

Three-dimensional foraging habitat use and niche partitioning in two sympatric seabird species, *Phalacrocorax auritus* and *P. penicillatus*

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ABSTRACT: Ecological theory predicts that co-existing, morphologically similar species will partition prey resources when faced with resource limitations. We investigated local movements, foraging dive behavior, and foraging habitat selection by breeding adults of 2 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. 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 riverine, mixed-estuarine, and nearshore marine habitats. Brandt's cormorant foraging areas were less expansive, were exclusively marine, and mostly overlapped with double-crested cormorant foraging areas. Within these 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. Brandt's cormorants also utilized a deeper, more benthic portion of the water column than did double-crested cormorants. Nevertheless, the substantial overlap in foraging habitat between the 2 cormorant species in the Columbia River estuary, particularly for Brandt's cormorants, suggests that superabundant prey resources allow these 2 large and productive cormorant colonies to coexist on a single island near the mouth of the Columbia River.

KEY WORDS: Spatial ecology · Niche partitioning · GPS · Temperature–depth recorder · TDR · Double-crested cormorant · Brandt's cormorant

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INTRODUCTION

Ecological theory predicts that for morphologically similar species of predators to occur sympatrically, they must partition prey resources, through either spatial, temporal, or dietary segregation, when those

resources are limited (Gause 1934, Pianka 1986, Holbrook & Schmitt 1989). Many seabirds nest in large multispecies colonies, often on islands which provide isolation from disturbance and terrestrial predators. Nesting seabirds are also constrained as central-place foragers by the need to defend nest sites and

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provision young (Masello et al. 2010, Paredes et al. 2012). Seabirds should minimize commuting time and distance between the nesting colony and foraging areas while also selecting foraging areas with limited competition in order to maximize foraging success and reduce energy expenditure (Schoener 1971, Mori & Boyd 2004). Seabird colonies, therefore, provide robust models to test theory and mechanisms of niche partitioning because they combine dense aggregations of marine predators with spatial constraints that potentially enhance interspecific competition for marine forage resources.

Previous studies of sympatrically nesting 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, 2016, Miller et al. 2010, Navarro et al. 2013). 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). However, superabundant prey availability may reduce the degree of resource partitioning in highly productive systems (Forero et al. 2004).

In this study, we focused on double-crested cormorants *Phalacrocorax auritus* and Brandt's cormorants *P. penicillatus*, 2 congeneric species that co-occur throughout much of the California Current system along the Pacific coast of North America (Wallace & Wallace 1998, Dorr et al. 2014). These 2 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 and interior lakes and rivers, and are considered aquatic ecosystem generalists (Dorr et al. 2014). In large lake systems in the northeastern USA, double-crested cormorants preferentially select shallower foraging habitats (Coleman et al. 2005, Dorr et al. 2014), and along the Pacific Coast of the USA, they are more likely to forage in estuaries than the other 2 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 are endemic to the California Current system (Wallace & 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 & 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 & 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).

Research was conducted at a mixed-species seabird colony on East Sand Island (ESI) in the Columbia River estuary at the border of Oregon and Washington states, USA. Double-crested cormorants nesting at ESI have previously been documented to forage predominantly in the freshwater and marine mixing zones within the Columbia River estuary (Anderson et al. 2004). Couch & Lance (2004) found that Brandt's cormorants nesting at ESI 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 ESI consume roughly an order of magnitude fewer salmonids per capita than do double-crested cormorants nesting in the same colony (BRNW 2014). We therefore predict 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 3-dimensional foraging behavior of seabirds at very high resolution (Grémillet et al. 1999, Daunt et al. 2003, Kokubun et al. 2010), and to compare foraging habitat use by sympatric seabird species (Kokubun et al. 2010). We used GPS tags with integrated environmental sensors to investigate foraging habitat use and resource partitioning by cormorant species nesting sympatrically at ESI.

The objectives of this study were to describe the foraging habitat use of double-crested and Brandt's cormorants nesting at ESI and to determine how, and

to what degree, these species 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 2 cormorant species utilize the vertical spatial dimension and 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 both of these cormorant species. We investigated hypotheses suggesting the maximum foraging segregation possible: (1) Habitat segregation: double-crested cormorants will forage across a wide range of habitat types, including freshwater and estuarine habitats, while Brandt's cormorants will utilize marine foraging habitats exclusively. (2) Spatial segregation: double-crested and Brandt's cormorants will use distinct foraging areas with low spatial overlap. (3) Vertical segregation: within areas of spatial overlap, double-crested and Brandt's cormorants will partition the water column vertically. Segregation could be caused by the local, ecological response of one species to the presence of the other (i.e. proximate competition); however, we also considered the alternative hypothesis that interspecific differences in foraging behavior are partly due to previously evolved foraging strategies and physiological adaptations for diving in these 2 cormorant species.

MATERIALS AND METHODS

Study area

ESI (46° 15' 46" N, 123° 59' 15" W) is located in the lower Columbia River estuary (river kilometer 7), straddling the border between Oregon and Washington. ESI is a semi-natural low-lying island, about 20 ha in area, which is comprised of mixed dune, forest, shrubland, and rocky habitat types and surrounded by extensive intertidal sand and mudflats. ESI is owned and managed by the US 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). The Columbia River estuary comprises many habitat types and supports a wide variety and abundance of forage fish species

(Bottom & 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* (BRNW 2015). ESI, located near the mouth of the estuary, is also a post-breeding roost site for more than 10 000 California brown pelicans *Pelecanus occidentalis californicus* (Wright et al. 2007), while the Columbia River plume supports dense foraging aggregations of sooty shearwaters *Puffinus griseus* and common murre *Uria aalge*. The west end of ESI is home to a large mixed-species colony of double-crested and Brandt's cormorants. The abundance of these congeners breeding on ESI, combined with the wide variety of available foraging habitat types for 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, Weitkamp et al. 2012). The productivity of marine habitats near the mouth of the Columbia River is enhanced by circulation 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 ESI, 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 & Wallace 1998).

Double-crested cormorants were first detected nesting on ESI 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 ESI on a pile dike off the west end of the island in 1997 (Couch & Lance 2004). In 2006, the Brandt's cormorant col-

ony shifted to ESI 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 an estimated 1629 pairs in 2014, making it one of the largest Brandt's cormorant colonies in Oregon (Naughton et al. 2007, BRNW 2015).

GPS tracking and environmental data logging

Brandt's and double-crested cormorants were captured and later recaptured 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 both the late incubation period and 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 ESI 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 sex determination (Avian Biotech International). Interspecific 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 3.1.2 (R Development Core Team 2014).

GPS data loggers (GPS-TDlog; Earth & Ocean Technologies) with integrated temperature and pressure sensors were affixed to 24 double-crested cormorants and 18 Brandt's cormorants. Loggers were mounted to plastic 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 stream-

lined composite housing measuring 55 mm \times 31 mm \times 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) 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. The combined weight of the GPS/data logger, attachment materials, VHF tag, and bands was less than 3% of the body mass of every transmitter-equipped cormorant.

GPS-TDlog tags were programmed to collect GPS data in 2 phases, normal and active. During the normal phase, locations were obtained once every 4 min. The active phase was triggered when a tag detected diving activity (based on pressure; dives deeper than approximately 0.5 m), and each active phase continued until dive activity had ceased for 2 min. During an active phase, tags were programmed to collect GPS locations either continuously, which resulted in approximately 1 location s^{-1} , or at a 2 s interval, which resulted in approximately 1 location every 5 s. To conserve battery life, tags were programmed 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 recorders (TDRs) sampled either once every second or once every 2 s 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 to retrieve the tag and download the data.

Logger data processing

Data collected by TDRs at 1 s intervals were subsampled to match the temporal resolution of the TDR data sampled at 2 s intervals, by removing data recorded on odd seconds. Pressure data were converted from bars to depth in meters using a conversion factor of 10.06 m bar^{-1} . This conversion factor represents a simple compromise between the standard conversion factors for freshwater (10.20 m bar^{-1} ; SBEI 2002) and saltwater (9.92 m bar^{-1} ; 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 0-offset correction with the package `diveMove` 1.3.9 (Luque 2007) in program R. This process followed the methods of Luque & 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 overplotted 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 2 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 s offset for temperature data, with the value at the offset point computed via monotonic Hermite interpolation (Fritsch & Carlson 1980), at a frequency of 20 Hz, within the subsurface portion of each dive. Hermite interpolation was performed using the function ‘`splinefun`’ in program R.

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. Potential error associated with rapidly moving birds was reduced by excluding dives when the previous GPS location was obtained more than 5 min before the dive began and the subsequent GPS location was obtained more than 1 min 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 satellite imagery from 2013 and 2014 (ESRI 2014). 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 s 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, USGS, pers. comm.). 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, Oregon, Skamokawa, Washington, or Toke Point, Washington (A. W. Stevens pers. comm.).

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 dive characteristic, 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 (KDEs) were generated in ArcMap 10.2.2 (ESRI 2014) using methods developed by MacLeod (2014). These methods utilized the ‘Kernel Interpolation with Barriers’ tool in the Spatial Analyst toolbox to generate a KDE 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 (MacLeod 2014, Sprogis et al. 2016). 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 0. We used a fixed bandwidth that was selected ad hoc, following methods of MacLeod (2014), with subsequent visual inspection (Wand & 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 0.7.3.0 (Beyer 2012). To evaluate foraging habitat diversity, we compared overall and core foraging areas to broadscale (static) salinity zones adapted from Simenstad et al. (1990) and Anderson et al. (2004) (Fig. 1).

Comparison of dive characteristics

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 dive characteristics that were measured once per individual, such as the proportion of benthic dives (Venables & Dichmont 2004, Kokubun et al. 2010). We used a binomial distribution for all GLMs and assessed significance using Wald tests.

GLMMs are related to GLMs, but allow for the incorporation and analysis of grouped or hierarchical data, such as multiple observations within individuals (Venables & Dichmont 2004). We used GLMMs to examine the effect of species on dive characteristics 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 package lme4 1.1-10 (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 5 tagged individuals, 2 data loggers failed to collect or record any data, and 5 data loggers failed to record environmental sensor data. Individual cormorants were tracked for between 3 and 5 d, and the median tracking period was slightly more than 4 d. 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 male and 8 female double-crested cor-

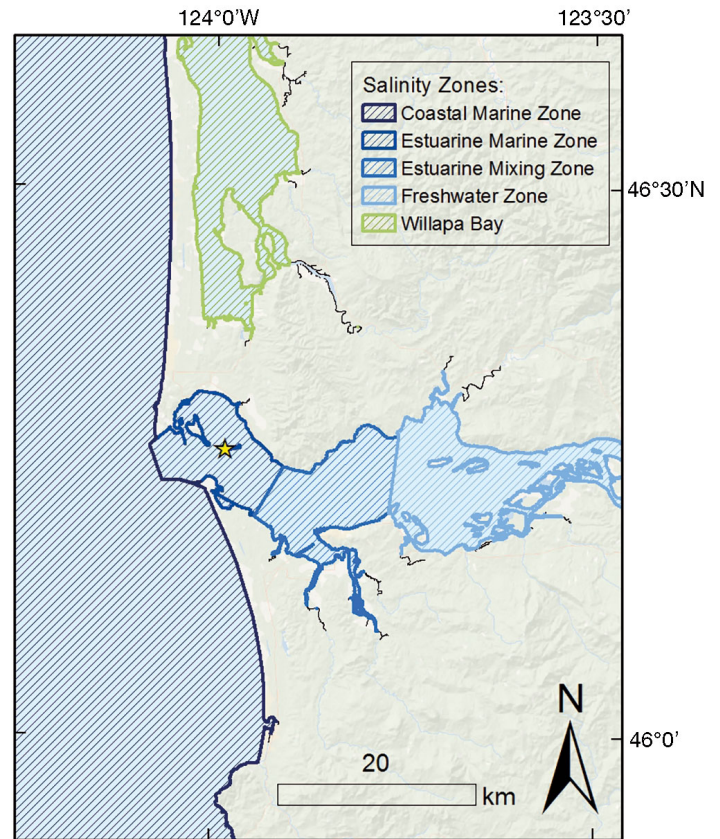


Fig. 1. Study area, showing major foraging habitats for double-crested and Brandt's cormorants nesting on East Sand Island (star) in the Columbia River estuary, based on salinity zones and adapted from Simenstad et al. (1990) as modified by Anderson et al. (2004)

morants, and 10 male and 4 female Brandt's cormorants, plus 1 Brandt's cormorant whose gender was undetermined. The body mass of double-crested cormorants ranged from 1850 to 2550 g, with a mean of 2272 g ($n = 17$), while that of Brandt's cormorants ranged from 1850 to 2700 g, with a mean of 2347 g ($n = 15$; Table 1). Mean body mass of Brandt's cormorants was not significantly greater than that of double-crested cormorants (Wilcoxon rank-sum test, $p = 0.12$).

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. Loggers from 17 double-crested cormorants recorded data from between 435 and 2267 dives ind.^{-1} , with a median of 1627 dives. Loggers from 15 Brandt's cormorants recorded data from 511 to 1040 dives ind.^{-1} ,

Table 1. Body mass 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. Body mass data for Brandt's cormorants includes 3 additional birds that were captured for this study, but did not contribute data to our analysis

	n	Body mass (g)		
		Max.	Min.	Mean \pm SD
Double-crested				
All	17	2550	1850	2260 \pm 164
Female	8	2350	1850	2164 \pm 163
Male	9	2550	2200	2356 \pm 113
Brandt's				
All	18	2700	1850	2220 \pm 285
Female	6	2050	1850	1946 \pm 66
Male	11	2700	2350	2493 \pm 131
Unknown	1	2450	2450	2450

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 of 13.9 m ind.⁻¹. 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 of 29.7 m ind.⁻¹.

Foraging area comparisons

Double-crested cormorants foraged across a broader area and used a wider range of marine and estuarine habitat types compared to Brandt's cormorants (Table 2). 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 (Figs. 2A & 3A). 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 3 prominent roost sites at the mouth of the Columbia River: the tip

Table 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 estimate (KDE) interpolation of dive locations

Habitat (salinity zone)	Double-crested		Brandt's	
	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

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 (Figs. 2B & 3B).

The overall area used for foraging by the tagged double-crested cormorants nesting on ESI (the area within the 95 % kernel density contour) was 451 km², more than 4 times greater than that of the tagged Brandt's cormorants (108 km²). Similarly, the core foraging area used by double-crested cormorants (the area within the 50 % kernel density contour) was 197 km², compared to 32 km² for Brandt's cormorants. Most of the overall foraging area and core foraging area used by Brandt's cormorants, 59.1 and 89.2 %, respectively, overlapped with those of double-crested cormorants. In contrast, the overall foraging area and core foraging area of double-crested cormorants only overlapped with those of Brandt's cormorants by 25.8 and 26.5 %, respectively (Table 3, Fig. 4). 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 ESI, by crossing the approximately 5 km wide strip of land separating Willapa Bay from the Columbia River estuary. Without crossing land, Willapa Bay is over 50 km from ESI. Double-crested cormorants were also observed crossing the Long Beach Peninsula between Willapa Bay and coastal

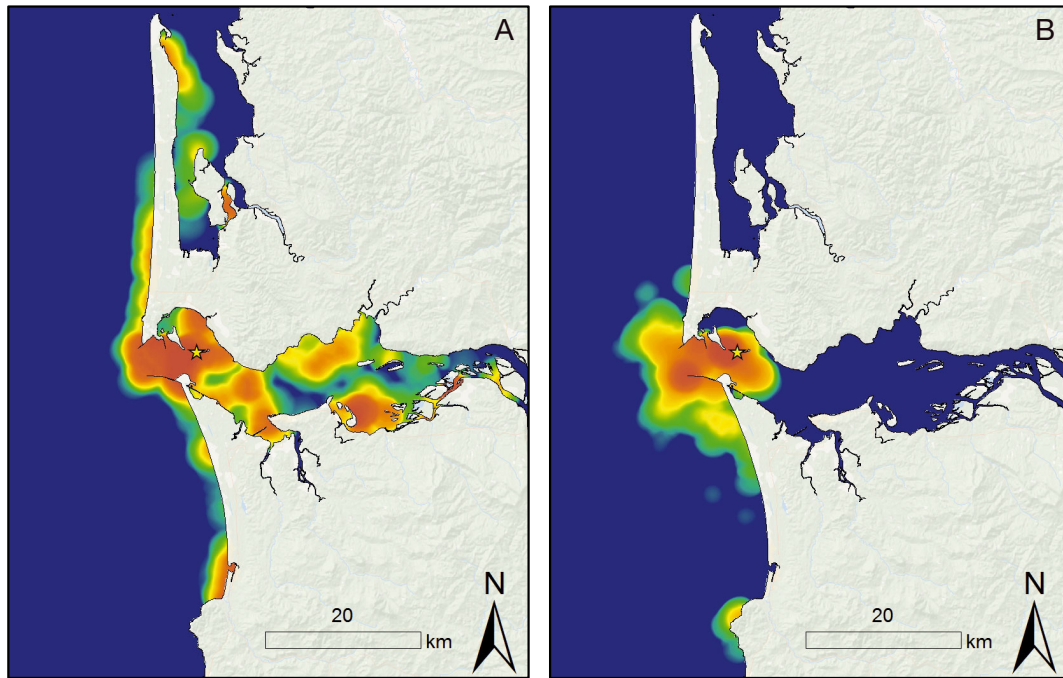


Fig. 2. Foraging areas used by (A) double-crested cormorants ($n = 17$ individuals) and (B) Brandt's cormorants ($n = 15$ individuals) nesting on East Sand Island (star) in the Columbia River estuary. Foraging areas were estimated using a kernel density interpolation approach, which accounted for hard boundaries to foraging activities, such as islands, jetties, and other land-masses. 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

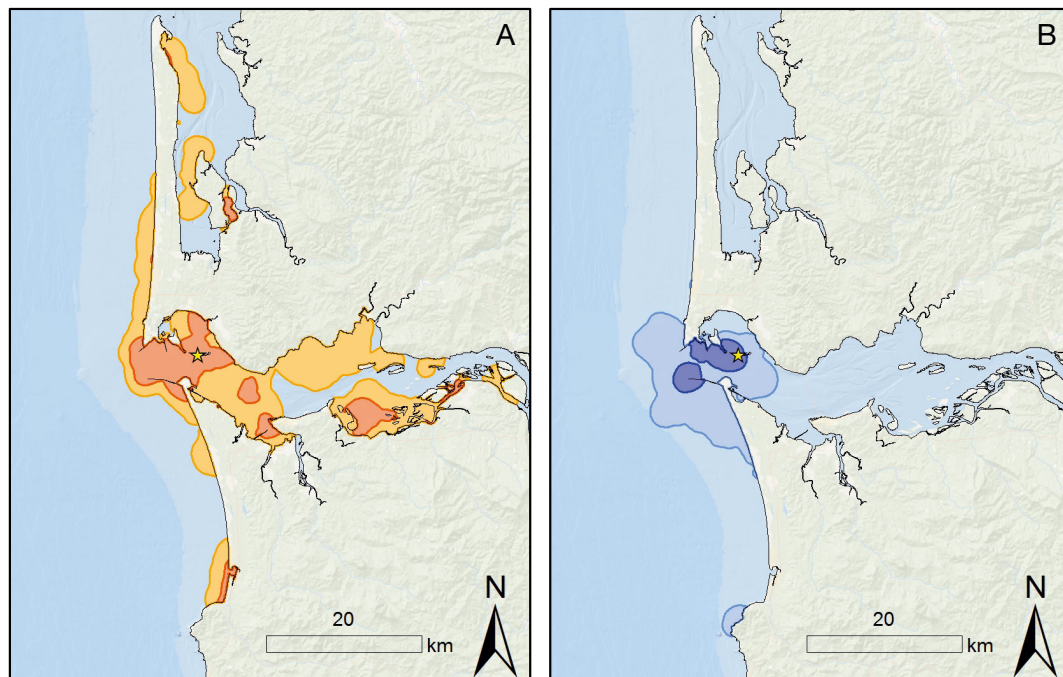


Fig. 3. Foraging areas used by (A) double-crested cormorants ($n = 17$ individuals) and (B) Brandt's cormorants ($n = 15$ individuals) nesting on East Sand Island (star) in the Columbia River estuary. Overall foraging area estimates (95% kernel density estimate, KDE) are indicated by lighter shaded areas, and core foraging area estimates (50% KDE) are indicated by darker shaded areas

Table 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 estimate (KDE) interpolation of dive locations

Foraging area	Overlap area (km ²)	Double-crested		Brandt's	
		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

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.

Comparisons of dive characteristics

Brandt's cormorants dove significantly deeper, dove in deeper locations, and made longer dives than double-crested cormorants (Table 4, Fig. 5). 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-

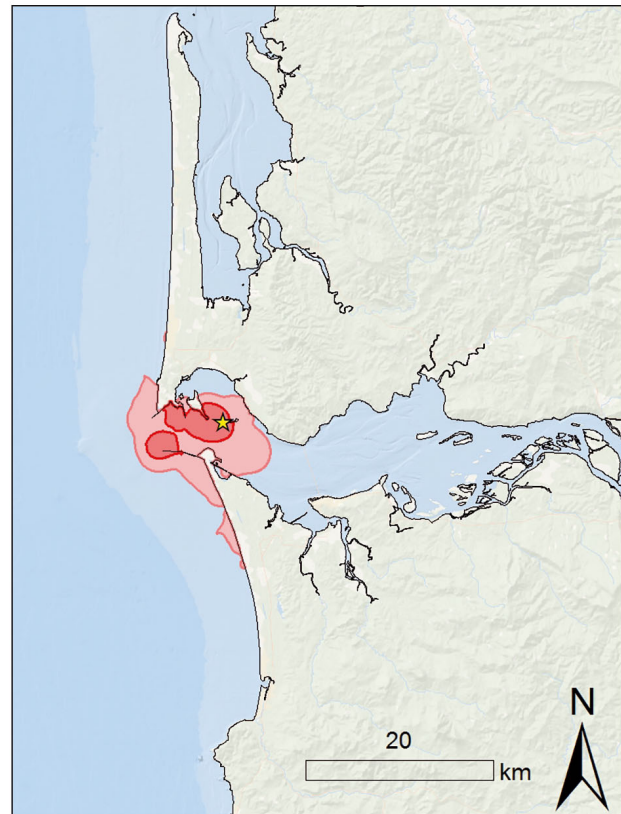


Fig. 4. Overlap in foraging areas used by double-crested cormorants (n = 17 individuals) and Brandt's cormorants (n = 15 individuals) nesting on East Sand Island (star) in the Columbia River estuary. Overlap in overall foraging area estimates (95 % kernel density estimate, KDE) is indicated by lighter shaded areas, and overlap in core foraging area estimates (50 % KDE) is indicated by darker shaded areas

Table 4. Comparison of dive characteristics (means ± SD) between double-crested cormorants (n = 17 birds) and Brandt's cormorants (n = 15). Model results for all dives and for dives within the area of 95 % overlap in foraging areas for the 2 species are presented separately. KDE: kernel density estimate; GLM: generalized linear model; GLMM: generalized linear mixed model; LRT: likelihood ratio test; W: Wald test. Model distributions are gamma (G) or binomial (B)

Parameter	Double-crested	Brandt's	Model used	Statistic	p
All dives					
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	$\zeta = 0.29$	0.776
Dives in area of 95 % KDE overlap					
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	$\zeta = 0.24$	0.810

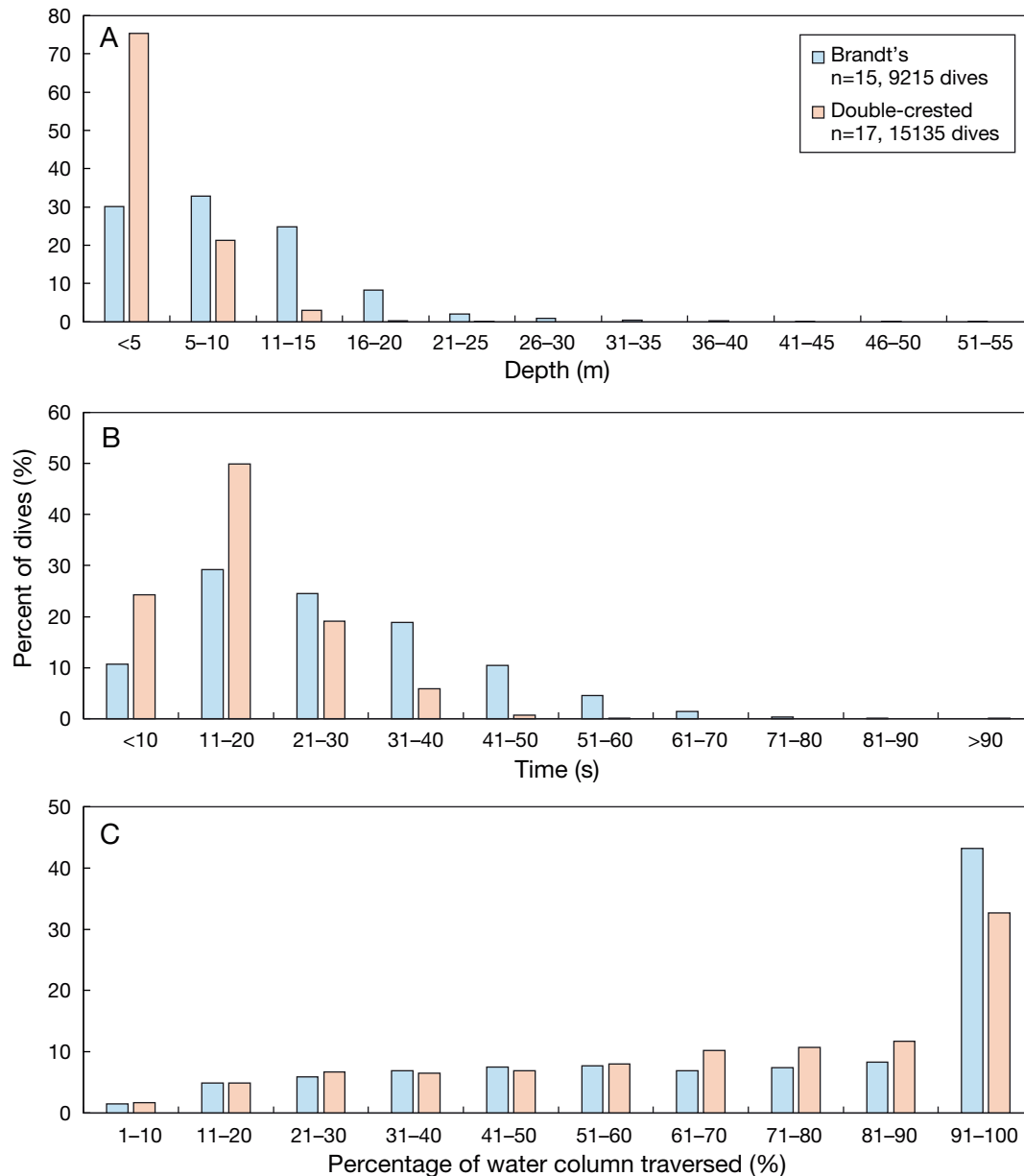


Fig. 5. Frequency distributions of dives against (A) dive depth, (B) dive duration, and (C) water column utilization for double-crested and Brandt's cormorants nesting at East Sand Island in the Columbia River estuary

crested cormorants dove into significantly warmer water than did Brandt's cormorants (dive bottom temperature; Table 4). Warmer water temperatures correlate with lower salinity in the Columbia River estuary system during the summer. We did not detect differences between the 2 cormorant species in the percentage of benthic dives or the percentage of the water column traversed during foraging dives (Table 4).

For dives occurring within the area of overlap between the 95% KDEs of the 2 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 4). There was, however, no interspecific difference in temperature at the bottom of dives in areas of overlap between the 95% KDEs. 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 4).

DISCUSSION

Segregation of 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 in a mixed-species colony on ESI, 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 used 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 4), which reflects the greater use of freshwater habitats by double-crested cormorants.

While avoidance of direct competition for food resources may partially explain the interspecific differences in foraging patterns that we found, 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 (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 geographic foraging ranges. Our observations are consistent with the alternative hypothesis that interspecific differences in foraging behavior may be partially due to previously evolved foraging strategies and physiological adaptations for diving in these 2 cormorant species.

Species-specific foraging patterns

Double-crested cormorants

Our results demonstrated that double-crested cormorants nesting at ESI used 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 USA. (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.

Some double-crested cormorants that nest on ESI visit interior rivers and lakes during the non-breeding season, and follow inland migration routes to reach wintering areas (Courtot et al. 2012). Therefore, at least a portion of the double-crested cormorants nesting on ESI are accustomed to traveling 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 ESI.

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 2 species (Ainley et al. 1981). There is currently only limited data on the diet of Brandt's cormorants at ESI, but Couch & Lance (2004) found that forage species present in the diet of Brandt's cormorants nesting on ESI 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). These prior diet results from ESI 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 salmonids with PIT tags recovered from the ESI 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 used 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 & Wallace 1998). Three tagged Brandt's cormorants made foraging trips to Tillamook Head, a prominent headland 35 km south of ESI with several surrounding rocky islets. In addition to foraging, all Brandt's cormorants that visited this area spent time roosting on at least 1 of 3 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 ESI, and the closest feature to the south is Tillamook Head. Brandt's cormorants may select foraging habitats adjacent to roost sites to facilitate drying, body warming, preening, and resting during or after foraging bouts, and prior to the return commute to the breeding colony (Cook & Leblanc 2007). 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 may instead be 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. However, additional data on the respective diets of these 2 cormorant species is needed to fully understand the potential degree of dietary segregation.

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 2 large and productive cormorant colonies to coexist on a single island near the mouth of the Columbia River.

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