

Recent Population Size, Trends, and Limiting Factors for the Double-Crested Cormorant in Western North America

The Faculty of Oregon State University has made this article openly available.
Please share how this access benefits you. Your story matters.

Citation	Adkins, J. Y., Roby, D. D., Lyons, D. E., Courtot, K. N., Collis, K., Carter, H. R., Shuford, W. D., & Capitolo, P. J. (2014). Recent population size, trends, and limiting factors for the double-crested cormorant in western North America. <i>Journal of Wildlife Management</i> , 78(7), 1131–1142. doi:10.1002/jwmg.737
DOI	10.1002/jwmg.737
Publisher	John Wiley & Sons Ltd.
Version	Version of Record
Terms of Use	http://cdss.library.oregonstate.edu/sa-termsfuse



Review

Recent Population Size, Trends, and Limiting Factors for the Double-Crested Cormorant in Western North America

JESSICA Y. ADKINS,¹ *Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA*

DANIEL D. ROBY,² *U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA*

DONALD E. LYONS,¹ *Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA*

KAREN N. COURTOT,² *Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA*

KEN COLLIS,¹ *Real Time Research, Inc., 52 SW Roosevelt Avenue, Bend, OR 97702, USA*

HARRY R. CARTER,¹ *Carter Biological Consulting, 1015 Hampshire Road, Victoria, BC V8S 4S8, Canada; and Department of Wildlife, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, USA*

W. DAVID SHUFORD,¹ *Point Blue Conservation Science, 3820 Cypress Drive #11, Petaluma, CA 94954, USA*

PHILLIP J. CAPITOLO,¹ *University of California, Institute of Marine Sciences, 100 Shaffer Road, Santa Cruz, CA 95060, USA*

ABSTRACT The status of the double-crested cormorant (*Phalacrocorax auritus*) in western North America was last evaluated during 1987–2003. In the interim, concern has grown over the potential impact of predation by double-crested cormorants on juvenile salmonids (*Oncorhynchus* spp.), particularly in the Columbia Basin and along the Pacific coast where some salmonids are listed for protection under the United States Endangered Species Act. Recent re-evaluations of double-crested cormorant management at the local, flyway, and federal level warrant further examination of the current population size and trends in western North America. We collected colony size data for the western population (British Columbia, Washington, Oregon, Idaho, California, Nevada, Utah, Arizona, and the portions of Montana, Wyoming, Colorado and New Mexico west of the Continental Divide) by conducting aircraft-, boat-, or ground-based surveys and by cooperating with government agencies, universities, and non-profit organizations. In 2009, we estimated approximately 31,200 breeding pairs in the western population. We estimated that cormorant numbers in the Pacific Region (British Columbia, Washington, Oregon, and California) increased 72% from 1987–1992 to circa 2009. Based on the best available data for this period, the average annual growth rate (λ) of the number of breeding birds in the Pacific Region was 1.03, versus 1.07 for the population east of the Continental Divide during recent decades. Most of the increase in the Pacific Region can be attributed to an increase in the size of the nesting colony on East Sand Island in the Columbia River estuary, which accounts for about 39% of all breeding pairs in the western population and is the largest known breeding colony for the species (12,087 breeding pairs estimated in 2009). In contrast, numbers of breeding pairs estimated in coastal British Columbia and Washington have declined by approximately 66% during this same period. Disturbance at breeding colonies by bald eagles (*Haliaeetus leucocephalus*) and humans are likely limiting factors on the growth of the western population at present. Because of differences in biology and management, the western population of double-crested cormorants warrants consideration as a separate management unit from the population east of the Continental Divide. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS cormorant, limiting factors, Pacific coast, *Phalacrocorax auritus*, population, status assessment.

The double-crested cormorant (*Phalacrocorax auritus*) in North America, like the great cormorant (*P. carbo*) in Europe and Asia, has long faced antipathy from humans, particularly

those in the commercial and sport fishing industries (Duffy 1995, Hatch 1995, Kirby et al. 1996, Frederiksen et al. 2001, Kameda et al. 2003). Arguably, cormorants may be considered sentinel species for fisheries–waterbird interactions around the world because the rise and fall of cormorant populations in many areas over the last century is reflective of human attitudes toward and tolerance of piscivorous waterbirds in general. Reduced reproduction and population declines from chemical pollution (especially organochlorines) in the Great Lakes, southern California,

Received: 15 August 2013; Accepted: 6 April 2014
Published: 7 June 2014

¹E-mail: adkinsjy@yahoo.com

²Present address: U.S. Geological Survey, Pacific Island Ecosystems Research Center, Kilauea Field Station, Hawaii National Park, HI 96718, USA

southern British Columbia, and elsewhere add additional strong arguments supporting the species' sentinel status (e.g., Gress et al. 1973, Gress 1995, Weseloh et al. 1995).

In western North America, stakeholders are concerned about the potential impact of predation by double-crested cormorants on juvenile salmonids (*Oncorhynchus* spp.), some of which are listed for protection under the United States Endangered Species Act (ESA), in the Columbia Basin and along the Pacific coast (Good et al. 2005, Ford 2011). The population size and status of the double-crested cormorant in western North America was first comprehensively examined during 1989–1992 (Carter et al. 1995). Since then, events have transpired that necessitate an updated review of the status of the species in this region. First, a Final Environmental Impact Statement (FEIS) completed in 2003 (United States Fish and Wildlife Service [USFWS] 2003) included a management plan for double-crested cormorants east of, but not west of, the Continental Divide. The FEIS expanded the Aquaculture Depredation Order first issued in 1998 and proposed a Public Resource Depredation Order, allowing the take of double-crested cormorants by state wildlife agencies, federally recognized tribes, and Animal and Plant Health Inspection Service, Wildlife Services without a federal permit in 24 states east of the Continental Divide. The Depredation Order is scheduled to expire in 2014 and the USFWS is considering revisions to the regulations governing the management of double-crested cormorants, which could involve changes to the provisions of the current Depredation Order to include states west of the Continental Divide. Additionally, a Pacific Flyway Plan (Pacific Flyway Council 2012), which provides a framework for managing double-crested cormorants to address depredation on fishery resources in the Pacific Flyway, was completed in 2012, and there have been recent calls for management of double-crested cormorants in the Columbia River basin to enhance restoration of ESA-listed salmonids (National Oceanic and Atmospheric Administration 2008, 2010), including potential lethal control. In light of these developments, an examination of the current population size and trends in western North America is needed and a more robust definition of the appropriate management unit should be developed.

As part of the first status assessment for double-crested cormorants in western North America, Carter et al. (1995) summarized available data up to 1992 on the size of breeding colonies for both coastal and inland areas of Alaska, British Columbia, Washington, Oregon, California, and northwestern Mexico (Baja California Norte, Baja California Sur, Sonora, and Sinaloa). An updated status assessment for the species in North America further summarized data from parts of the Pacific Coast region during the mid to late 1990s (Wires et al. 2001, Wires and Cuthbert 2006). An update of the status in British Columbia included survey data up to 2000 (Chatwin et al. 2002, Moul and Gebauer 2002). In 2003, coordinated colony surveys in the Pacific Coast region were initiated by cooperators from federal and state agencies and universities. Inland colonies were not included in the surveys, however, and the compiled results were not widely

disseminated (but see Capitolo et al. 2004; M. Naughton, USFWS, unpublished data). Consequently, the status of the double-crested cormorant in western North America has not been evaluated or updated since at least 2003.

Carter et al. (1995) noted that the population of double-crested cormorants on the Pacific coast of North America had expanded dramatically since the early 20th century and was likely to continue to expand. This trend apparently reflects considerable population recovery following a series of enhanced protections afforded the species, including 1) protection of breeding colonies within wildlife refuges, reserves, parks, and other managed areas, especially in the United States (Carter et al. 1995); 2) protection of double-crested cormorants in the United States and Mexico under the Migratory Bird Treaty Act, as amended in 1972, as well as various other legal protections of breeding and foraging habitats from the 1970s to present (Carter et al. 1995, Wires and Cuthbert 2006); and 3) the restriction of dichlorodiphenyltrichloroethane (DDT) use in 1972, which had negatively affected colonies in southern California and northwestern Baja California Norte (Gress et al. 1973). Double-crested cormorant sub-populations in certain areas (e.g., coastal British Columbia and coastal Washington), however, have experienced less recovery or more recent declines (Carter et al. 1995, Chatwin et al. 2002, Moul and Gebauer 2002).

The objectives of our study were to 1) locate active colony sites of at least modest size (>25 breeding pairs) through aircraft-, boat-, and ground-based surveys and collaboration with other agencies and individuals; 2) estimate the size of breeding colonies and the western population as a whole; 3) assess trends for local or regional sub-populations and for the entire western population; and 4) develop a more robust definition of the appropriate management units.

STUDY AREA

For the purposes of this study, we considered the western population to include all breeding colonies of double-crested cormorants within British Columbia, Washington, Oregon, Idaho, California, Nevada, Utah, Arizona, and the portions of Montana, Wyoming, Colorado, and New Mexico that lie west of the Continental Divide (Fig. 1). We accepted the traditional subspecies delineation between birds in Alaska and British Columbia (and thus the conterminous U.S.; Hatch 1995, Hatch and Weseloh 1999), which was supported strongly by analyses of genetic structure within the species' range (Mercer et al. 2013). Thus, we did not attempt to collect current data on the status of double-crested cormorants breeding in Alaska. Similarly, we did not include the area east of the Continental Divide because evidence indicates very limited connectivity between this population and the western population (Mercer et al. 2013). Finally, we excluded double-crested cormorants nesting in northwestern Mexico in this study because of the lack of availability of recent and possibly future survey data and greatly differing management of colonies in that region.

The Pacific Region, as defined in this study, included all breeding colonies of double-crested cormorants within

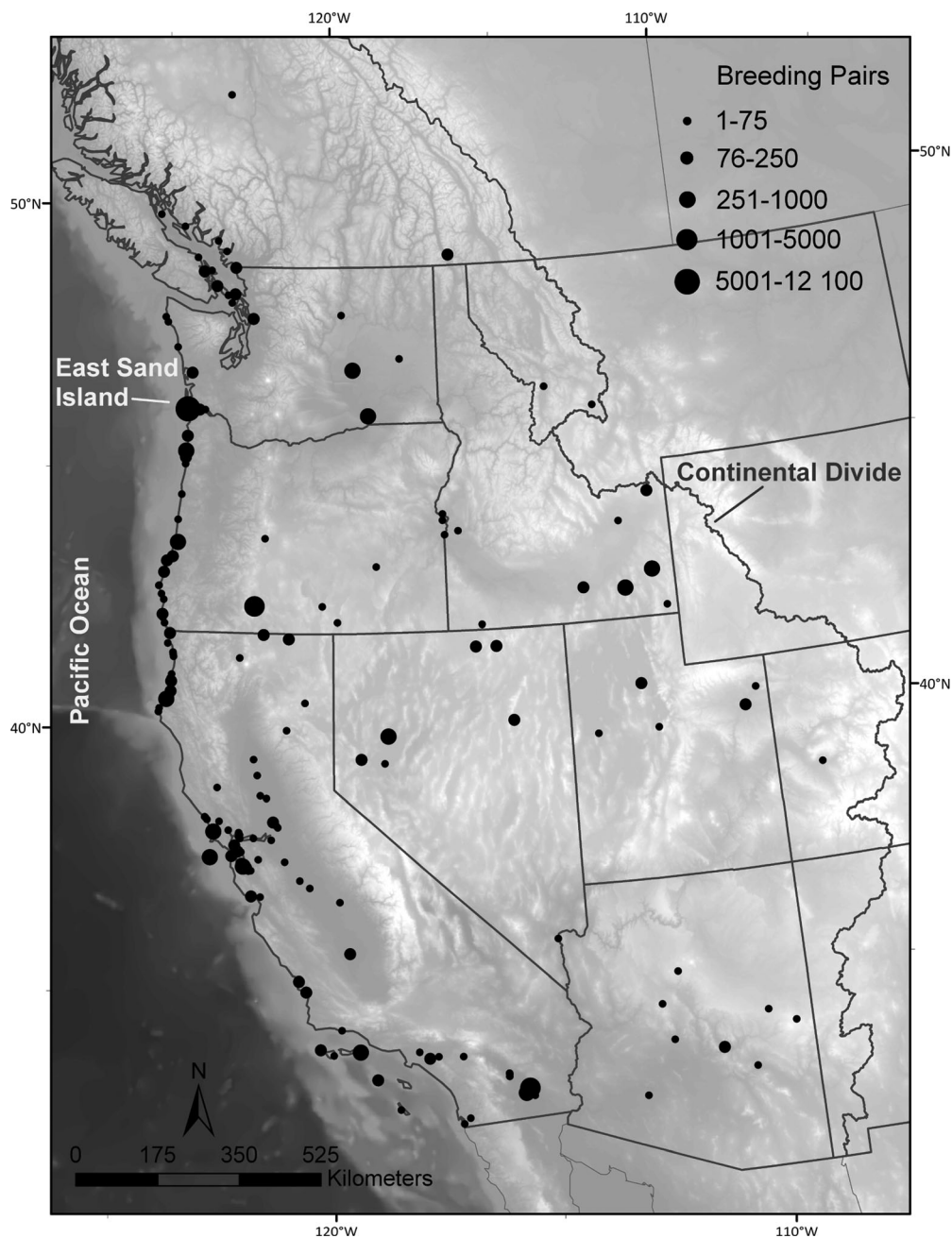


Figure 1. Distribution and relative size of double-crested cormorant breeding colonies in the western population at the time of most recent surveys (1998–2010; Adkins and Roby 2010; D. D. Roby, U.S. Geological Survey, unpublished data).

British Columbia, Washington, Oregon, and California. This differs from the treatment by Carter et al. (1995), which also included Alaska and northwestern Mexico. To enable like comparisons, we excluded the latter 2 areas from the totals in Carter et al. (1995) when comparing them to data for the sub-population from the Pacific Region of this study.

Sub-regional designations are those used in Carter et al. (1995), except as follows. We omitted the Washington sub-region Columbia River Mouth and the name of the Oregon sub-region Columbia River Mouth was changed to Columbia River Estuary. All navigational markers located in the Columbia River estuary or near the mouth of the

Columbia River are included here in the Oregon sub-region Columbia River Estuary.

As defined here, inland refers to colony sites located in freshwater areas of the coastal states (Washington, Oregon, and California) and British Columbia; interior refers to colony sites located in freshwater areas of the interior states (Idaho, Montana, Nevada, Utah, Colorado, Wyoming, New Mexico, and Arizona).

METHODS

We collected survey and colony size data during the breeding season or obtained survey and colony data from cooperating

government agencies, universities, and non-profit organizations. Observers counted or carefully estimated attended or well-built nests during aerial, boat, and ground surveys or by directly counting such nests from film or digital photographs taken during aerial surveys. For colonies with more than 1 species of nesting cormorant, experienced observers determined colony size using aerial photographs of a resolution high enough to differentiate between species (e.g., using nest structure type, gular pouch color, plumage) as well as differences in nest habitat, nest spacing, and phenology. Standardized methods for identifying different cormorant species in aerial photographs have been used in coastal California since 1989 (Carter et al. 1992, 1996; Capitolo et al. 2004). All research involving the use of live animals followed protocols approved by the Institutional Animal Care and Use Committee at Oregon State University.

To estimate the size of the western population and the Pacific Region, we used colony size data from 2009, when available. When 2009 data were lacking, we used data from adjacent years. These included 1999 estimates for the Central Valley area of inland California, 2008 estimates for all of coastal California and inland British Columbia, and a 2010

estimate for Mullet Island at the Salton Sea, California (33.22°N, 115.61°W; Tables 1 and 2). We calculated the average annual growth rate (λ) for the Pacific Region using the circa 1992 regional sub-population estimate (from Carter et al. 1995, modified as noted) and the circa 2009 estimate, assuming a uniform growth rate during the intervening 17 years.

We assessed sub-regional and local sub-population trends (including trends by province or state) by comparing the most recent data with previously published or unpublished data. See Adkins and Roby (2010) for data for individual colonies (and data sources) used to calculate population and sub-population estimates. Some areas of the western United States were experiencing moderate to severe drought during the 1987–1992 and 2009 survey periods (Carter et al. 1995, Shuford and Henderson 2010b, Christian-Smith et al. 2011). Drought conditions could have affected presence of breeding birds and colony size estimates at inland and interior sites during these time periods.

Some of our sub-regional estimates were incomplete (underestimates) because of 1) a lack of estimates for a large number of sites, 2) a missing estimate for a site likely to

Table 1. Estimated double-crested cormorant breeding pairs in coastal sub-regions of British Columbia, Washington, Oregon, and California in 1987–1992 and 1998–2009. Years with few or no data are omitted. An empty cell indicates no data recorded at that site in that year. Totals in parentheses are incomplete because of missing data. We used numbers with asterisks (*) to calculate population and sub-population estimates. See Adkins and Roby (2010) for a complete list of colonies.

Location	1987–1992 ^a	1998	1999	2000	2003	2008	2009
British Columbia ^b							
Northern Strait of Georgia	124	46	47	113			24
Gulf Islands	1,729	540	285	458			316
Vancouver Area	128			46			63
Coastal British Columbia total	1,981	(586)	(332)	617			403*
Washington ^c							
San Juan Islands	25	120	95		718		595
Juan de Fuca Strait East	528	166	82		156		28
Olympic Peninsula Outer Coast	571	210	101				75
Grays Harbor	440		5		80		90
Coastal Washington total	1,564	(496)	(283)		(954)		788*
Oregon ^d							
Columbia River Estuary	3,364	7,270	6,561	7,373	11,040	11,315	12,346
Northern Coast	983				788		737
Central Coast	599				52		31
Southern Coast	1,357				1,376		1,616
Coastal Oregon total	6,303				13,256		14,730*
California ^e							
Northern Coast—North Section	1,210				2,111	1,235	
Northern Coast—South Section	182				326	390	
Central Coast—Outer Coast North	475				581	560	
Central Coast—San Francisco Bay	1,261				2,201	1,450	
Central Coast—Outer Coast South	164				652	584	
Southern Coast	1,113				704 ^f	775	
Coastal California total	4,405				6,575	4,994*	

^a British Columbia data from Moul and Gebauer (2002); all other data from Carter et al. (1995), with modification to the Columbia River Estuary sub-region to allow direct comparison, but see Capitolo et al. (2004) for revised California numbers and detailed estimation methods.

^b T. Chatwin, British Columbia Ministry of the Environment, personal communication; Chatwin et al. (2001); Moul and Gebauer (2002); H. R. Carter, Carter Biological Consulting, unpublished data; and D. D. Roby, U.S. Geological Survey, unpublished data.

^c M. Naughton, USFWS, unpublished data; and D. D. Roby, unpublished data.

^d M. Naughton, unpublished data; Naughton et al. (2007); S. Stephens, USFWS, unpublished data; and D. D. Roby, unpublished data.

^e Capitolo et al. (2004); H. R. Carter and P. J. Capitolo, University of California, unpublished data; M. Elliott, Point Blue Conservation Science, personal communication; L. Harvey, Channel Islands National Park, unpublished data; C. Robinson-Nilsen, San Francisco Bay Bird Observatory, personal communication; D. Suddjian, Santa Cruz Bird Club, personal communication.

^f 2001 data.

Table 2. Estimated double-crested cormorant breeding pairs in inland areas of British Columbia, Washington, Oregon, and California, and interior states or portions thereof that lie west of the Continental Divide in 1987–1992 and 1998–2009. Years with few or no data are omitted. An empty cell indicates no data recorded at that site in that year. Totals in parentheses are incomplete because of missing data. We used numbers with asterisks (*) to calculate population and sub-population estimates. See Adkins and Roby (2010) for a complete list of colonies.

Location	1987–1992 ^a	1998	1999	2003	2005	2006	2007	2008	2009
British Columbia ^b	4 ^c	9	10	25	59	117	99	123*	
Washington ^d	(425)			(250)	1,218	1,554	1,367	1,428	1,196*
Oregon ^e	(725)		913	(883)					1,041*
California ^f									
Northeastern ^g	(680)	(280)	574 ^h	(521)					259*
Central Valley Area	(317)	781 ^h	633 ^{h*}						
Southern Interior	(62)	(3,359)	5,658						4,184 ^{i*}
Idaho ^j						1,008	(1,180)	(1,418)	1,613*
Montana ^k						17			32*
Nevada ^l		911	1,677		(269)	(720)	(872)	(165)	660*
Utah ^m									177*
Colorado ⁿ					21	18	19	29	41*
Arizona ^o						(78)	(9)	(125)	325*

^a Carter et al. (1995), unless otherwise noted.

^b British Columbia Conservation Data Centre (2008); M. Machmer, Pandion Ecological Research, personal communication; Moul and Gebauer (2002); J. Steciw, British Columbia Ministry of the Environment, personal communication; and Van Damme (2004).

^c Moul and Gebauer (2002), 1983 estimate.

^d D. D. Roby, U.S. Geological Survey, unpublished data.

^e P. Milburn, Oregon Department of Fish and Wildlife, personal communication; M. Naughton, USFWS, unpublished data; D. D. Roby, unpublished data; Shuford et al. (2006); Shuford and Henderson (2010b).

^f C. Robinson-Nilsen, San Francisco Bay Bird Observatory, personal communication; Shuford et al. (2006); Shuford (2010a); Shuford and Henderson (2010b); D. Woolington, USFWS, personal communication.

^g The first comprehensive survey of this region in 1997 estimated 1,415 breeding pairs, 69% of which nested at Sheepy Lake in Lower Klamath NWR (Shuford 2010a). Total number of breeding pairs in 1998 and 1999 were greatly affected by low numbers at Sheepy Lake due to high water levels inundating the nesting site.

^h Data missing from 1 colony site with ≤ 11 breeding pairs in adjacent years.

ⁱ 2010 estimate; estimate includes only the Mullet Island, Salton Sea breeding colony; minimum estimate, aerial survey and photography were completed in late March, after the peak in breeding at this site; D. D. Roby, unpublished data.

^j C. Moulton, Idaho Department of Fish and Game, personal communication.

^k C. Wightman, Montana Fish, Wildlife, and Parks, personal communication.

^l D. Withers, USFWS, personal communication; J. Jeffers, Nevada Department of Wildlife, personal communication; and P. Bradley, Nevada Department of Wildlife, personal communication; includes M. Naughton, unpublished data.

^m S. Jones, USFWS, personal communication; J. Neill, Utah Division of Wildlife Resources, personal communication; and J. Cavitt, Weber State University, personal communication.

ⁿ J. Beason, Rocky Mountain Bird Observatory, personal communication.

^o T. Corman, Arizona Game and Fish Department, personal communication.

represent a large portion of breeding pairs for the area, or 3) only a visual approximation of breeding pairs was available for a given site(s), rather than a precise count (Tables 1 and 2). Missing data were of little consequence for coastal sites in the western population because coastal areas are typically surveyed more comprehensively and more frequently, and data were sufficiently complete to allow comparisons between years. Inland and interior sites were more problematic because these regions are surveyed more sporadically and data were unavailable for multiple years included in this study, which precluded an evaluation of trends in sub-regional or local sub-populations in most instances.

RESULTS

Western Population and Pacific Region

We estimated the 2008–2010 western population of double-crested cormorants to consist of 31,199 breeding pairs. Of these, about 39% (12,087) nested on East Sand Island (46.26°N, 123.97°W; Fig. 1) in the Columbia River Estuary sub-region, 28% (8,828) at other coastal colony sites, and 33% (10,284) at inland or interior colony sites. Of the latter,

Mullet Island in the Salton Sea (Southern Interior sub-region of California) accounted for 13% (4,184) and colonies in the interior states accounted for 9% (2,848) of the western population total.

We estimated 28,351 breeding pairs for the Pacific Region inland and coastal sites combined, a 72% increase from about 16,466 breeding pairs in the late 1980s and early 1990s (Carter et al. 1995, Moul and Gebauer 2002). Approximately 43% and 15% of the 2008–2010 total Pacific Region sub-population nested on East Sand Island and on Mullet Island, respectively, compared to about 20% in the Columbia River Estuary (including East Sand Island) and a negligible percent at the Salton Sea (including Mullet Island) in 1987–1992 (Carter et al. 1995).

Based on the best available data for 1987–1992 (Carter et al. 1995, Moul and Gebauer 2002) and circa 2009 (this study, see immediately above), our estimated average annual growth rate (λ) for the Pacific Region sub-population was 1.03 (3% annual increase). For comparison, the likely composite λ for the population in central and eastern North America during the 1960s to the 1990s was approximately 1.07 (Sauer et al. 1997, Hatch and Weseloh 1999).

Sub-Population Trends by Province or State

British Columbia.—In 2009, 403 breeding pairs of double-crested cormorants were estimated at 7 sites in coastal British Columbia (Table 1), down from 617 breeding pairs at 11 sites in 2000 (Table 1). The 2009 estimate for coastal British Columbia was down approximately 80% from the peak of 1,981 breeding pairs at 11 sites in 1987 (Table 1; Moul and Gebauer 2002). Numbers of breeding pairs in inland British Columbia, however, grew from 9 pairs at 1 site in 1998 to 123 pairs at 2 sites in 2008 (Table 2).

Washington.—In 2009, 788 breeding pairs were estimated at 9 sites in coastal Washington (Table 1). Direct comparisons between 2009 counts and any of the 3 other counts in the previous 11 years were problematic because not all coastal Washington colony sites were surveyed in any 1-year (Table 1). Estimated breeding pairs during 1998–2009, however, were down from the 1,564 breeding pairs counted at 21 sites in 1991–1992 (Carter et al. 1995); the 2009 estimate was a 50% decrease from 1991–1992.

In 2009, 1,196 breeding pairs were estimated at 4 sites in inland Washington (Table 2). The number of breeding cormorants in this region, although currently stable, has grown from around 425 breeding pairs at 1 site in 1991 (Carter et al. 1995).

Oregon.—In 2009, 14,730 breeding pairs were estimated at 26 sites in coastal Oregon (Table 1), up about 134% from the 1991–1992 estimate of 6,303 breeding pairs at 25 sites (modified from Carter et al. 1995). One colony, East Sand Island in the Columbia River Estuary sub-region, supported 82% of breeding pairs in 2009, compared to 53% in 1991–1992 (Carter et al. 1995). The East Sand Island double-crested cormorant colony increased in size by nearly a factor of 6 from 2,026 breeding pairs in 1991 (Carter et al. 1995) to 12,087 breeding pairs in 2009, whereas the numbers of double-crested cormorants breeding elsewhere along the Oregon coast remained stable or declined slightly during this time period (Table 1).

The dataset on breeding colony size for inland Oregon is problematic, with some missing data in most years and variation in survey methods complicating comparisons. In 2009, when a comprehensive aerial survey and direct counts of the associated digital photographs were conducted, 1,041 breeding pairs were estimated at 7 sites (Table 2). A suite of sub-colonies in the Upper Klamath National Wildlife Refuge (NWR) constituted 82% of all breeding pairs and has been the primary nesting site in inland Oregon since at least 1999 (Shuford et al. 2006; USFWS, unpublished data). The 2009 estimate for the Upper Klamath NWR was up from the 1992 estimate of 485 pairs (Carter et al. 1995) and the 1999 estimate of 500 pairs (M. Naughton, unpublished data). The 1992 and 1999 estimates were approximate visual estimates completed during aerial surveys, however, compared to the more precise 2009 estimate. The 1992 estimate was also low compared to earlier years because of changing water levels (Carter et al. 1995) and numbers nesting in this area can vary a great deal annually (W. D. Shuford, Point Blue Conservation Science, unpublished data). A second previously important colony site was on Malheur Lake in

Malheur NWR, which was last known to be active in 1999, when 259 pairs nested there (M. Naughton, unpublished data). Double-crested cormorants have not nested at Malheur Lake for several years because the area no longer has trees or emergent marsh vegetation (e.g., hardstem bulrush [*Schoenoplectus acutus*]) available for nesting habitat (T. Bodeen, USFWS, personal communication; Cornely et al. 1993).

California.—In 2008, 4,994 breeding pairs were estimated at 48 sites along the California coast (Table 1). The 2008 estimate was down from the 2001–2003 estimate of 6,575 breeding pairs at 45 sites (Table 1; Capitolo et al. 2004) and similar to the 1989–1991 estimate of 4,405 breeding pairs at 39 sites (Carter et al. 1995). Despite the similarity in nesting numbers in coastal California in 1989–1991 and 2008, local changes occurred. Increases were evident in the Northern Coast—South Section sub-region (approx. 114%) and in the Central Coast—Outer Coast South sub-region (approx. 256%), whereas numbers in the Southern Coast sub-region were down 35% in 2008 compared to 1991 (Table 1).

For inland California, a comprehensive recent estimate was available for only the Northeastern sub-region where in 2009, 259 breeding pairs were estimated at 5 sites (Table 2; Shuford and Henderson 2010b), down from estimates between 1992 and 2003 (Table 2). Comparisons are problematic, however, because data were missing for some sites in all years between 1992 and 2003 (Table 2; Carter et al. 1995) and the 2009 breeding season followed a 3-year drought, which affected foraging and nesting habitat in the region (Shuford and Henderson 2010b).

The Salton Sea in inland southern California has been an intermittent breeding site for double-crested cormorants since the lake was formed by flooding of the Colorado River in 1905–1907 (Molina and Sturm 2004, Shuford 2010a). Nesting at this site has been especially sporadic over the last 2 decades. Only 57 pairs nested there in 1988 (Carter et al. 1995), and none nested during 1989–1994 (Molina and Sturm 2004). Fifty-six pairs re-established nesting in 1995 (Shuford 2010a) and by 1999 numbers had increased rapidly to an estimated 5,425 breeding pairs, primarily on Mullet Island (Shuford et al. 2002, Molina and Sturm 2004). This increase was followed by a severe decline in nesting numbers, with total breeding failure in 2000 (Shuford 2010a), and no cormorant nesting was observed at Mullet Island in 2001–2002 (Molina and Sturm 2004). No data were available for 2003–2009; however, in 2010 a minimum of 4,184 breeding pairs were estimated at Mullet Island, making it the second largest breeding colony in the western population (Table 2).

Interior states.—Data on double-crested cormorant breeding colonies for the interior states portion of the range of the western population were limited because colonies are not typically surveyed on an annual basis. Consequently, these data were insufficient for assessing long-term population trends. Brief state summaries are provided below. No known breeding colonies are located west of the Continental Divide in either New Mexico or Wyoming (Wires et al. 2001; A. Orabona, Wyoming Game and Fish Department, personal communication).

West of the Continental Divide in Colorado and Montana, 1 and 3 active breeding colonies were documented in 2009, respectively (Adkins and Roby 2010). A single western Colorado colony has been known since 2005, when 21 breeding pairs were recorded, compared to 41 breeding pairs in 2009 (Table 2). Thirty-two pairs nested at 2 of 3 sites in western Montana in 2009 (Table 2); breeding was confirmed at the third site, but no estimate of colony size recorded. In 2006, breeding at this third site was limited to a single pair.

In Idaho, approximately 1,613 breeding pairs were estimated at 11 sites in 2009 (Table 2). Since 2006, between 1,000 and 1,613 pairs have nested at up to 11 sites in Idaho, with the majority breeding at the Blackfoot and American Falls reservoirs and at Minidoka NWR (Adkins and Roby 2010).

In Nevada, 660 breeding pairs were estimated at 6 sites in 2009 (Table 2), down from the estimate of 1,677 breeding pairs at 4 sites in 1999 (Table 2). This decline is due in part to fewer cormorants nesting at Anaho Island on Pyramid Lake (39.58°N, 119.31°W) in recent years (D. Withers, USFWS, personal communication). Additionally, the Humboldt Sink colony (39.59°N, 118.37°W) can range from being inactive in dry years (e.g., 2009) to holding approximately 50% of all breeding pairs in the state when inundated with water, roughly once or twice every 5 years (J. Jeffers, Nevada Department of Wildlife, personal communication).

In Utah, 177 breeding pairs were estimated at 5 sites in 2009 (Table 2). Data from previous years were not available for this state.

In Arizona, 325 breeding pairs were estimated at 6 sites in 2009 (Table 2), the highest estimate in the state during the last 4 years. However, 2 to 5 more sites were surveyed in 2009 than in previous years.

DISCUSSION

Population Trends

Although the Pacific Region sub-population and, by extension, the double-crested cormorant western population grew between 1987–1992 and 2009, it grew at a lower rate than the exponential population expansion observed east of the Continental Divide (Sauer et al. 1997, Hatch and Weseloh 1999). Growth in the western population can be attributed primarily to the increase in size of 1 breeding colony, at East Sand Island in the Columbia River estuary, where more than a third of the western population nested in 2009. The East Sand Island colony grew steadily from 1997–2007 (Roby et al. 2011) and has thrived because of ample habitat for ground-nesting, abundant food supply, few mammalian predators, low rates of human disturbance, and possibly the greater security from predation by bald eagles (*Haliaeetus leucocephalus*) afforded by this large and dense colony. Annual changes between 1987–1992 and 2009 at other colonies within the western population are not well known but were likely variable across the region. The East Sand Island breeding colony is currently the largest known for the species (F. Cuthbert, University of Minnesota, personal communication). The Mullet Island colony in the

Salton Sea also contributed substantially to the growth of the Pacific Region sub-population and the western population and is the largest inland colony west of the Continental Divide (this study).

In some regions of the western population declines have occurred. Total numbers of colony sites and breeding pairs at many of the ground-nesting island colonies in coastal British Columbia and Washington have declined. Colonies located on cliffs and artificial structures are increasing both in size and number (Adkins and Roby 2010), however, likely because such breeding habitats provide some refuge from bald eagle harassment and human disturbance (Chatwin et al. 2002, Moul and Gebauer 2002). Bald eagle and boat disturbances that flushed cormorants from their nests were common in protected coastal waters of Washington during the early 1990s (U. Wilson, USFWS, personal communication; Carter et al. 1995); both factors likely contributed to colony declines at some sites (Carter et al. 1995). Wilson (1991) documented that double-crested cormorants bred in reduced numbers on the outer Washington coast during strong El Niño years and subsequent years, whereas they consistently bred in inner waters during these periods. This may indicate movements by some birds to inner estuarine waters during strong El Niño events, as was also suspected in San Francisco Bay, California, during 1982–1983 (Carter et al. 1995).

In southern California, numbers were down in 2008 compared to 1991. Reduced numbers have been most evident at Prince Island (San Miguel Island; 34.05°N, 120.33°W) and Santa Barbara Island (33.47°N, 119.03°W), but new colonies also have formed since the late 1990s along the Santa Barbara County mainland coast and at San Clemente Island (32.90°N, 118.50°W). As part of a potentially genetically distinct population (Mercer et al. 2013), colonies in southern coastal California interact with colonies in northwestern Mexico. In particular, colonies on the northwest coast of Baja California Norte grew rapidly in the decade preceding 2003 (Gress et al. 2005), and some birds from the northern Channel Islands may have moved to or recruited at northwestern Baja California colonies, as well as at new locations in southern California. Similar patterns have been observed for the Brandt's cormorant (*P. penicillatus*), with new colony formations along the southern California mainland and an apparent shift of the Channel Islands sub-population nearshore and south (P.J. Capitolo, University of California, and H. R. Carter, Carter Biological Consulting, unpublished data). Pelagic cormorant (*P. pelagicus*) numbers at Anacapa Island (34.01°N, 119.42°W) have been relatively stable between 1991 and 2008 (F. Gress, California Institute of Environmental Studies, personal communication).

Cormorants nesting at inland and interior sites are subjected to the dramatic effects of fluctuating water levels on the availability of nesting and foraging habitat from water management in some areas and severe drought. Improved monitoring of trends in the numbers of nesting double-crested cormorants is needed to better assess short- and long-term trends of cormorants breeding at inland and interior sites.

Management Unit

Results from leg-band recovery (Clark et al. 2006) and satellite-tracking (Courtot et al. 2012) studies of cormorants marked in the Columbia River estuary indicate strong connectivity between birds from the Columbia River estuary and colonies in the Salish Sea region of northern Washington and southern British Columbia (i.e., the northern limit of the western population). Individuals from the East Sand Island colony, however, have also dispersed toward the southern (southeastern California) limits of the range of the western population along the Pacific coast during the non-breeding season (Courtot et al. 2012). Both studies indicated more limited movement by individuals from the Columbia River estuary to regions east of the Cascade and Sierra Nevada mountain ranges.

Molecular genetic analyses of the currently recognized subspecies of double-crested cormorant have been conducted since previous regional or national status assessments were completed. Waits et al. (2003) and Green et al. (2006) restricted their analyses to the relationship of cormorants in the southeastern versus northeastern United States and found a lack of support for delineation below the species level between these regions. Mercer et al. (2013) analyzed samples of individuals from throughout North America and found little support for recognition of separate subspecies within the continental United States and Canada, outside of Alaska, indicating a lack of connectivity between the western population and Alaska. Although they did not find a distinct genetic break between individuals from east and west of the Continental Divide consistent with the currently recognized subspecies *P. a. auritus* and *P. a. albociliatus*, the level of interchange required to prevent genetic differentiation between populations east and west of the Divide would not necessarily affect either population from a demographic standpoint (Wright 1931, Slatkin 1985, Mills and Allendorf 1996, Mercer et al. 2013).

Some evidence of either a lack of or limited connectivity between the western population and populations east of the Continental Divide is provided by 1) band recovery studies (Ainley and Boekelheide 1990, Dolbeer 1991, King et al. 2010), 2) differences in population growth rates (Sauer et al. 1997, Hatch and Weseloh 1999, this study), 3) regional declines observed within the western population (this study), and 4) the low densities of breeding and few overwintering individuals within the Intermountain West (Adkins and Roby 2010, this study). Additional information is needed to better understand the degree of connectivity between southern California and northwestern Mexico. However, we contend that the many difficulties of obtaining and interpreting past and future data on status in northwestern Mexico strongly supports establishing the southern limit of the western population at the United States–Mexico border. Considering major differences between populations and management of the double-crested cormorant, we believe that defining the western population as a separate management unit from other populations in Alaska, the remaining conterminous United States, Canada, and northwestern Mexico warrants further consideration.

Limiting Factors

Since the early 1990s, various previous impacts to double-crested cormorants in the Pacific Region have been reduced greatly or ceased entirely to the point that they no longer limit the sub-population; these include colony disturbances to prevent breeding, habitat loss, introduced mammalian predators on islands, unauthorized shooting, organochlorine pollutants, oil spills, and gill-net fishing (see Carter et al. 1995 for a summary, Adkins and Roby 2010). Below, we discuss the 3 main limiting factors at present.

Predation.—Carter et al. (1995) noted that disturbance by bald eagles, along with human disturbance, at 2 colonies in northern Washington had contributed to complete nesting failure in 1990–1992. Small colony sizes or absence of nesting altogether also occurred at these colonies in 2008 and 2009, concurrent with observations of bald eagles at most of these sites during aerial surveys. Moul and Gebauer (2002) and Chatwin et al. (2002) observed similar effects at colonies in southern British Columbia, where double-crested cormorants appear to be increasing their use of cliff-face and human-made structures for colony sites, apparently to gain greater protection from bald eagles. Parrish (1995) and Parrish et al. (2001) observed that bald eagles negatively affected a common murre (*Uria aalge*) breeding colony on the northern outer coast of Washington. Bald eagle disturbance and predation and the associated nest predation by gulls (*Larus* spp.) caused complete breeding failure at the large Caspian tern (*Hydroprogne caspia*) colony on East Sand Island in 2011 (D. D. Roby, U.S. Geological Survey, unpublished data). Disturbance and predation pressure from bald eagles apparently caused double-crested cormorants nesting at East Sand Island to use a smaller area and to nest in higher densities during 2005–2011 compared to previous years (Roby et al. 2011; D. D. Roby, unpublished data). Bald eagle impacts may limit the size and productivity of the East Sand Island colony in the future, despite the availability of suitable habitat to support the continued growth of this immense colony.

Similar to trends for double-crested cormorants, bald eagle numbers have recovered to a large extent in recent years following the reduction of DDT use in the early 1970s and the greater protection afforded to the species and its nest sites from the United States Endangered Species Act (1967–2007; USFWS 2010). As bald eagle numbers continue to increase, predation pressure will continue to restrict nesting opportunities for double-crested cormorants in southern British Columbia, Washington, and Oregon, and eagle impacts may extend into and throughout California and much of northern Baja California, if bald eagles fully reoccupy their historical range. Only colony sites that offer structural or other forms of protection from bald eagle predation for nesting individuals may be used in the future.

Human disturbance.—Although the impact of direct human harassment and disturbance on double-crested cormorant populations has been reduced in the United States since 1972, when they were first protected under the Migratory Bird Treaty Act, nesting cormorants still are affected by human disturbance, particularly during the early

incubation and early nestling-rearing stages (Ellison and Cleary 1978, Hatch and Weseloh 1999). The effects of human disturbance have been well-documented at colonies in British Columbia (Verbeek 1982, Rodway 1991, Chatwin et al. 2002, Moul and Gebauer 2002) and are thought to have contributed to nesting failure and colony abandonment at sites in Washington in the recent past (Henny et al. 1989, Carter et al. 1995). Human presence at active breeding colonies and the resulting disturbance have been documented recently at colonies in northern California (P.J. Capitolo, unpublished data). Greater use of artificial habitats in central California since the 1980s (Carter et al. 1995) has led to increased disturbance from maintenance and nearby construction activities at certain bridges, navigational markers, and transmission towers, most notably the imminent replacement of the San Francisco-Oakland Bay Bridge (which hosts one of the largest colonies in the state) after a decade of construction activities (Stenzel et al. 1995, Rauzon et al. 2001, Capitolo et al. 2004). Many current cormorant colony sites are located in federal, state, and provincial protected areas, where access by the public is technically prohibited or restricted. East Sand Island is owned by the United States Army Corps of Engineers (USACE 2013) and the public has not had access during the nesting season. With expanding human populations along the coast and the increasing perception that double-crested cormorants represent a threat to sport and commercial fisheries throughout the range of the western population, however, human disturbance could increase and pose a significant threat to this population in the future. This could be of particular consequence in the absence of new rules and restrictions or if enforcement is limited. Nesting colonies on artificial habitats (e.g., bridges, dredge spoil islands, navigational markers, power transmission towers) used by humans or accessed for maintenance are particularly vulnerable.

Climate.—As colonially nesting waterbirds, double-crested cormorants congregate in areas with ample food resources and are dependent on the stability and predictability of those resources for successful breeding. Changes in ocean conditions (e.g., timing of the onset of upwelling) and climatic shifts (e.g., La Niña and ENSO events) off the Pacific coast influence population dynamics of double-crested cormorants and other seabirds (Ainley and Boekelheide 1990, Wilson 1991, Veit et al. 1996, Sydeman et al. 2001, Lyons 2010), as well as the forage fish communities on which cormorants rely (Emmett and Brodeur 2000, Chavez et al. 2003, Emmett et al. 2006, Barth et al. 2007). For example, a record late onset of upwelling in 2005 corresponded with massive seabird mortality events and breeding failures along the coasts of Washington, Oregon, and California, although impacts on double-crested cormorants were not noted (Sydeman et al. 2006, Parrish et al. 2007). Unusual mortality events were not observed at the double-crested cormorant colony at East Sand Island, which appeared to be buffered to a certain extent by more stable food resources associated with the Columbia River estuary (Anderson et al. 2004). Coastal nesting double-crested cormorants also may be less

vulnerable to forage base changes compared to other piscivorous seabird species because of their diverse diet and use of varied marine and freshwater foraging habitats.

Double-crested cormorants breeding at many inland sites appear to face less stable and predictable food resources and nesting sites because of severe drought or flooding in some years (Carter et al. 1995, Roby et al. 2011). Recent nesting at the Salton Sea, the largest inland breeding site for double-crested cormorants in California during some years, is likely driven by the introduced tilapia (*Tilapia* spp.) population in the lake (Molina and Sturm 2004), which in turn is susceptible to high temperature and salinity levels (Sardella et al. 2007). Additionally, current water levels in the Salton Sea are receding, in part because of municipal reallocation, and it is unclear how long the lake will continue to support fish populations. Mammalian tracks were observed on Mullet Island, the primary cormorant nesting site in the area, during the 2013 breeding season (W. D. Shuford, unpublished data), indicating that water depth adjacent to the island is no longer sufficient to provide a suitable barrier to mammalian predators.

MANAGEMENT IMPLICATIONS

East Sand Island is currently home to more than a third of all double-crested cormorant breeding pairs in the western population. No site elsewhere in the region has the combination of factors necessary to sustain a super colony of this size. The forage base supports >50,000 piscivorous birds that breed or roost at East Sand Island every summer, including Caspian terns, double-crested cormorants, Brandt's cormorants, brown pelicans (*Pelecanus occidentalis*), and gulls (Roby et al. 2010). The sheer number of double-crested cormorants may have helped insulate the colony from the impact of predation and disturbance by bald eagles (D. D. Roby, unpublished data), and the island has been well protected from human disturbance because of the presence of researchers throughout the breeding season since 1999. Double-crested cormorants from the Columbia River estuary have demonstrated a strong connectivity with coastal breeding sites to the north but less so with southern coastal and inland or interior sites (Clark et al. 2006, Courtot et al. 2012). The number of coastal colonies to the north of East Sand Island has declined by approximately 50% since the early 1990s, and numbers nesting at the remaining northern coastal sites have also declined, resulting in a 66% decline in numbers of breeding pairs within this sub-population. If management is employed to dissuade double-crested cormorants from nesting at East Sand Island in an effort to reduce their impact on ESA-listed juvenile salmonids, some individuals may likely disperse northward to prospect for breeding sites (Courtot et al. 2012). We are unclear how successful dispersal to these areas would be, however, given the declines in this region. Because of the unique characteristics of the double-crested cormorant colony at East Sand Island and the tenuous status of colonies elsewhere, the future of this colony will likely influence the entire western population. To identify future changes in the size or distribution of the western population,

a census (e.g., Pacific Flyway Council 2013) should be completed following management induced or naturally occurring (i.e., large-scale bald eagle disturbance resulting in colony abandonment) events that affect the status of the East Sand Island double-crested cormorant colony.

ACKNOWLEDGMENTS

We are extremely grateful to the following individuals who contributed data, comments, or contributed to the original unpublished report in other ways: D. Battaglia, J. Beason, T. Bodeen, P. Bradley, R. Bradley, J. Cavitt, T. Chatwin, T. Corman, M. Elliott, A. Evans, F. Gress, S. Haig, L. Harvey, J. Jahncke, J. Jeffers, S. Jones, P. Loschl, R. Lowe, M. Machmer, G. McChesney, D. Mercer, P. Milburn, K. Molina, C. Moulton, M. Naughton, A. Orabona, J. Neill, M. Rauzon, C. Robinson-Nilsen, J. Steciw, S. Stephensen, D. Suddjian, Y. Suzuki, W. B. Tyler, C. Wightman, D. Withers, and D. Woolington. We would like to thank many seasonal employees, staff, and graduate students for their valuable assistance, particularly B. Courtot, D. Craig, C. Gilbert, C. Hand, L. Kerr, T. Marcella, A. Myers, and R. Suryan. This paper benefited from comments provided by M. McDowell, T. Messmer, L. Wires, and 2 anonymous reviewers. Funding was provided by the U.S. Army Corps of Engineers, Portland District, Portland, Oregon (Geoff Dorsey and Paul Schmidt).

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.
- Ainley, D. G., and R. J. Boekelheide. 1990. Seabirds of the Farallon Islands. Stanford University Press, Stanford, California, USA.
- Anderson, C. D., D. D. Roby, and K. Collis. 2004. Conservation implications of the large colony of double-crested cormorants on East Sand Island, Columbia River estuary, Oregon, USA. *Waterbirds* 27:155–160.
- Barth, J. A., B. A. Menge, J. Lubchenco, F. Chan, J. M. Bane, A. R. Kirincich, M. A. McManus, K. J. Nielsen, S. D. Pierce, and L. Washburn. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. *Proceedings of the National Academy of Sciences, USA* 104:3719–3724.
- British Columbia Conservation Data Centre. 2008. BC Species and Ecosystems Explorer. British Columbia Ministry of the Environment, Victoria, British Columbia, Canada. <<http://a100.gov.bc.ca/pub/eswp/>>. Accessed 12 May 2009.
- Capitolo, P. J., H. R. Carter, R. J. Young, G. J. McChesney, W. R. McIver, R. T. Golightly, and F. Gress. 2004. Changes in breeding population size of Brandt's and double-crested cormorants in California, 1975–2003. Department of Wildlife, Humboldt State University, Arcata, California, USA.
- Carter, H. R., G. J. McChesney, D. L. Jaques, C. S. Strong, M. W. Parker, J. E. Takekawa, D. L. Jory, and D. L. Whitworth. 1992. Breeding populations of seabirds in California, 1989–1991. Vols 1 and 2. Unpublished draft final report, U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, Dixon, California, USA.
- Carter, H. R., G. J. McChesney, J. E. Takekawa, L. K. Ochikubo, D. L. Whitworth, T. W. Keeney, W. R. McIver, and C. S. Strong. 1996. Population monitoring of seabirds in California: 1993–1995 aerial photographic surveys of breeding colonies of common murre, Brandt's cormorants and double-crested cormorants. Unpublished final report, U.S. Geological Survey, California Science Center, Dixon, California, USA.
- 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.
- Chatwin, T. A., M. H. Mather, and T. D. Giesbrecht. 2001. Double-crested and pelagic cormorant inventory in the Strait of Georgia in 2000. Unpublished Report, Ministry of Environment, Lands, and Parks, Victoria, British Columbia, Canada.
- Chatwin, T. A., M. H. Mather, and T. D. Giesbrecht. 2002. Changes in pelagic and double-crested cormorant nesting populations in the Strait of Georgia, British Columbia. *Northwestern Naturalist* 83:109–117.
- Chavez, F. P., J. Ryan, S. E. Lluch-Cota, and C. M. Niquen. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299:217–221.
- Christian-Smith, J., M. Levy, and P. H. Gleick. 2011. Impacts of the California drought from 2007–2009. Unpublished Report, Pacific Insite, Oakland, California, USA.
- Clark, A. C., T. M. Kollasch, and D. A. Williamson. 2006. Movements of double-crested cormorants fledged on the Columbia River estuary. *Northwestern Naturalist* 87:150–152.
- Cornely, J. E., S. P. Thompson, C. J. Henny, and C. D. Littlefield. 1993. Nests and eggs of colonial birds nesting in Malheur Lake, Oregon, with notes on DDE. *Northwestern Naturalist* 74:41–48.
- 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.
- Dolbeer, R. A. 1991. Migration patterns of double-crested cormorants east of the Rocky Mountains. *Journal of Field Ornithology* 62:83–93.
- Duffy, D. C. 1995. Why is the double-crested cormorant a problem? Insights from cormorant ecology and human sociology. *Colonial Waterbirds* 18:25–32.
- Ellison, L. N., and L. Cleary. 1978. Effects of human disturbance on breeding of double-crested cormorants. *Auk* 95:510–517.
- Emmett, R. L., and R. D. Brodeur. 2000. Recent changes in the pelagic nekton community off Oregon and Washington in relation to some physical oceanographic conditions. *North Pacific Anadromous Fisheries Commission Bulletin No. 2*: 11–20.
- Emmett, R. L., G. K. Krutzikowsky, and P. Bentley. 2006. Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: relationship to oceanographic conditions, forage fishes, and juvenile salmonids. *Progress in Oceanography* 68:1–26.
- Ford, M. J., editor. 2011. Status review update for Pacific salmon and steelhead listed under the Endangered Species Act: Pacific Northwest. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-113, Seattle, Washington, USA.
- Frederiksen, M., J. D. Lebreton, and T. Bregnballe. 2001. The interplay between culling and density-dependence in the great cormorant: a modelling approach. *Journal of Applied Ecology* 38:617–627.
- Good, T. P., R. S. Waples, and P. Adams, editors. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-66, Seattle, Washington, USA.
- Green, M. C., J. L. Waits, M. L. Avery, M. E. Tobin, and P. L. Leberg. 2006. Microsatellite variation of double-crested cormorant populations in eastern North America. *Journal of Wildlife Management* 70:579–583.
- Gress, F. 1995. Organochlorines, eggshell thinning, and productivity relationships in brown pelicans breeding in the Southern California Bight. Dissertation, University of California, Davis, USA.
- Gress, F., E. Palacios, A. L. Harvey, L. Alfaro, D. W. Anderson, and E. González. 2005. Status of brown pelicans and three species of cormorants in the Mexican portion of the Southern California Bight, 2002–2003. Unpublished report, California Institute of Environmental Studies, Davis, USA.
- Gress, F., R. W. Risebrough, D. W. Anderson, L. F. Kiff, and J. R. Jehl. 1973. Reproductive failures of double-crested cormorants in southern California and Baja California. *Wilson Bulletin* 85:197–208.
- Hatch, J. J. 1995. Changing populations of double-crested cormorants. *Colonial Waterbirds* 18:8–24.
- Hatch, J. J., and D. V. Weseloh. 1999. Double-crested cormorant (*Phalacrocorax auritus*). *Birds of North America*. <<http://bna.birds.cornell.edu/bna/species/441>>. Accessed 30 Sep 2009.

- 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 north-western Washington. *Colonial Waterbirds* 12:198–206.
- Kameda, K., A. Ishida, and M. Narusue. 2003. Population increase of the great cormorant *Phalacrocorax carbo hanedae* in Japan: conflicts with fisheries and trees and future perspectives. *Vogelwelt* 124:27–33.
- King, D. T., B. F. Blackwell, B. S. Dorr, and J. L. Belant. 2010. Effects of aquaculture on migration and movement patterns of double-crested cormorants. *Human-Wildlife Conflicts* 4:77–86.
- Kirby, J. S., J. S. Holmes, and R. M. Sellers. 1996. Cormorants *Phalacrocorax carbo* as fish predators: an appraisal of their conservation and management in Great Britain. *Biological Conservation* 75:191–199.
- 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, USA.
- Mercer, D. M., S. M. Haig, and D. D. Roby. 2013. Phylogeography and population genetic structure of double-crested cormorants (*Phalacrocorax auritus*). *Conservation Genetics* 14:823–846.
- Mills, L. S., and F. W. Allendorf. 1996. The one-migrant-per-generation rule in conservation and management. *Conservation Biology* 10:1509–1518.
- Molina, K. C., and K. K. Sturm. 2004. Annual colony site occupation and patterns of abundance of breeding cormorants, herons, and ibis at the Salton Sea. *Studies in Avian Biology* 27:42–51.
- Moul, I. E., and M. B. Gebauer. 2002. Status of the double-crested cormorant in British Columbia, B.C. Wildlife Working Report. No. WR-105. Ministry of Water, Land, and Air Protection, Biodiversity Branch, Victoria, British Columbia, Canada.
- National Oceanic and Atmospheric Administration. 2008. Consultation on remand for operation of the Federal Columbia River Power System, 11 Bureau of Reclamation projects in the Columbia Basin and ESA section 10(a)(I)(A) permit for Juvenile Fish Transportation Program (revised and reissued pursuant to court order, NWF v. NMFS, Civ. No. CV 01-640-RE [D. Oregon]). National Marine Fisheries Service, Northwest Region, Seattle, Washington, USA.
- National Oceanic and Atmospheric Administration. 2010. Supplemental consultation on remand for operation of the Federal Columbia River Power System, 11 Bureau of Reclamation projects in the Columbia Basin and ESA section 10(a)(I)(A) permit for Juvenile Fish Transportation Program. National Marine Fisheries Service, Northwest Region, Seattle, Washington, USA.
- Naughton, M. B., D. S. Pitkin, R. W. Lowe, K. J. So, and C. S. Strong. 2007. Catalog of Oregon seabird colonies. U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication FWS/BTP-R1009-2007, Washington, D.C., USA.
- Pacific Flyway Council. 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.
- Pacific Flyway Council. 2013. A monitoring strategy for the western population of double-crested cormorants within the Pacific Flyway. Pacific Flyway Council, U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- Parrish, J. K. 1995. Influence of group size and habitat type on reproductive success on common murre (*Uria aalge*). *Auk* 112:390–401.
- Parrish, J. K., N. Bond, H. Nevins, N. Mantua, R. Loeffel, W. T. Peterson, and J. T. Harvey. 2007. Beached birds and physical forcing in the California Current System. *Marine Ecology Progress Series* 352:275–288.
- Parrish, J. K., M. Marvier, and R. T. Paine. 2001. Direct and indirect effects: interactions between bald eagles and common murre. *Ecological Applications* 11:1858–1869.
- Rauzon, M. J., W. J. Sydeman, M. L. Elliott, and J. Roth. 2001. Population size and breeding success of double-crested cormorants (*Phalacrocorax auritus*) on the Richmond-San Rafael Bridge, California, in 2000. Unpublished Report, San Francisco State University, Department of Biology, San Francisco, California, USA and Point Reyes Bird Observatory, Stinson Beach, California, USA.
- Roby, D. D., K. Collis, J. Y. Adkins, M. Correll, K. Courtot, B. Cramer, N. Hostetter, P. Loschl, D. E. Lyons, T. Marcella, Y. Suzuki, J. Tennyson, A. Evans, M. Hawbecker, J. Shegby, and S. Sebring. 2010. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River: Final 2009 Annual Report. Bird Research Northwest, Bend, Oregon, USA.
- Roby, D. D., K. Collis, D. E. Lyons, J. Y. Adkins, P. Loschl, Y. Suzuki, D. Battaglia, T. Marcella, T. Lawes, A. Peck-Richardson, L. Bayliss, L. Faulquier, D. Harvey, E. Tompkins, J. Tennyson, A. Evans, N. Hostetter, B. Cramer, and M. Hawbecker. 2011. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River: Final 2010 Annual Report. Bird Research Northwest, Bend, Oregon, USA.
- Rodway, M. S. 1991. Status and conservation of breeding seabirds in British Columbia. Pages 43–102 in J. P. Croxall, editor. Seabird status and conservation: a supplement. International Council for Bird Preservation, Cambridge, United Kingdom.
- Sardella, B. A., V. Matey, and C. J. Brauner. 2007. Coping with multiple stressors: physiological mechanisms and strategies in fishes of the Salton Sea. *Lake and Reservoir Management* 23:518–527.
- Sauer, J. R., J. E. Hines, G. Gough, I. Thomas, and B. G. Peterjohn. 1997. The North American Breeding Bird Survey results and analysis. Version 96.4. Patuxent Wildlife Research Center, Laurel, Maryland, USA. <<http://www.mbr-pwrc.-usgs.gov/bbs/bbs.html>>. Accessed 30 Sep 2009.
- Shuford, W. D. 2010a. Inland-breeding pelicans, cormorants, gulls, and terns in California: a catalogue, digital atlas, and conservation tool. Wildlife Branch, Nongame Wildlife Program Report 2010-01. California Department of Fish and Game, Sacramento, USA.
- Shuford, W. D., and R. P. Henderson. 2010b. Surveys of colonial waterbirds in northeastern and east-central California in 2009. Unpublished report to the U.S. Fish and Wildlife Service, Region 8, Sacramento, California, USA.
- Shuford, W. D., D. L. Thomson, D. M. Mauser, and J. Beckstrand. 2006. Abundance and distribution of nongame waterbirds in the Klamath Basin of Oregon and California from comprehensive surveys in 2003 and 2004. Final Report to U.S. Fish and Wildlife Service, Klamath Basin National Wildlife Refuge Complex, Tulelake, California, USA.
- Shuford, W. D., N. Warnock, K. C. Molina, and K. K. Sturm. 2002. The Salton Sea as critical habitat to migratory and resident waterbirds. *Hydrobiologia* 473:255–274.
- Slatkin, M. 1985. Gene flow in natural populations. *Annual Review of Ecology and Systematics* 16:393–430.
- Stenzel, L. E., H. R. Carter, R. P. Henderson, S. D. Emslie, M. J. Rauzon, G. W. Page, and P. Y. O'Brien. 1995. Breeding success of double-crested cormorants in the San Francisco Bay area, California. *Colonial Waterbirds* 18:216–224.
- Sydeman, W. J., R. W. Bradley, P. Warzybok, C. L. Abraham, J. Jahncke, K. D. Hyrenbach, V. Kousky, J. M. Hipfner, and M. D. Ohman. 2006. Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual atmospheric blocking? *Geophysical Research Letters* 33: 1–5.
- Sydeman, W. J., M. M. Hester, J. A. Thayer, F. Gress, P. Martin, and J. Buffa. 2001. Climate change, reproductive performance and diet composition of marine birds in the southern California Current System, 1969–1997. *Progress in Oceanography* 49:309–329.
- U.S. Army Corps of Engineers [USACE]. 2013. Draft Environmental Assessment- Adaptively manage predation on Caspian terns in the lower Columbia River Estuary. U.S. Army Corps of Engineers, Portland, Oregon, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2003. Double-crested cormorant management in the United States Final Environmental Impact Statement. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, Virginia, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2010. Post-delisting monitoring plan for the bald eagle (*Haliaeetus leucocephalus*) in the contiguous 48 states. U.S. Fish and Wildlife Service, Divisions of Endangered Species and Migratory Birds, and State Programs, Midwest Regional Office, Twin Cities, Minnesota, USA.
- Van Damme, L. M. 2004. First breeding record of the double-crested cormorant in the Creston Valley, British Columbia. *Blue Jay* 62:79–83.
- Veit, R. R., P. Pyle, and J. A. McGowan. 1996. Ocean warming and long-term change in pelagic bird abundance within the California Current System. *Marine Ecology Progress Series* 139:11–18.
- Verbeek, N. A. M. 1982. Egg predation by northwestern crows: its association with human and bald eagle activity. *Auk* 99:347–352.

- Waits, J. L., M. L. Avery, M. E. Tobin, and P. L. Leberg. 2003. Low mitochondrial DNA variation in double-crested cormorants in eastern North America. *Waterbirds* 26:196–200.
- Weseloh, D. V., P. J. Ewins, J. Sturges, P. Mineau, C. A. Bishop, S. Postupalsky, and J. P. Ludwig. 1995. Double-crested cormorants of the Great Lakes: changes in population size, breeding distribution and reproduction output between 1913 and 1991. *Colonial Waterbirds* 18: 48–59.
- Wilson, U. W. 1991. Responses of three seabird species to El Niño events and other warm episodes on the Washington coast, 1979–1990. *Condor* 93:853–858.
- 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 (*Phalacrocorax auritus*) in North America. Final Report to U.S. Fish and Wildlife Service. University of Minnesota, St. Paul, USA.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–259.

Associate Editor: Terry Messmer.