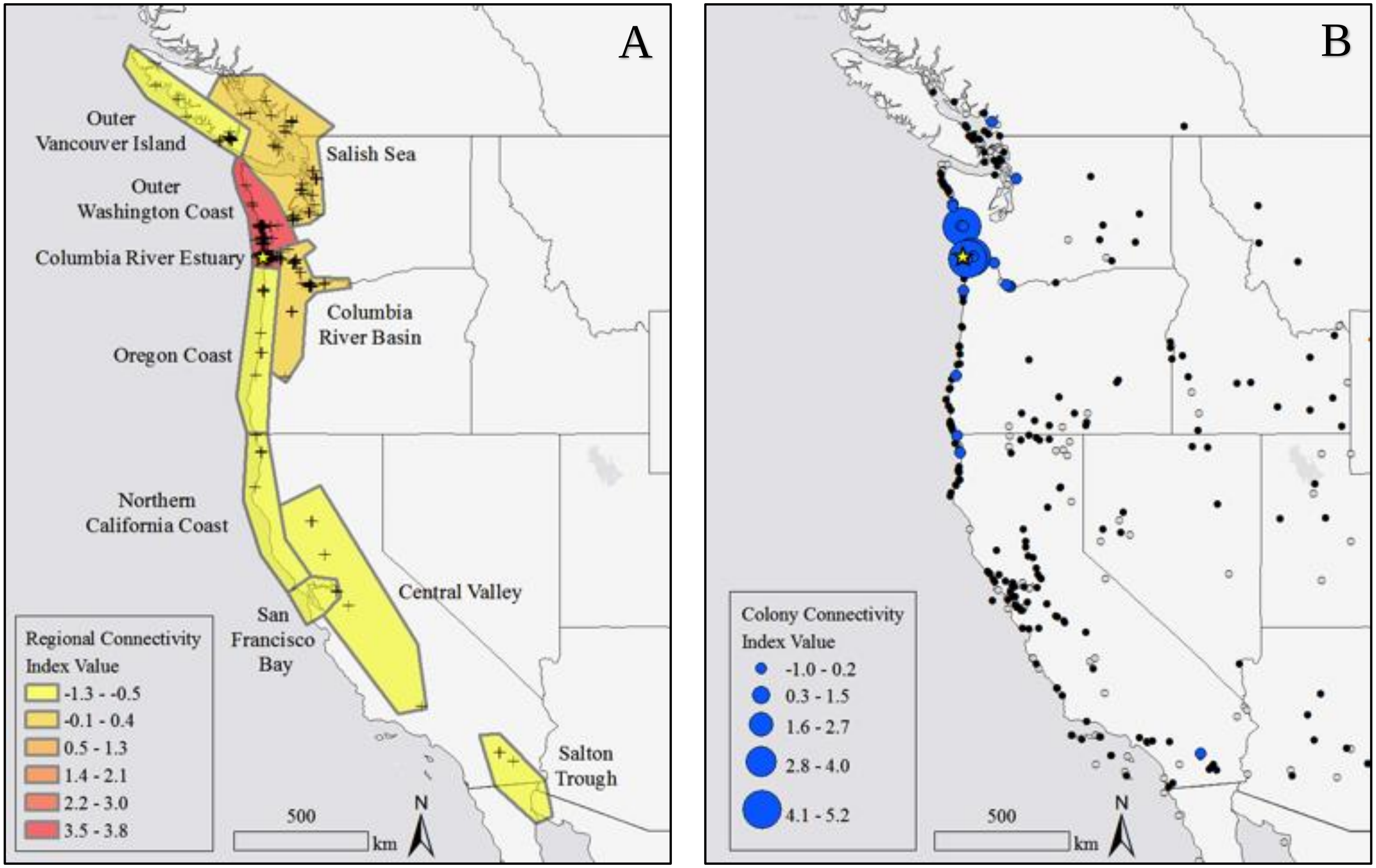

Figure 3.2. Relative regional connectivity (A) based on roost locations (+) during the breeding season for double-crested cormorants satellite-tagged at East Sand Island (n = 84) in 2012 and 2013, represented by shaded regions. Colony connectivity (B) during the same period is depicted by graduated blue circles. Distributions of active (●) and historical (○) colony locations for the western North America breeding population that were not visited by satellite-tagged cormorants from East Sand Island during this period are also shown.

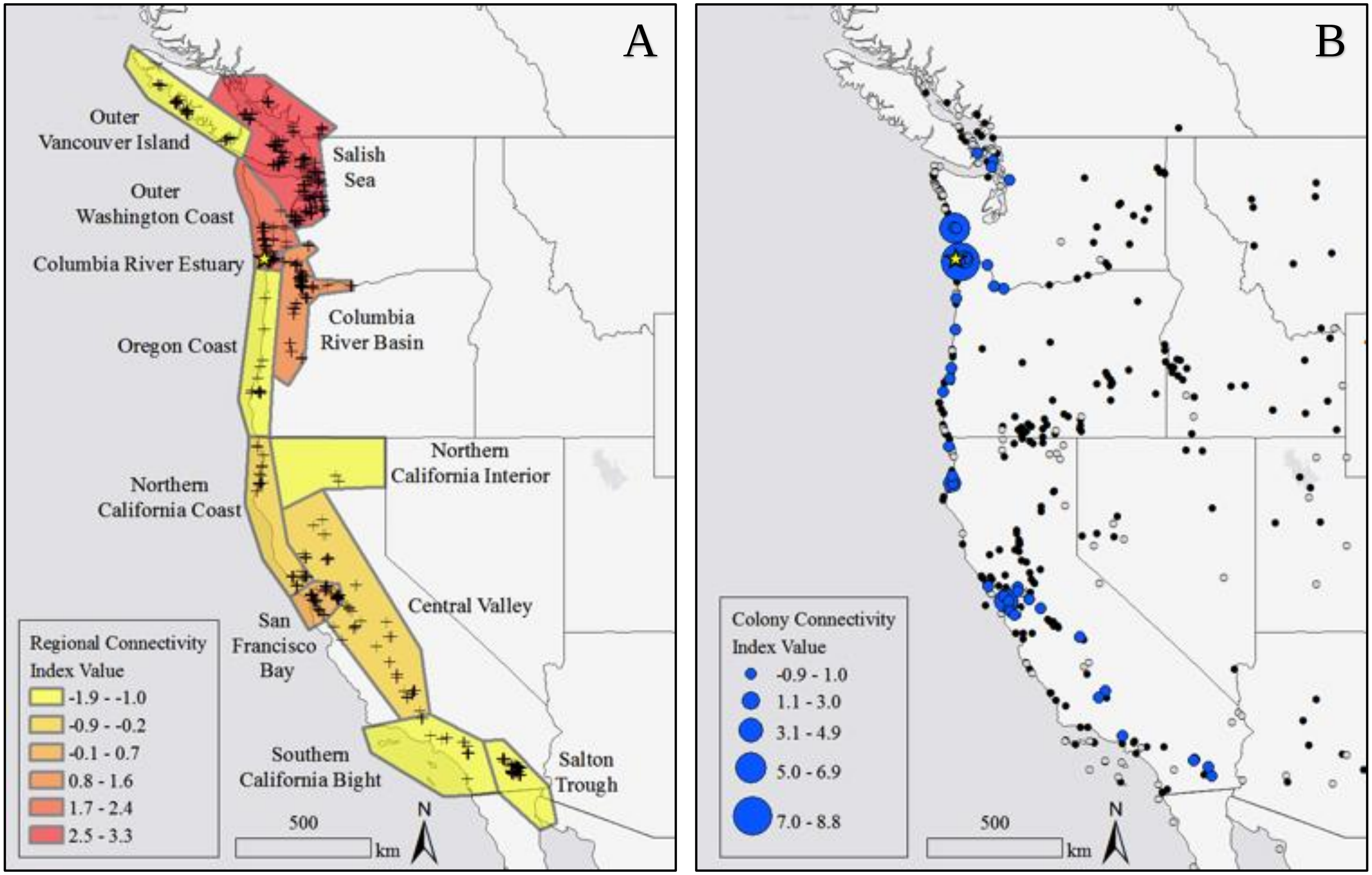

Figure 3.3. Relative regional connectivity (A) based on roost locations (+) during the non-breeding season for double-crested cormorants satellite-tagged at East Sand Island (n = 80) in 2012 and 2013, represented by shaded regions. Colony connectivity (B) during the same period is depicted by graduated blue circles. Distributions of active (●) and historical (○) colony locations for the western North America breeding population that were not visited by satellite-tagged cormorants from East Sand Island during this period are also shown.

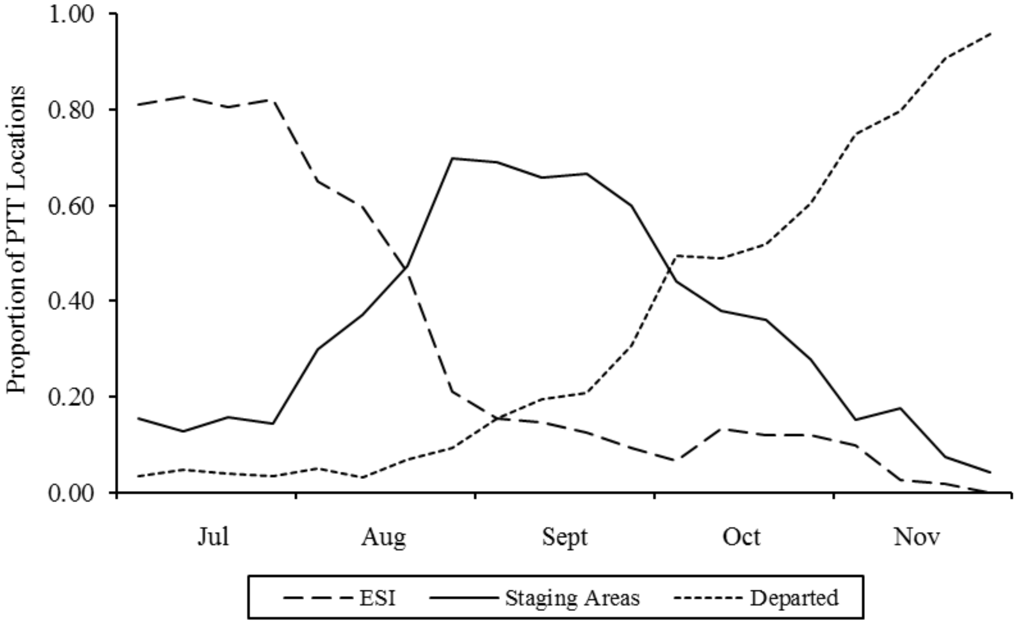

Figure 3.4. The proportion of location fixes for double-crested cormorants that were satellite-tagged (PTT) on East Sand Island and subsequently detected during late summer and fall at either East Sand Island (ESI), staging areas near ESI, or other regions more removed from ESI (departed). Detections from July through November are plotted, a period of time covering the transition from the breeding season to the non-breeding season.

CHAPTER 4: SYNOPSIS AND CONCLUSIONS

Adam G. Peck-Richardson

This thesis is comprised of two distinct studies that utilized miniaturized telemetry tags to study the foraging ecology and movement patterns of cormorants nesting at East Sand Island (ESI) in the Columbia River estuary. The first study, presented in Chapter 2, investigated the breeding-season foraging ecology and resource partitioning of two congeneric species of cormorants, Brandt's cormorant (*Phalacrocorax penicillatus*) and double-crested cormorant (*P. auritus*), nesting in a mixed species colony on ESI. The second study, presented in Chapter 3, investigated potential dispersal during the breeding season and subsequent post-breeding dispersal movements by double-crested cormorants that were captured and tagged on ESI during the pre-breeding period. Information on the colony connectivity and regional connectivity of double-crested cormorants from this colony was intended to inform managers evaluating potential management actions to reduce consumption by cormorants of ESA-listed juvenile salmonids in the Columbia River estuary. Taken together, the two studies significantly advance our understanding of cormorant ecology within the Pacific Flyway, the respective niches of the two cormorant species, and the importance of coastal estuaries as nesting and foraging habitat for both species.

My study of cormorant foraging ecology is the first to use a combination of GPS and temperature-depth data loggers to describe double-crested cormorant and Brandt's cormorant foraging distributions and habitat use in high resolution. This robust data set allowed me to not only describe and compare species-specific foraging areas across the geographic plane, it also allowed me to detect interspecific differences in habitat use as a function of depth in the water column. My results revealed that double-crested cormorants and Brandt's cormorants, breeding at a mixed-species colony on ESI in the Columbia River estuary, used foraging habitat differently. The core foraging areas and overall foraging areas of the two species overlapped to a considerable extent; however, double-crested cormorants foraged over a much larger area than Brandt's cormorants, and utilized a much wider variety of estuarine habitat types. Conversely, Brandt’s cormorants foraged across a smaller area and almost exclusively in marine habitats. Moreover, in areas where the two species overlapped, they used different microhabitats for foraging.

Double-crested cormorant use of freshwater and mixed estuarine habitats and shallower dive locations compared to Brandt’s cormorants was consistent with prior studies that found double-crested cormorants preferentially selected shallower foraging habitats (Coleman et al. 2005, Dorr et al. 2014) and are more likely to forage in estuaries along the West Coast of the U.S. than other cormorant species (Ainley et al. 1981). Across their range, double-crested cormorants exploit many shallow-water habitats where the capacity for deep dives may confer little or no advantage while foraging for fish (Dorr et al. 2014). Consequently, behavioral and physiological traits that support deep diving may not be subject to strong selection pressure in double-crested cormorants throughout much of their range. Therefore, the interspecific differences in foraging habitat selection observed in my study may be a function of evolutionary divergence and, despite the high degree of overlap in foraging areas between the two species, suggest there is limited direct competition for prey resources between the two cormorant species nesting on East Sand Island in the Columbia River estuary.

Previous studies of the foraging patterns of double-crested cormorants nesting at East Sand Island reported that they disproportionately utilized freshwater habitats early in the nesting season, and then shifted more to marine habitats later in the nesting season (Anderson et al. 2004, Lyons et al. 2007). This mid-nesting season shift in foraging distribution corresponds with the seasonal decline in abundance of out-migrating juvenile salmonids in the Columbia River estuary (Lyons et al. 2007, Weitkamp et al. 2012), and also corresponds with the seasonal decline in the prevalence of juvenile salmonids in the diet of double-crested cormorants nesting on East Sand Island (Lyons

2010). Marine forage fish comprise the majority of the diet of double-crested cormorants nesting on ESI during the latter part of the nesting season (Collis et al. 2002, Lyons 2010). The freshwater foraging distribution of double-crested cormorants observed in our study is consistent with previous studies in the Columbia River estuary, and suggests that double-crested cormorants nesting at this colony exploit seasonally abundant out-migrating juvenile salmonids as they pass through the estuary (Anderson et al. 2004, Lyons et al. 2007).

Previous research on the feeding ecology of Brandt's and double-crested cormorants along the Pacific Coast found almost no overlap in diet composition between the two species (Ainley et al. 1981). Couch and Lance (2004), however, found that the prey species represented in the diet of Brandt's cormorants nesting on East Sand Island overlapped almost completely with those in the diet of double-crested cormorants nesting on the same island (relative proportions of prey in the diet of each species could not be directly compared due to methodological differences, however). A general similarity in diet between the two cormorant species nesting at East Sand Island is consistent with the foraging patterns observed in my study, where the foraging area of Brandt's cormorants mostly overlapped with that of double-crested cormorants. Subsequent studies using juvenile salmonid PIT tags recovered from the East Sand Island cormorant colony indicated that Brandt's cormorants consumed approximately an order of magnitude fewer salmonids per individual compared to double-crested cormorants (BRNW 2014). This is consistent with our findings that Brandt's cormorants did not forage in freshwater estuarine habitats where they would be more likely to encounter juvenile salmonids relative to other potential prey types. Instead, they foraged overwhelmingly in marine habitats, tended to select deeper dive locations, and utilized a deeper portion of the water column compared with double-crested cormorants, all behavioral traits that would be expected to result in relatively fewer encounters with juvenile salmonids.

I also observed a high degree of intraspecific overlap in the foraging patterns of individual double-crested cormorants and Brandt’s cormorants that were GPS-tagged during the same time periods. Individuals from each species that were tracked utilized very similar foraging areas and commuted along similar routes on the same day, but at different times throughout the day. Local foraging areas shifted between days and these patterns were not apparent between species, only within species. While this study did not endeavor to analyze these patterns, these preliminary results suggest that individuals may share information about foraging locations with conspecifics at a breeding colony.

Resource partitioning among sympatric species may not be primarily a function of proximate competition for limited resources, but instead a function of evolutionary divergence. Species-specific evolutionary constraints were likely a causal mechanism for the observed inter-specific habitat segregation in this study. Furthermore, there may be little overlap in diet when there is an abundant prey resource that one species is better adapted to exploit, as appeared to be the case for double-crested cormorants preying on juvenile salmonids in the Columbia River estuary. It is also likely that superabundant forage fish resources at the mouth of the Columbia River have allowed a large colony of Brandt’s cormorants to form on an island where they share the majority of their foraging habitat with a similar-sized and far more numerous congener.

Results of my study on dispersal of double-crested cormorants from the colony on East Sand Island support the hypothesis that individuals nesting at this colony have high connectivity with regions and colonies across the full latitudinal extent of the range of the western North America population of the species. Furthermore, ESI cormorants visited regions and colonies throughout this range during both the breeding and non-breeding periods. Visits to regions and colonies during the breeding period could provide a cormorant with information on breeding activity and nesting success, information that could inform decisions about where to attempt to nest if the cormorant lost its current nesting site. Overall, double-crested cormorants nesting at ESI demonstrated the greatest connectivity with the Salish Sea, the outer Washington coast, and the lower Columbia River, but also visited sites throughout California. Cormorant detections away from ESI were particularly clustered around major coastal estuary systems. Despite this pattern of broad regional connectivity, no cormorants tagged on ESI were detected east of the Cascade or Sierra Nevada mountain ranges, supporting previous evidence of limited connectivity between the coastal and interior subpopulations within the western North America population (Courtot et al. 2012, Mercer et al. 2013). Furthermore, cormorants tagged in the present study had surprisingly low regional and colony connectivity with the Oregon Coast, despite numerous active and historical colonies in that region, as well as proximity to the colony at ESI.

Results of the study described in Chapter 3 were generally consistent with a previous study of post-breeding dispersal from ESI by Courtot et al. (2012), which found that the great majority of double-crested cormorants nesting at ESI migrated either north or south from the Columbia River estuary to overwinter. Fall migration occurred after departing late summer/early fall staging areas either in estuaries on the outer Washington coast or in the Columbia River estuary. Surprisingly, very few tagged cormorants remained in the Columbia River estuary through the non-breeding season. Also, cormorants dispersing north or south of the Columbia River estuary did not mix after departing the staging areas; southward migrating individuals did not visit regions to the north during winter, and northward migrating individuals did not visit regions to the south.

Staging area use was a major driver of regional and colony connectivity during both the breeding and non-breeding periods. Cormorant detections at staging areas in the upper Columbia River estuary, Willapa Bay, and Grays Harbor peaked from late August through early October, spanning both the breeding and non-breeding periods. High connectivity index values with the outer Washington coast and elsewhere in the Columbia River estuary during the non-breeding period were due to the high proportion of tagged individuals that staged in these two regions during fall (59% for each region), before moving to regions where they overwintered. The proportion of weighted detections in these two regions during the non-breeding period was low, however; only 12% of detections during the non-breeding period were from the outer Washington coast and only 7% of detections were from the Columbia River estuary. Tagged cormorants eventually departed these fall staging areas and overwintered elsewhere to the north or south. No tagged cormorants overwintered along the outer Washington coast and only two tagged individuals overwintered in the Columbia River estuary.

ESI has supported the largest breeding colony of double-crested cormorants in western North American and is likely the only site in this region that provides the necessary combination of abundant forage fish resources and ample nesting habitat secure from human disturbance and mammalian predators to support such a large colony. Furthermore, the large size of the ESI cormorant colony likely serves to dilute the impact of disturbance and predation from bald eagles (*Haliaeetus leucocephalus*) and other secondary nest predators, such as gulls (*Larus* spp.) and corvids (Family: Corvidae). Regional natural resource managers have established a goal of reducing the number of double-crested cormorant nesting pairs at the ESI colony by *ca.* 60% in order to limit the colony's impact on survival of ESA-listed juvenile salmonids out-migrating to the North Pacific. To accomplish this goal, management agencies implemented a four-year plan beginning in 2015 to cull *ca.* 11,000 adult double-crested cormorants in the lower Columbia River estuary, as well as oil or otherwise destroy 72.5% of the cormorant nests on ESI during the 2015-2018 breeding seasons. Phase two of this management plan would be implemented once the colony size was reduced to *ca.* 5,600 breeding pairs, and would consist of a reduction in nesting habitat in order to maintain the ESI double-crested cormorant colony at this size in perpetuity. During the 2016 nesting season, as lethal management actions were underway, the entire ESI cormorant colony abandoned nesting from mid-May until late June, when some cormorants returned to the colony and attempted to re-nest. The cause of this abrupt and temporary colony abandonment remains undetermined. It is in the context of this management and other potential disturbance factors that understanding the possible dispersal choices of double-crested cormorants nesting at ESI is important. The ESI double-crested cormorant colony remains the largest colony for this species in western North America and formerly represented *ca.* 40% of the regional population (Adkins et al. 2014).

My study demonstrated that double-crested cormorants are highly motivated to continue nesting at ESI and, in 2013, nearly all tagged individuals returned to the colony where they were captured despite being caught, handled, tagged, and forced to relocate to a new nesting area on ESI. Nevertheless, the 2013 management feasibility study did not restrict nesting habitat sufficiently to preclude even a small proportion of the cormorant colony from nesting on ESI colony, and a record number of double-crested cormorants nested on ESI that year. In order for habitat management to substantially reduce the size of the cormorant colony at ESI, the amount of suitable nesting habitat would need to be restricted to a much smaller area than the 2013 feasibility study attempted to do.

If management actions or other disturbances result in the dispersal of nesting double-crested cormorants from ESI, it cannot be definitively predicted where these individuals would be most likely to prospect for future nesting opportunities, although several results of this study inform that question. My study has demonstrated high connectivity between ESI and potential breeding sites elsewhere in the Columbia River estuary, as well as the nearby Grays Harbor estuary on the outer Washington coast. These regions apparently do not have sufficient unoccupied and suitable nesting habitat to support large increases in double-crested cormorant nesting populations; land-based predators, human disturbance, and/or high rates of bald eagle depredation are likely limiting factors. I also demonstrated high connectivity of the ESI double-crested cormorant colony with coastal regions throughout the range of the western North America population, and the highest connectivity was with major estuary systems. I did not detect strong connectivity with the Oregon Coast, however, or with interior regions east of the Cascade-Sierra Nevada mountain divide, suggesting immigration to these regions would be limited. Finally, the initial two-week dispersal period occurred very early in the nesting season, and it is possible that dispersal patterns would be different if double-crested cormorants had departed from ESI later in the nesting season. To fully understand the potential dispersal and redistribution of ESI cormorants in response to future disturbances, either management-related or natural, I recommend regular comprehensive region-wide breeding population censuses, as well as continued research on cormorant movements following reduction in available nesting habitat at ESI.

The combined results from the two studies described in this thesis demonstrate the importance of large coastal estuaries in the life history of the double-crested cormorant population in western North America. Estuaries are often a nexus of superabundant prey resources because they provide access to riverine and estuarine, as well as marine, forage fish species. Diverse prey resources from each of these multiple habitats also provide a degree of insulation from seasonal and inter-annual variation in availability of particular prey types that may be driven by large-scale climatic forcing, such as the Pacific Decadal Oscillation (PDO), El Nino-Southern Oscillation (ENSO), or global climate change (Brodeur et al. 2005), which may have different and potentially asynchronous impacts on those distinct habitats. Coastal regions are less affected by drought conditions that may limit availability of water, nesting habitat, and freshwater fish prey in interior regions. Estuaries may locally enhance marine productivity or provide refugia for marine forage fishes during years when coastal upwelling and upwelling-dependent productivity is otherwise suppressed (Brodeur et al. 2005, Litz et al. 2014). Our tracking results, combined with this understanding of estuarine productivity, highlight the outsized role that estuaries play in supporting the western North America population of double-crested cormorants. This conclusion also suggests the hypothesis that over the long term, coastal areas may function as demographic sources of individuals to less productive interior portions of the breeding range of the western North America population.

Estuaries may also play an increasingly important role in supporting Brandt's cormorant populations. Brandt's cormorants are infrequent estuarine inhabitants and the nesting colony on ESI is the largest for the species located within an estuary during our study period. The expansion of the Brandt's cormorant colony at ESI could be the result of a region-wide population expansion and subsequent movement of individuals into peripheral habitat, but there is little evidence of such a population increase (Naughton et al. 2007). Increased numbers at ESI could also be the result of a distributional shift due to natural or human disturbance at other colonies (Adkins et al. 2014). Regardless of cause, this shift may offer several benefits to the Brandt's cormorants nesting in the region. Heightened estuarine productivity supports superabundant prey resources within the Columbia River estuary and allows large colonies of double-crested and Brandt's cormorants to coexist at a shared colony despite potential interspecific competition for prey resources. Nesting sympatrically within a larger seabird colony (double-crested cormorants outnumber Brandt's cormorants by approximately an order of magnitude at East Sand Island) likely also affords a degree of security from predation by bald eagles. Furthermore, as with double-crested cormorants, estuaries may provide refugia for Brandt's cormorant breeding populations in years of poor coastal marine productivity.

LITERATURE CITED

Adkins, J. Y., D. D. Roby, D. E. Lyons, K. N. Courtot, K. Collis, H. R. Carter, W. D. Shuford, and P. J. Capitolo. 2014. Recent population size, trends, and limiting factors for the double-crested cormorant in western North America. Journal of Wildlife Management 78:1131–1142.

Ainley, D. G. 1984. Cormorants. Pages 92-101 *in* Seabirds of the eastern North Pacific and Arctic waters. (Haley, D., ed.) Pacific Search Press, Seattle, Washington, USA.

Anderson, C. D., D. D. Roby, and K. Collis. 2004. Foraging patterns of male and female double-crested cormorants nesting in the Columbia River estuary. Canadian Journal of Zoology 82:541–554.

Bird Research Northwest [BRNW]. 2014. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River, Final 2013 Annual Report. Bonneville Power Administration, U.S. Army Corps of Engineers, and Grant County Public Utility District, Portland, Oregon, USA. <www.birdresearchnw.org>. Accessed 18 Jan 2017.

Brodeur, R. D., J. P. Fisher, R. L. Emmett, C. A. Morgan, and E. Casillas. 2005. Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. Marine Ecology Progress Series 298:41-57.

Coleman, J. T. H., M. E. Richmond, L. G. Rudstam, and P. M. Mattison. 2005. Foraging location and site fidelity of the Double-Crested Cormorant on Oneida Lake, New York. Waterbirds 28:498–510.

Collis, K., D. D. Roby, D. P. Craig, S. Adamany, J. Y. Adkins, and D. E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: Implications for losses of juvenile salmonids to avian predation. Transactions of the American Fisheries Society 131:537–550.

Couch, S. L. L., and M. M. Lance. 2004. Diet composition and breeding success of Brandt's cormorants in the Columbia River estuary. Northwestern Naturalist 85:62–66.

Courtot, K. N., D. D. Roby, J. Y. Adkins, D. E. Lyons, D. T. King, and R. S. Larsen. 2012. Colony connectivity of Pacific Coast double-crested cormorants based on post-breeding dispersal from the region's largest colony. Journal of Wildlife Management 76:1462–1471.

Dorr, B. S., J. J. Hatch, and D. V. Weseloh. 2014. Double-crested cormorant (*Phalacrocorax auritus*). The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://birdsna.org/Species-Account/bna/species/doccor>. Accessed 18 Jan 2017.

Litz, M. N. C., R. L. Emmett, P. J. Bentley, A. M. Claiborne, C. Barceló. 2014. Biotic and abiotic factors influencing forage fish and pelagic nekton community in the Columbia River plume (USA) throughout the upwelling season 1999–2009. ICES Journal of Marine Science 71:5-18.

Lyons, D. E. 2010. Bioenergetics-based predator-prey relationships between piscivorous birds and juvenile salmonids in the Columbia River estuary. Dissertation, Oregon State University, Corvallis, Oregon, USA.

Lyons, D. E., D. D. Roby, and K. Collis. 2007. Foraging patterns of Caspian terns and double-crested cormorants in the Columbia River estuary. Northwest Science 81:91–103.

Mercer, D. M., S. M. Haig, and D. D. Roby. 2013. Phylogeography and population genetic structure of double-crested cormorants (*Phalacrocorax auritus*). Conservation Genetics 14:823–836.

Naughton, M., D. S. Pitkin, R. W. Lowe, K. J. So, and C. S. Strong. 2007. Catalog of Oregon Seabird Colonies. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Washington, D.C., USA.

Weitkamp, L. A., P. J. Bentley, and M. N. C. Litz. 2012. Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. Fishery Bulletin 110:426–450.

BIBLIOGRAPHY

Adams, J., C. MacLeod, R. M. Suryan, K. D. Hyrenbach, and J. T. Harvey. 2012. Summer-time use of west coast US national marine sanctuaries by migrating sooty shearwaters (*Puffinus griseus*). Biological Conservation; Seabirds and Marine Protected Areas Planning 156:105–116.

Adkins, J. Y., and D. D. Roby. 2010. A status assessment of the double-crested cormorant (*Phalacrocorax auritus*) in western North America: 1998-2009. Unpublished Report to the U.S. Army Corps of Engineers. U.S. Geological Survey, Corvallis, Oregon, USA.

Adkins, J. Y., D. D. Roby, D. E. Lyons, K. N. Courtot, K. Collis, H. R. Carter, W. D. Shuford, and P. J. Capitolo. 2014. Recent population size, trends, and limiting factors for the double-crested cormorant in western North America. Journal of Wildlife Management 78:1131–1142.

Ainley, D. G., D. W. Anderson, and P. R. Kelly. 1981. Feeding ecology of marine cormorants in southwestern North America. Condor 83:120–131.

Ainley, D. G. 1984. Cormorants. Pages 92-101 *in* Seabirds of the eastern North Pacific and Arctic waters. (Haley, D., ed.) Pacific Search Press, Seattle, Washington, USA.

Anderson, C. D., D. D. Roby, and K. Collis. 2004. Foraging patterns of male and female double-crested cormorants nesting in the Columbia River estuary. Canadian Journal of Zoology 82:541–554.

Argos. 2007. Argos user’s manual. Collecte Localisation Satellites. Ramonville Saint-Agne, France. <http://www.argos-system.org/manual>. Accessed 18 Jan 2017.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-48.

Bird Research Northwest [BRNW]. 2013. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River, Final 2012 Annual Report. Bonneville Power Administration, U.S. Army Corps of Engineers, and Grant County Public Utility District, Portland, Oregon, USA. <www.birdresearchnw.org>. Accessed 18 Jan 2017.

Bird Research Northwest [BRNW]. 2014. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River, Final 2013 Annual Report. Bonneville Power Administration, U.S. Army Corps of Engineers, and Grant County Public Utility District, Portland, Oregon, USA. <www.birdresearchnw.org>. Accessed 18 Jan 2017.

Bird Research Northwest [BRNW]. 2015. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River, Final 2014 Annual Report. Bonneville Power Administration, U.S. Army Corps of Engineers, and Grant County Public Utility District, Portland, Oregon, USA. <www.birdresearchnw.org>. Accessed 18 Jan 2017.

Bottom, D. L., and K. K. Jones. 1990. Species composition, distribution, and invertebrate prey of fish assemblages in the Columbia River estuary. Progress in Oceanography 25:243–270.

Brodeur, R. D., J. P. Fisher, R. L. Emmett, C. A. Morgan, and E. Casillas. 2005. Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. Marine Ecology Progress Series 298:41-57.

Carter, H. R., A. L. Sowls, M. S. Rodway, U. W. Wilson, R. W. Lowe, G. J. McChesney, F. Gress, and D. W. Anderson. 1995. Population size, trends, and conservation problems of the double-crested cormorant on the Pacific coast of North America. Colonial Waterbirds 18:189–215.

Coleman, J. T. H., M. E. Richmond, L. G. Rudstam, and P. M. Mattison. 2005. Foraging location and site fidelity of the Double-Crested Cormorant on Oneida Lake, New York. Waterbirds 28:498–510.

Collis, K., D. D. Roby, D. P. Craig, S. Adamany, J. Y. Adkins, and D. E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: Implications for losses of juvenile salmonids to avian predation. Transactions of the American Fisheries Society 131:537–550.

Couch, S. L. L., and M. M. Lance. 2004. Diet composition and breeding success of Brandt's cormorants in the Columbia River estuary. Northwestern Naturalist 85:62–66.

Courtot, K. N., D. D. Roby, J. Y. Adkins, D. E. Lyons, D. T. King, and R. S. Larsen. 2012. Colony connectivity of Pacific Coast double-crested cormorants based on post-breeding dispersal from the region's largest colony. Journal of Wildlife Management 76:1462–1471.

Courtot, K. N., D. D. Roby, L. H. Kerr, D. E. Lyons, and J. Y. Adkins. 2016. A low-disturbance capture technique for ground-nesting double-crested cormorants (*Phalacrocorax auritus*). Waterbirds 3:193–198.

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79:2415–2428.

Daunt, F., G. Peters, B. Scott, D. Gremillet, and S. Wanless. 2003. Rapid-response recorders reveal interplay between marine physics and seabird behaviour. Marine Ecology Progress Series 255:283–288.

Day, J. W., Jr., B .C. Crump, W. M. Kemp, and A. Yanez-Arancibia, editors. 2013. Estuarine ecology. Second Edition. Wiley-Blackwell, Hoboken, New Jersey, USA.

Dorr, B. S., J. J. Hatch, and D. V. Weseloh. 2014. Double-crested cormorant (*Phalacrocorax auritus*). The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://birdsna.org/Species-Account/bna/species/doccor>. Accessed 18 Jan 2017.

Duerr, A. E., T. M. Donovan, and D. E. Capen. 2007. Management-induced reproductive failure and breeding dispersal in double-crested cormorants on Lake Champlain. Journal of Wildlife Management 71:2565–2574.

Evans, A. F., N. J. Hostetter, D. D. Roby, K. Collis, D. E. Lyons, B. P. Sandford, R. D. Ledgerwood, and S. Sebring. 2012. Systemwide evaluation of avian predation on juvenile salmonids from the Columbia River based on recoveries of passive integrated transponder tags. Transactions of the American Fisheries Society 141:975-989.

Faraway, J. J. 2006. Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Chapman & Hall/CRC Press, Boca Raton, Florida, USA.

Fritsch, F. N., and R. E. Carlson. 1980. Monotone piecewise cubic interpolation. SIAM Journal on Numerical Analysis 17:238–246.

Gremillet, D., R. P. Wilson, S. Storch, and Y. Gary. 1999. Three-dimensional space utilization by a marine predator. Marine Ecology Progress Series 183:263–273.

Guillaumet, A., B. S. Dorr, G. Wang, and T. J. Doyle. 2014. The cumulative effects of management on the population dynamics of the double-crested cormorant (*Phalacrocorax auritus*) in the Great Lakes. Ibis 156:141–152.

Guillaumet, A., B. Dorr, G. Wang, J. D. Taylor, R. B. Chipman, H. Scherr, J. Bowman, K. F. Abraham, T. J. Doyle, and E. Cranker. 2011. Determinants of local and migratory movements of Great Lakes double-crested cormorants. Behavioral Ecology 22:1096–1103.

Hamer, K. C., E. M. Humphreys, S. Garthe, J. Hennicke, G. Peters, D. Gremillet, R. A. Phillips, M. P. Harris, and S. Wanless. 2007. Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. Marine Ecology Progress Series 338:295–305.

Hatch, J. J. 1995. Changing populations of double-crested cormorants. Colonial Waterbirds 18:8–24.

Hedenström, A., and T. Alerstam. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227–234.

Hénaux, V., T. Bregnaballe, and J. D. Lebreton. 2007. Dispersal and recruitment during population growth in a colonial bird, the great cormorant (*Phalacrocorax carbo sinensis*). Journal of Avian Biology 38:44–57.

Henny, C. J., L. J. Blus, S. P. Thompson, and U. W. Wilson. 1989. Environmental contaminants, human disturbance and nesting of double-crested cormorants in northwest Washington. Colonial Waterbirds 12:198-206.

Holbrook, S. J., and R. J. Schmitt. 1989. Resource overlap, prey dynamics, and the strength of competition. Ecology 70:1943–1953.

Horton, C. A. 2014. Top-down influences of bald eagles on common murre populations in Oregon. Thesis, Oregon State University, Corvallis, Oregon, USA.

Huyer, A. 1983. Coastal upwelling in the California Current System. Progress in Oceanography 12:259–284.

Kennedy, M., and H. G. Spencer. 2014. Classification of the cormorants of the world. Molecular Phylogenetics and Evolution 79:249-257.

King, D. T., M. E. Tobin, and M. Bur. 2000. Capture and telemetry techniques for double-crested cormorants (*Phalocrocorax auritus*). Pages 54-57 *in* Proceedings of the 19th Vertebrate Pest Conference, University of California, Davis, USA.

Kokubun, N., A. Takahashi, Y. Mori, S. Watanabe, and H.-C. Shin. 2010. Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. Marine Biology 157:811–825.

Kokubun, N., T. Yamamoto, N. Sato, Y. Watanuki, A. Will, A. S. Kitaysky, and A. Takahashi. 2016. Foraging segregation of two congeneric diving seabird species breeding on St. George Island, Bering Sea. Biogeosciences 13:2579–2591.

Kudela, R. M., A. R. Horner-Devine, N. S. Banas, B. M. Hickey, T. D. Peterson, R. M. McCabe, E. J. Lessard, et al. 2010. Multiple trophic levels fueled by recirculation in the Columbia River plume. Geophysical Research Letters 37:L18607.

Litz, M. N. C., R. L. Emmett, P. J. Bentley, A. M. Claiborne, C. Barceló. 2014. Biotic and abiotic factors influencing forage fish and pelagic nekton community in the Columbia River plume (USA) throughout the upwelling season 1999–2009. ICES Journal of Marine Science 71:5-18.

Luque, S. P., and R. Fried. 2011. Recursive filtering for zero offset correction of diving depth time series with GNU R Package diveMove. PLoS ONE 6:e15850.

Lyons, D. E. 2010. Bioenergetics-based predator-prey relationships between piscivorous birds and juvenile salmonids in the Columbia River estuary. Dissertation, Oregon State University, Corvallis, Oregon, USA.

Lyons, D. E., D. D. Roby, and K. Collis. 2007. Foraging patterns of Caspian terns and double-crested cormorants in the Columbia River estuary. Northwest Science 81:91–103.

MacLeod, C. D. 2014. An introduction to using GIS in marine biology: supplementary workbook four: Investigating home ranges of individual animals. Pictish Beast Publications, Glasgow, U.K.

Mercer, D. M., S. M. Haig, and D. D. Roby. 2013. Phylogeography and population genetic structure of double-crested cormorants (*Phalacrocorax auritus*). Conservation Genetics 14:823–836.

Moul, I. E., and M. B. Gebauer. 2002. Status of the double-crested cormorant in British Columbia. British Columbia Ministry of Water, Land and Air Protection, Biodiversity Branch, Victoria, British Columbia, Canada.

Miller, A. K., M. A. Kappes, S. G. Trivelpiece, and W. Z. Trivelpiece. 2010. Foraging-niche separation of breeding gentoo and chinstrap penguins, South Shetland Islands, Antarctica. Condor 112:683–695.

National Audubon Society [NAS]. 2013. Important Bird Areas in the U.S., East Sand Island. National Audubon Society, Manhattan, New York, USA. <netapp.audubon.org/IBA/Reports/3604/>. Accessed 18 Jan 2017.

National Oceanic and Atmospheric Administration [NOAA]. 2014. Federal Columbia River power system 2014 supplemental biological opinion. National Marine Fisheries Service, Northwest Region, Seattle, Washington, USA.

Naughton, M., D. S. Pitkin, R. W. Lowe, K. J. So, and C. S. Strong. 2007. Catalog of Oregon Seabird Colonies. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Washington, D.C., USA. <http://www.fws.gov/uploadedFiles/Catalog_of_Oregon_Seabird_Colonies_1-TOC.pdf>. Accessed 18 Jan 2017.

Navarro, J., S. C. Votier, J. Aguzzi, J. J. Chiesa, M. G. Forero, and R. A. Phillips. 2013. Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. PLoS ONE 8:e62897.

Pacific Flyway Council [PFC]. 2012. Pacific flyway plan: a framework for the management of double-crested cormorant depredation on fish resources in the Pacific flyway. Pacific Flyway Council, U.S. Fish and Wildlife Service, Portland, Oregon, USA.

Parrish, J. K., M. Marvier, and R. T. Paine. 2001. Direct and indirect effects: interactions between bald eagles and common murres. Ecological Applications 11:1858-1869.

Saunders, P. M. 1981. Practical conversion of pressure to depth. Journal of Physical Oceanography 11:573–574.

Scherr, H., J. Bowman, and K. F. Abraham. 2010. Migration and winter movements of double-crested cormorants breeding in Georgian Bay, Ontario. Waterbirds 33:451–460.

Schjørring, S., J. Gregersen, and T. Bregnaballe. 1999. Prospecting enhances breeding success of first-time breeders in the great cormorant (*Phalacrocorax carbo sinensis*). Animal Behaviour 57:647–654.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369–404.

Sea-Bird Electronics, Inc [Sea-Bird]. 2002. Application note no. 69, conversion of pressure to depth. Sea-Bird Electronics Inc., Bellevue, Washington, USA. <http://www.seabird.com/sites/default/files/documents/appnote69.pdf.>. Accessed 18 Jan 2017.

Simenstad, C. A., L. F. Small, C. D. McIntire, D. A. Jay, and C. Sherwood. 1990. Columbia River estuary studies: an introduction to the estuary, a brief history, and prior studies. Progress in Oceanography 25:1-13.

Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7:533–555.

Trivelpiece, W. Z., S. G. Trivelpiece, and N. J. Volkman. 1987. Ecological segregation of Adelie, gentoo, and chinstrap penguins at King George Island, Antarctica. Ecology 68:351–361.

U.S. Fish and Wildlife Service [USFWS]. 2003. Final environment impact statement: double-crested cormorant management in the United States. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, Virginia, USA.

U.S. Fish and Wildlife Service [USFWS]. 2005. Record of decision: Caspian tern management to reduce predation of juvenile salmonids in the Columbia River estuary, final environmental impact statement. U.S. Fish and Wildlife Service, Migratory Birds and Habitat Programs, Portland, Oregon, USA.

U.S. Army Corps of Engineers [USACE]. 2015. Final environmental impact statement: double-crested cormorant management plan to reduce predation of juvenile salmonids in the Columbia River estuary. U.S. Army Corps of Engineers, Portland District, Portland, Oregon, USA.

U.S. Army Corps of Engineers [USACE]. 2017. Double-crested cormorant monitoring report, avian predation program monitoring, draft report. U.S. Army Corps of Engineers, Portland District, Portland, Oregon, USA.

Venables, W. N., and C. M. Dichmont. 2004. GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fisheries Research 70:319–337.

Wallace, E. A. H., and G. E. Wallace. 1998. Brandt’s cormorant (*Phalacrocorax penicillatus*). The Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://birdsna.org/Species-Account/bna/species/doccor>. Accessed 18 Jan 2017.

Wand, M. P., and M. C. Jones. 1994. Kernel smoothing. Chapman & Hall/CRC Press, Boca Raton, Florida, USA.

Weber, T. P., B. J. Ens, and A. I. Houston. 1998. Optimal avian migration: a dynamic model of fuel stores and site use. Evolutionary Ecology 12:377–401.

Weitkamp, L. A., P. J. Bentley, and M. N. C. Litz. 2012. Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. Fishery Bulletin 110:426–450.

Weitkamp, L. A., T. P. Good, D. E. Lyons, and D. D. Roby. 2016. The influence of environmental variation on the Columbia River estuarine fish community: implications for predation on juvenile salmonids. North Pacific Anadromous Fish Commission Bulletin 6:33-44.

Wilks, D. S. 2011. Statistical methods in the atmospheric sciences. Academic Press, Cambridge, Massachusetts, USA.

Wires, L. R. 2014. The double-crested cormorant: plight of a feathered pariah. Yale University Press, New Haven, Connecticut, USA.

Wires, L. R., and F. J. Cuthbert. 2006. Historic populations of the double-crested cormorant (*Phalacrocorax auritus*): implications for conservation and management in the 21st century. Waterbirds 29:9–37.

Wires, L. R., and F. J. Cuthbert. 2010. Characteristics of double-crested cormorant colonies in the U.S. Great Lakes island landscape. Journal of Great Lakes Research 36:232–241.

Wires, L. R., F. J. Cuthbert, D. R. Trexel, and A. R. Joshi. 2001. Status of the double-crested cormorant (*Phalocrocorax auritus*) in North America. Final Report to U.S. Fish and Wildlife Service. University of Minnesota, St. Paul, USA.

Wood, A. G., B. Naef-Daenzer, P. A. Prince, and J. P. Croxall. 2000. Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. Journal of Avian Biology 31:278–286.

Wright, H. W. 1913. The birds of San Martin Island, lower California. Condor 15:207–210.

Wright, S. K., D. D. Roby, and R. G. Anthony. 2007. Responses of California brown pelicans to disturbances at a large Oregon roost. Waterbirds 30:479-487.

Zamon, J. E., E. M. Phillips, and T. J. Guy. 2014. Marine bird aggregations associated with the tidally-driven plume and plume fronts of the Columbia River. Deep Sea Research II: Topical Studies in Oceanography, Fronts, Fish and Top Predators 107:85–95.