Marine Mammal Science

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ARTICLE OPEN ACCESS

Evaluating Seasonal vs. Spatial Extrapolation for Cetacean Distribution Models in the California Current

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Received: 17 July 2024 | **Revised:** 7 April 2025 | **Accepted:** 6 May 2025

Funding: This project was funded by the Navy, Commander, U.S. Pacific Fleet, and by the National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS), Southwest Fisheries Science Center (SWFSC).

Keywords: cetacean distribution | Dall's porpoise | extrapolation | fin whale | generalized additive model | habitat-based density model | Pacific white-sided dolphin | pelagic conservation | short-beaked common dolphin | species distribution model

ABSTRACT

Species distribution models (SDMs) have been developed for multiple cetacean species within the California Current Ecosystem (CCE) from shipboard survey data collected by the Southwest Fisheries Science Center (SWFSC) in summer and fall, thus limiting the ability to inform management decisions in cool seasons when abundance and distribution patterns are substantially different. Winter and spring SDMs have been developed for a few species using California Cooperative Oceanic Fisheries Investigations (CalCOFI) shipboard survey data, but model predictions are limited to the waters off southern and central California. In this study, winter and spring density estimates for the entire CCE study area were made from SWFSC summer and fall model predictions (temporal extrapolation) and CalCOFI winter and spring model predictions (spatial extrapolation) for short-beaked common dolphin (*Delphinus delphis delphis*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), Dall's porpoise (*Phocoenoides dalli*), and fin whale (*Balaenoptera physalus*). The performance of the models was compared based on available abundance estimates and documented distribution patterns in the cool seasons. Results reveal species-specific ecological factors to consider when extrapolating model predictions temporally or spatially, including whether a given study area includes a species "core habitat", and whether static variables should be included when a species exhibits temporal distribution shifts.

1 | Introduction

Effective marine species management and conservation measures require spatially- and temporally-explicit predictions of species abundance and distribution. Species distribution models (SDMs) have been established as important tools for marine conservation and management because they can be used to predict abundance and distribution patterns of seabirds, fish, sea turtles, cetaceans, and other species (Abrahms et al. 2019; Becker et al. 2016, 2022; Eguchi et al. 2017; Gilles et al. 2011; Hammond et al. 2013; Hazen et al. 2017, 2018; Louzao et al. 2006; Oppel et al. 2012; Redfern et al. 2013; Torres et al. 2015; Welch

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et al. 2019). Habitat-based density models, which integrate environmental data into SDMs, are particularly useful in the marine environment where many species exhibit dynamic changes in abundance and distribution in response to changing oceanic conditions within a given region (Becker et al. 2014, 2017, 2018; Cañadas and Hammond 2008; Gilles et al. 2016; Roberts et al. 2016).

Ideally, SDMs would be developed based on data specific to each area and season of interest; however, financial and logistical constraints often limit data collection to a subset of regions or time periods. Extrapolation of model predictions, either spatially or temporally, may be necessary to support management decisions when no alternatives are available (Mannocci et al. 2015; Roberts et al. 2016; Wang et al. 2021). Such extrapolated predictions, when applied with care from solidly developed SDMs, are often considered superior to having no information to support conservation or management decisions (Bouchet et al. 2019; Forbes and Calow 2002; Mannocci et al. 2017; Miller et al. 2004).

As human populations and their impacts on marine species grow, conservation demands will likely increase the interest in extrapolating SDMs to novel regions and time periods; however, model transferability has only been assessed for a few marine species (e.g., Mannocci et al. 2017; Redfern et al. 2017; Torres et al. 2015). Torres et al. (2015) evaluated extrapolated predictions of gray petrel (*Procellaria cinerea*) habitat use across the Southern Hemisphere and found that in novel ecosystems the SDMs could identify potential distributions (where a species could live) but were not able to predict realized distributions (where a species actually occurs relative to available habitat). Redfern et al. (2017) evaluated the transferability of blue whale (*Balaenoptera musculus*) SDMs from two well-sampled ecosystems to a data-poor ecosystem and found that ecosystem-specific models were not transferable, while models developed using data from two diverse ecosystems performed better. Most of the marine studies to date have focused on extrapolations from well surveyed regions to poorly surveyed regions that are separated geographically from one another, rather than temporal or spatial extrapolations within a specific ecosystem (e.g., Mannocci et al. 2015; Redfern et al. 2017). In ecosystems that exhibit substantial temporal and spatial variability in oceanic conditions, it is important to assess the accuracy of both temporal and spatial extrapolations, particularly where extrapolation is required to meet critical management needs.

In the California Current Ecosystem (CCE), a long history of studies has documented dynamic changes in cetacean abundance and distribution associated with seasonal and interannual variability in oceanic conditions throughout the region (Becker et al. 2014, 2017, 2018, 2020; Boyd et al. 2018; Campbell et al. 2015; Dohl et al. 1978; Douglas et al. 2014; Forney and Barlow 1998; Hazen et al. 2017). SDMs have been developed for many cetacean species in the CCE using systematic survey data collected by the Southwest Fisheries Science Center (SWFSC) off the U.S. West Coast since 1991 (Barlow et al. 2009; Becker et al. 2010, 2012, 2016, 2020; Forney 2000; Forney et al. 2012; Redfern et al. 2013). The majority of the 1991–2018 SWFSC survey effort (Figure 1) has been limited to the summer and fall months, because weather conditions during winter and spring are too rough for ship-based surveys. Density predictions based on SDMs developed from summer and fall survey data have been used for multiple management applications, for example, to assess ship-strike risk for large whales (Redfern et al. 2013, 2019; Rockwood et al. 2017); to evaluate the risk of chronic shipping noise on cetaceans in Southern California (Redfern et al. 2017); and to evaluate potential impacts to cetaceans from conducting Navy at-sea training and testing activities (Becker et al. 2016, 2018, 2020, 2022; Forney et al. 2012; U.S. Department of the Navy 2015, 2017). These SDMs allow the assessment of anthropogenic activities during summer and fall, but potential impacts during winter and spring are not adequately captured. Becker et al. (2014) evaluated seasonal extrapolations for three cetacean species and showed that such extrapolations can be informative for some species, particularly when the range of covariates used to construct the model is similar to that observed in the alternate season. However, the study also illustrated the risk of extrapolating outside of the modeled covariate space, underscoring the need for further studies to assess when and how extrapolations can be made reliably across space and time.

In the present study, we compare the performance of temporally extrapolated cetacean SDM predictions (from summer and fall to winter and spring seasons) to those that are spatially extrapolated within a season from one portion of the CCE study area to the entire CCE region. For simplicity, "warm season" refers to summer and fall while "cool season" refers to winter and spring (U.S. Department of the Navy 1977). Our comparison uses two sets of cetacean surveys: (1) the 1991–2018 CCE-wide summer and fall surveys conducted by SWFSC that have formed the basis for the SDMs described in Becker et al. (2012, 2014, 2016, 2020), and (2) the 2005–2020 marine mammal surveys conducted during quarterly California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises off southern and central California (Campbell et al. 2015; Douglas et al. 2014). A subset of the latter data (2005 to 2015) was previously used to develop winter and spring SDMs for short-beaked common dolphin (*Delphinus delphis delphis*), Dall's porpoise (*Phocoenoides dalli*), and humpback whale (*Megaptera novaeangliae*) (Becker et al. 2017). Those results provided the first spatially explicit density predictions for these species off central and southern California during the cool seasons and confirmed that abundance and distribution patterns differed markedly from those documented for summer and fall. However, since the CalCOFI study area covers only a portion of the CCE study area (Figure 1), seasonal variability in species abundance and distribution patterns north of 38° N was not captured.

The analysis presented below examines whether temporal or spatial extrapolations can be used to provide seasonally resolved SDMs for the entire CCE region, filling a data gap that is increasingly important for management of anthropogenic activities along the U.S. West Coast. Sample sizes were sufficient to compare extrapolated model results for four taxonomically and ecologically diverse species: short-beaked common dolphin, Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), Dall's porpoise, and fin whale (*Balaenoptera physalus*).

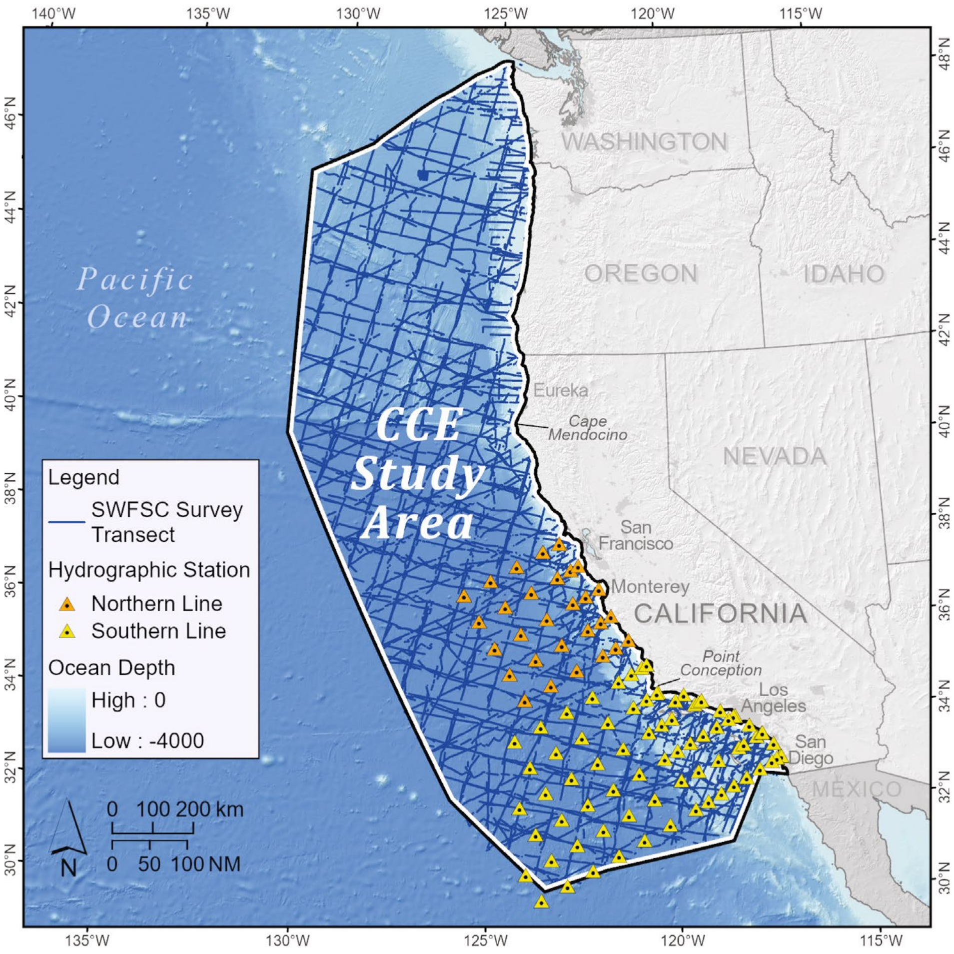

FIGURE 1 | The Southwest Fisheries Science Center California Current Ecosystem (CCE) approximate 1,141,800 km^2 study area off the U.S. West Coast and on-effort tracklines completed during the 1991–2018 surveys (dark blue lines). The smaller California Cooperative Oceanic Fisheries Investigations (CalCOFI) approximate 385,460 km^2 study area encompasses the CalCOFI sampling stations (yellow and orange triangles); surveys are conducted along the southwest to northeast parallel lines running between the sampling stations. The main six southern CalCOFI transect lines are surveyed quarterly, and an additional five northern lines are surveyed less frequently and only during the winter and spring (refer to Table 2).

1.1 | Species Overview

Below is a brief summary of information on what is currently known about the distribution, abundance, and trends of the four species examined, to provide ecological context for this analysis.

1.1.1 | Short-Beaked Common Dolphin

During the late 1970s and early 1980s along the U.S. West Coast, short-beaked common dolphins were sighted primarily south of Point Conception (Dohl et al. 1983), but since the early 2000s they have been commonly encountered as far north as 42° N (Hamilton et al. 2009), and occasionally as far north as 48° N (Forney 2007). Seasonal distribution shifts are pronounced, with a significant southerly shift south of Point Arguello in the winter (Becker et al. 2014; Campbell et al. 2015; Forney and Barlow 1998). Short-beaked common dolphins are a warm temperate to tropical species, and based on habitat models developed using line-transect survey data off the U.S. West Coast from 1991 to 2018, densities are greatest when waters are warmest (Barlow et al. 2009; Becker et al. 2010, 2016, 2014, 2018, 2020; Forney and Barlow 1998). Barlow (2016) noted a nearly monotonic increase in the abundance of short-beaked common dolphins from 1991 to 2014 off the U.S. West Coast in summer and fall. Predictions from habitat-based density models indicate a similar increase in summer and fall short-beaked dolphin abundance off the U.S. West Coast from 1996 to 2018, with the most recent (2018) abundance estimate of 1,056,308 (CV = 0.207) (Barlow 2016; Becker et al. 2020; Carretta et al. 2023). However, the increase in short-beaked common dolphin abundance could be due to a northward movement of animals from waters off Mexico, and additional analyses are required to better assess potential population trends (Barlow 2016; Becker et al. 2022).

1.1.2 | Pacific White-Sided Dolphin

Pacific white-sided dolphins are found in cold temperate waters across the northern rim of the Pacific Ocean as far north as the southern Bering Sea and as far south as the Gulf of California off Mexico (Jefferson et al. 2015). Forney and Barlow (1998) found significant north/south shifts in the seasonal distribution of Pacific white-sided dolphins off California, with animals moving north into Oregon and Washington waters during summer and showing increased abundance in the Southern California Bight during winter. During the unusually warm water conditions present in 2014, there were few sightings of Pacific white-sided dolphins off central and southern California (Barlow 2016). There is considerable seasonal and annual variability in the abundance and distribution of Pacific white-sided dolphins off the U.S. West Coast, and no long-term population trends have been identified (Carretta et al. 2023). Based on data collected in summer and fall, the most recent (2018) abundance estimate for Pacific white-sided dolphins off California, Oregon, and Washington is 34,999 (CV = 0.222) (Becker et al. 2020; Carretta et al. 2023).

1.1.3 | Dall's Porpoise

Dall's porpoises are one of the most common odontocete species in North Pacific waters, occurring primarily between 30° N and 62° N, although during unusually cool water periods they occur as far south as 28° N (Jefferson et al. 2015). The distribution of Dall's porpoises off the U.S. West Coast is highly variable between years, most likely due to changes in oceanographic conditions (Barlow et al. 2009; Becker et al. 2016, 2018, 2020; Forney 2000; Forney et al. 2012). North–south movements in California, Oregon, and Washington have been observed, with Dall's porpoises shifting their distribution southward during cooler-water periods on both interannual and seasonal time scales (Becker et al. 2014, 2018; Boyd et al. 2018; Forney and Barlow 1998). Based on habitat models developed using 1991–2018 survey data collected in waters off the U.S. West Coast during summer and fall, Dall's porpoise density was greatest in shelf and slope waters, and decreased substantially in waters warmer than approximately 17°C (Barlow et al. 2009; Becker et al. 2020, 2016, 2020; Forney et al. 2012). During ship surveys conducted quarterly off southern California from 2004 to 2008, Dall's porpoises were encountered year-round, with highest encounters during the cold-water months (Douglas et al. 2014). Given the substantial variability in the abundance and distribution of Dall's porpoises off the U.S. West Coast, no long-term population trends have been identified (Carretta et al. 2023). Based on data collected in summer and fall, the most recent (2018) abundance estimate for Dall's porpoises off California, Oregon, and Washington is 16,498 animals (CV = 0.608) (Becker et al. 2020; Carretta et al. 2023).

1.1.4 | Fin Whale

Fin whales exhibit complex movement patterns within the California Current Ecosystem, and do not appear to follow the typical baleen whale migration model. Satellite tracking shows that the movements of fin whales off the U.S. West Coast are highly variable, exhibiting both long-range movements along the entire coast as well as short seasonal trips in spring and fall (Falcone and Schorr 2014; Mate et al. 2015; Scales et al. 2017). In summer and fall, fin whales are broadly distributed in relatively high densities off the U.S. West Coast, with aggregations of fin whales present year-round in southern and central California (Barlow et al. 2009; Becker et al. 2016, 2018, 2020; Calambokidis et al. 2024; Campbell et al. 2015; Dohl et al. 1983; Douglas et al. 2014; Forney and Barlow 1998; Scales et al. 2017). Sightings from year-round surveys off southern California from 2004 to 2013 show fin whales farther offshore in summer and fall and closer to shore in winter and spring (Campbell et al. 2015; Douglas et al. 2014). Analysis of long-term photo identification data suggests that two overlapping populations of fin whales occur off the U.S. West Coast, a transient population with broad seasonal movements that range from the Southern California Bight north to waters off Washington and a year-round resident population within the Southern California Bight that exhibits seasonal inshore and offshore shifts in distribution (Falcone et al. 2022). Analyses of line-transect survey data collected during summer and fall between 1991 and 2018, including design-based estimates, habitat-based density models, and Bayesian trend analyses, indicate that fin whale abundance in the California Current increased during this period (Becker et al. 2020; Moore and Barlow 2011; Nadeem et al. 2016). Based on data collected in summer and fall, the most recent (2018) abundance estimate for fin whales off California, Oregon, and Washington is 11,065 (CV = 0.405) (Becker et al. 2020; Carretta et al. 2023).

2 | Material and Methods

2.1 | Study Area and Field Methods

The California Current Ecosystem (CCE) study area includes waters off the U.S. West Coast out to approximately 555 km offshore, while the CalCOFI study area is approximately one third the size of the CCE study area, encompassing 11 transect lines that run roughly perpendicular to the coast between sampling stations off southern and central California (Figure 1). Cetacean sighting data collected by the Southwest Fisheries Science Center (SWFSC) during systematic ship surveys within waters of the CCE from 1991 to 2018 (Table 1) were used to develop summer and fall SDMs, following the methods of Becker et al. (2020), but with a different set of covariates, as described below. The winter and spring SDMs were developed using cetacean sighting data collected during quarterly CalCOFI cruises conducted from 2005 to 2020 (Table 2), following the methods of Becker et al. (2017), again with a different set of covariates. While there was some temporal variation in the timing of the cruises, winter surveys were generally conducted in January and February, and spring surveys in March and April. The CalCOFI cruises were conducted along six main transect lines located off Southern California, with lines increasing in length from north to south (470–700 km; Figure 1). There are five additional transect lines located off central California that were surveyed less frequently (Figure 1, Table 2). Cetacean sighting data collected on all the lines were included in this study to capture the broadest possible range of habitat types in the models. Both the SWFSC summer and fall and CalCOFI winter and spring surveys were conducted using line-transect methods (Buckland et al. 2001), although protocols varied somewhat as summarized below.

2.1.1 | SWFSC Summer and Fall Surveys

Each survey used a NOAA research vessel and a team of six experienced visual observers. For each rotation, three observers

TABLE 1 | Cetacean and ecosystem assessment surveys conducted during 1991–2018 and used to develop the summer and fall habitat-based density models for the California Current Ecosystem study area.

Survey	Dates	Effort (km)	Regions	Source
CAMMS91	Jul–Nov 1991	10,353.60	California	Hill and Barlow (1992)
PODS93	Jul–Nov 1993	6437.40	California/Baja	Mangels and Gerrodette (1994)
ORCAWALE96	Jul–Nov 1996	15,530.80	WA, OR, CA	von Saunder and Barlow (1999)
ORCAWALE01	Jul–Dec 2001	10,343.40	WA, OR, CA	Appler et al. (2004)
CSCAPE05	Jul–Dec 2005	10,221.90	WA, OR, CA	Forney (2007)
ORCAWALE08	Jul–Nov 2008	12,242.30	WA, OR, CA	Barlow et al. (2010)
DELPHINUS09	Sept–Dec 2009	4389.10	CenCA, SoCA, Baja	Chivers et al. (2010)
CalCurCEAS14	Aug–Dec 2014	10,205.40	WA, OR, CA	Barlow (2016)
CCES18	June–Dec 2018	9554.70	Canada. WA, OR, CA, Baja	Henry et al. (2020)
Total		89,278.60		

Note: Regions covered within the study area: WA, Washington; OR, Oregon; CA, California; CenCA, Central California; SoCA, Southern California; Baja, Baja California, Mexico.

stationed on the flying bridge of the ship visually searched for and recorded cetacean sightings between 0° and 90° to port and starboard using standard line-transect protocols. The height of the flying bridge varied between the four vessels used on these surveys, but this was found to be the least important factor affecting perpendicular sighting distances on SWFSC shipboard line-transect surveys (Barlow et al. 2001). Port and starboard observers searched with pedestal-mounted 25×150 binoculars, and a center-stationed third observer searched by eye or with handheld 7×50 binoculars. Sightings were recorded along with distance and direction from the vessel, from which perpendicular sighting distance was calculated. For sightings that were within three nautical miles (5.6 km) perpendicular of the transect, the ship would typically divert "off-effort" to approach the animals for species identification and group size estimation. All observers independently provided best, high, and low group size estimates and percentages of each species identified within the group. For each observer, the best estimate was multiplied by the estimated percentage of each species, and the resulting numbers were averaged across all observers (i.e., arithmetic mean) to obtain a single group size estimate for each sighting. The survey protocols were the same for all years and are described in more detail elsewhere (e.g., Barlow and Forney 2007; Kinzey et al. 2000).

2.1.2 | CalCOFI Winter and Spring Surveys

Six different research vessels were used during the 2005–2020 survey period, but Douglas et al. (2014) found no significant difference in perpendicular sighting distances for vessels with varying platform height. All surveys were conducted in passing mode (i.e., the vessel was not diverted for species identification or group size enumeration following a sighting) with two dedicated observers searching for cetaceans using the unaided eye and 7×50 handheld binoculars. Sighting, group size estimates, effort, and weather data were systematically logged and entered into an electronic record. We included only sightings made when two observers were on effort on the standard CalCOFI lines, excluding transits. Detailed descriptions of the survey protocol can be found in Douglas et al. (2014) and Campbell et al. (2015).

2.2 | Data Processing and Habitat Variables

To create samples for both the SWFSC summer and fall and CalCOFI winter and spring SDMs, continuous portions of on-effort survey tracklines were divided into approximate 5-km segments using methods described by Becker et al. (2010). The 5-km segment length was selected to be fine enough to capture finer-scale changes in habitat conditions in the CCE study area (e.g., bathymetry), and coarse enough to reduce the number of segments with no sightings (Barlow et al. 2009). Only on-effort data collected in Beaufort sea state conditions ≤ 5 within the CCE study area were used in model development. The total number of species-specific sightings and associated average group size estimates were assigned to each segment, and habitat covariates were derived based on the segment's geographical midpoint.

Environmental variables from a data-assimilative CCE implementation of the Regional Ocean Modeling System (ROMS), produced by the University of California Santa Cruz Ocean Modeling and Data Assimilation group (Moore et al. 2011), were used as dynamic predictors, as they have proven effective in SDMs for this study area (Abrahms et al. 2019; Becker et al. 2016, 2017, 2018, 2020; Hazen et al. 2018; Lezama-Ochoa et al. 2024). Daily averages for each variable at the approximate 10 km $\times$10 km pixel (i.e., picture element) resolution of the ROMS output were used in the models. The suite of potential dynamic predictors included sea surface temperature (SST) and its standard deviation (SSTsd; calculated for a 3×3-pixel box around the modeling segment midpoint), mixed layer depth (MLD, defined by a 0.5°C deviation from the SST), sea surface height (SSH), and the standard deviation of sea surface height (SSHsd; also calculated for a 3×3-pixel box around the modeling segment midpoint). Water depth was also included as a

TABLE 2 | Cetacean survey data used to develop the winter and spring habitat-based density models for the California Cooperative Oceanic Fisheries Investigations (CalCOFI) study area.

Year	Dates	Region
2005	Jan 4–19	South
	Apr 15–30	
2006	Feb 4–25	Full
	Apr 1–17	
2007	Jan 12–Feb 2	Full
	Mar 28–Apr 16	
2008	Jan 8–24	South
	Mar 25–Apr 6	
2009	Jan 8–22	South
	Mar 7–21	
2010	Jan 13–Feb 4	Full
2011	Jan 12–Feb 6	Full
2012	Jan 27–Feb 3	South
	Mar 26–Apr 3	
2013	Jan 11–31	Full
	Apr 6–29	
2014	Jan 29–Feb 4	South
	Mar 28–Apr 17	
2015	Jan 15–Feb 7	Full
	Apr 4–19	
2016	Jan 7–24	Full
	Apr 1–21	
2017	Jan 5–19	Full
	Mar 28–Apr 19	
2018	Feb 1–9	Full
	Apr 5–26	
2019	Feb 6–12	South
	Apr 2–17	
2020	Jan 4–21	South

Note: Entries under "Region" indicate if there was effort on only the six main CalCOFI southern transect lines ("South") or on all 11 transect lines, including the five northern CalCOFI transect lines ("Full"; see Figure 1).

potential predictor, derived from the ETOPO1 1-arc-min global relief model (Amante and Eakins 2009). All covariate values were obtained for the midpoint of each transect segment.

Unlike previous SDMs developed using the same SWFSC CCE survey data (e.g., Becker et al. 2020), none of the models were offered spatial (latitude, longitude) or temporal (year) covariates because these terms can limit a model's forecasting ability (Becker et al. 2018). For example, if latitude was included in the CalCOFI winter and spring models, it would preclude making predictions outside of that original spatial domain into the broader CCE study area. Further, year can act as a proxy for a dynamic variable, which in this case could confound the spatial and seasonal extrapolations.

2.3 | Modeling Methods

2.3.1 | General Approach

To provide temporal extrapolations, we developed habitat-based models of cetacean density using sighting data collected from SWFSC surveys conducted throughout the CCE study area in summer and fall between 1991 and 2018 (Table 1). Given that the CalCOFI surveys are conducted quarterly, we initially investigated the potential for combining the SWFSC and CalCOFI summer and fall data into a single model, using the summer and fall sighting data to evaluate performance. We found that the summer and fall distribution patterns predicted from the combined model results were not as accurate as models built only with the SWFSC data. Since the CalCOFI survey data provided a relatively minor contribution to the sample sizes available from the SWFSC data, and predictive power did not increase using a combined model, we developed the summer and fall models using only the SWFSC data. For the spatial extrapolations, we built models from 29 CalCOFI shipboard surveys conducted during winter and spring between 2005 and 2020 (Table 2).

Using a well-established Generalized Additive Modeling (GAM; Wood 2017) framework based on distance sampling (Buckland et al. 2001), models were fit for four species with sufficient sample sizes available in both datasets for modeling (Table 3): short-beaked common dolphin, Pacific white-sided dolphin, Dall's porpoise, and fin whale. Habitat variables included both static and dynamic predictors shown to be important in previous SDMs (e.g., Becker et al. 2014, 2016; Hazen et al. 2017). We thus produced two sets of models for each species: (1) a summer and fall model that covered the entire CCE study area, and (2) a winter and spring model that only covered the more limited CalCOFI study area off central/southern California (Figure 1). Both the SWFSC summer and fall models and the CalCOFI winter and spring models were then used to predict on habitat conditions from December to February ("winter") and March to May ("spring") for waters throughout the CCE study area from 2017 to 2021 using techniques designed to reduce or avoid spatial and temporal extrapolation artifacts (Bouchet et al. 2019). The resulting models provided a comparison of temporal (seasonal) extrapolations from the SWFSC summer and fall models and spatial extrapolations from the CalCOFI winter and spring models. Spatial distribution patterns and study area abundance estimates derived from the two sets of model predictions were evaluated based on what is currently known about species occurrence off the U.S. West Coast in the cool seasons.

2.3.2 | Detection Parameters

Two detection parameters are required to estimate density from line-transect surveys: (1) the effective strip width (*ESW*), which provides a measure of the distance from the trackline at which species were seen based on the probability detection function,

TABLE 3 | Number of sightings (# sights) and average group size (Avg. GS) of cetacean species observed during the Southwest Fisheries Science Center (SWFSC) 1991–2018 summer/fall and California Cooperative Oceanic Fisheries Investigations (CalCOFI) 2005–2020 winter/spring shipboard surveys for which habitat-based density models were developed.

		SWFSC Summer/Fall		CalCOFI Winter/ Spring	
Common name	**Taxonomic name**	**# Sights**	**Avg. GS**	**# Sights**	**Avg. GS**
Short-beaked common dolphin	*Delphinus delphis delphis*	1034	155.73	256	81.73
Pacific white-sided dolphin	*Lagenorhynchus obliquidens*	296	54.7	48	34.72
Dall's porpoise	*Phocoenoides dalli*	678	3.72	88	6.35
Fin whale	*Balaenoptera physalus*	558	2.06	39	1.64

Note: All sightings were made while on systematic effort in Beaufort sea states ≤ 5 within the species-specific truncation distances (see text for details).

and (2) $g(0)$, the probability of detection directly on the transect line. Following the methods of Becker et al. (2016), species-specific and segment-specific estimates of both *ESW* and $g(0)$ were incorporated into the summer and fall models based on the recorded detection conditions on that segment and using coefficients estimated specifically for the CCE dataset based on methods of Barlow et al. (2011) for *ESW* and Barlow (2015) for $g(0)$. For those segments where the average Beaufort sea state was 0 ($<1\%$ of the segments), $g(0)$ was assumed to be 1, that is, that all animals directly on the transect line were detected.

Only data from winter and spring were used to fit the winter and spring models; however, detection functions were fit to the full (year-round) 2005–2020 CalCOFI sighting data following methods of Becker et al. (2017) to increase the sample size for fitting the detection functions. The summer and fall CalCOFI data provided an additional 196 short-beaked common dolphin, 28 Pacific white-sided dolphin, 7 Dall's porpoise, and 180 fin whale sightings. Both half-normal and hazard-rate key functions with no adjustment terms were fit, and Akaike's information criterion (AIC; Akaike 1973) and visual inspection of the detection plots (Thomas et al. 2010) were used to select the best model. Given the influence of Beaufort sea state on detectability (Barlow 2015; Barlow et al. 2001, 2011), there is potential for heterogeneity in detection functions to bias results (Rexstad et al. 2023); therefore, detection functions were generated with Beaufort sea state as a covariate (Buckland et al. 2001; Marques et al. 2007) using the R packages *mrds* (v. 2.2.3) and *Distance* (v. 1.0.2). Species-specific and segment-specific estimates of *ESW* were then incorporated into the models based on the recorded sea state conditions on that segment.

The segment-specific estimates of g(0) derived specifically for the SWFSC CCE dataset and based on methods of Barlow (2015) were also applied to the winter and spring CalCOFI dataset. These $g(0)$ estimates are expected to be minimum corrections (i.e., likely underestimate density) for the two-person observer team during CalCOFI surveys, because the estimates based on Barlow (2015) were for a 3-person observer team including two observers searching with pedestal-mounted 25 × 150 binoculars.

2.3.3 | Additional Correction Factors

Conducting surveys in passing mode limits the ability of observers to positively identify species, resulting in a large number of unidentified large whales and unidentified common dolphins (either *D. delphis delphis* or *D. delphis bairdii*). All of the CalCOFI winter and spring surveys were conducted in passing mode, as was some of the effort on the summer and fall 2018 SWFSC survey. Omitting these “unidentified large whale” and “unidentified common dolphin” sightings from the modeling datasets would have resulted in an underestimation of animal density for fin whales and short-beaked common dolphins. To reduce this potential downward bias, species-specific correction factors were applied to all CalCOFI segments and to passing-mode segments of the SWFSC 2018 survey to account for unidentified animals, using the methods described in Becker et al. (2017) and Becker et al. (2020).

For both the large whale and common dolphin groups, the correction factor c was estimated from the sighting data according to the simplified formula:

$$c = 1 + \frac{t_{unid}}{t_{tgt} + t_{oth}} \tag{1}$$

where t_{tgt} is the number of individuals identified as the target species, t_{oth} is the number of individuals identified as other species within the broader species group, and t_{unid} is the number of unidentified individuals in that species group. Due to the potential effect of Beaufort sea state on detectability (Barlow 2015; Barlow et al. 2001, 2011), the correction factors were evaluated to determine if they varied by sea state. If so, separate correction factors were developed by sea state; otherwise, a single correction factor was applied. The correction factors were applied to the numbers of animals estimated per segment in the SDMs for short-beaked common dolphins and fin whales (see Equation 2 below).

2.3.4 | Habitat Models

Modeling methods largely followed those described in Becker et al. (2020) for the summer and fall models and Becker et al. (2017) for the winter and spring models. For both sets of models, GAMs were developed in R (v. 4.0.2; R Core Team 2022) using the package “*mgcv*” (v. 1.8–31; Wood 2011). Restricted maximum likelihood (REML) was used to obtain parameter estimates (Marra and Wood 2011). The shrinkage approach of Marra and Wood (2011) was used to potentially remove terms from each model by modifying the smoothing penalty, allowing the smooth effect to be shrunk to zero. Additionally, to avoid overfitting, an iterative forwards/backwards selection process was used to remove variables that had p-values > 0.05 (Redfern et al. 2017; Roberts et al. 2016).

Two different species-specific modeling frameworks were used, depending on group size characteristics. For all species except the short-beaked common dolphin, GAMs were fit using the number of individuals of the given species per transect segment as the response variable using all transect segments and a Tweedie distribution to account for overdispersion. For the short-beaked common dolphin, a species that has very large and variable group sizes (e.g., 1 to 2000 animals per sighting), a separate group encounter rate model was developed. The group encounter rate model was built using all transect segments, regardless of whether they included sightings, using the groups sighted per segment as the response variable and a Tweedie distribution to account for overdispersion (Miller et al. 2013). The expected group size based on the size bias regression method (Buckland et al. 2001; Thomas et al. 2010) was then used in the density equation (see Equation 2 below). The full suite of potential habitat predictors was offered to both the group encounter rate and single response GAMs.

Predictions from the final models were incorporated into the standard line-transect equation (Buckland et al. 2001) to estimate density (D; number of animals per km^2):

$$D_i = \frac{n_i \bullet s_i \bullet c_i}{A_i} \tag{2}$$

where i is the segment, n is the number of sightings on segment i, s is the average group size (i.e., number of a given species present in a group) on segment i, c is the species-specific correction factor for unidentified common dolphins or large whales (derived in Equation 1 and assumed to be 1 for all other species) based on sea state conditions on segment i, and A is the effective area searched for segment i:

$$A_i = 2 \bullet L_i \bullet ESW_i \bullet g(0)_i \tag{3}$$

where L_i is the length of the effort segment i, ESW_i is the effective strip half-width, and $g(0)_i$ is the probability of detection on the transect line.

Model performance was evaluated using established metrics, including the percentage of explained deviance, the area under the receiver operating characteristic curve (AUC; Fawcett 2006), the true skill statistic (TSS; Allouche et al. 2006), and visual inspection of predicted and observed distributions during the 1991–2018 summer and fall and 2005–2020 winter and spring cetacean surveys (Barlow et al. 2009; Becker et al. 2016, 2017; Forney et al. 2012). AUC measures the accuracy of predicting observed presences and absences; values range from 0 to 1, where a score > 0.5 indicates better than random skill. TSS accounts for both false negative and false positive errors and ranges from -1 to $+1$, where $+1$ indicates perfect agreement and values of zero or less indicate a performance no better than random. To calculate TSS, the sensitivity-specificity sum maximization approach (Liu et al. 2005) was used to define thresholds for transforming species densities to presence/absence.

In addition, the model-based abundance estimates for the respective summer and fall and winter and spring study areas based on the sum of individual modeling segment predictions were compared to standard line-transect estimates derived from the same dataset used for modeling in order to assess potential bias in the habitat-based model predictions (Becker et al. 2022). The standard line-transect estimates were derived from the survey data using Equations (2) and (3) above, but without the inclusion of habitat predictors (i.e., observed rather than predicted densities).

For each species, the final models were used to predict density in each cell of a 10 × 10 km grid throughout the CCE study area for distinct daily averages of environmental conditions in winter (December–February) and spring (March–May) for the last 5 years (2017–2021). While the survey data do not cover this exact time period, we selected the most recent 5 years for predictions since they are most relevant for management purposes and previous work has demonstrated that the models are able to capture interannual variability within the study area (Becker et al. 2018). Prior to making the predictions, the extrapolation detection tool in the R package "*dsmextra*" (Bouchet et al. 2020) was used to assess the source and extent of extrapolation in the winter and spring predictions for both sets of models. Pixels with habitat covariates outside the space of the data used to build the respective models were then eliminated from each of the daily surfaces, as this is a simple and effective method for avoiding extrapolation (Bouchet et al. 2019).

The separate daily 10-km resolution grid predictions were averaged to produce spatially-explicit grids of mean winter and spring species density and measures of uncertainty. For each of the four species there were thus two separate predictions for each seasonal period based on predictions from either the SWFSC summer and fall model (hereafter "seasonally extrapolated models") and the CalCOFI winter and spring models (hereafter "spatially extrapolated models").

As an initial validation step, we used data from the four most recent winter and spring CalCOFI surveys (2017–2020; data were not available for 2021) to evaluate the seasonal extrapolation of the SWFSC summer and fall models within the CalCOFI study area. For each species, both the seasonally and spatially extrapolated models were used to estimate abundance specifically for the CalCOFI study area, and ratios of the yearly estimates were computed. In addition, sightings from the 2017–2020 CalCOFI surveys were overlaid on the seasonally extrapolated density surfaces to compare predicted and observed distributions for each year.

2.3.5 | Model Uncertainty

Variation in environmental conditions has been one of the greatest sources of uncertainty when predicting density as a function of habitat variables in highly dynamic ecosystems such as the California Current, and this variation has been used in previous publications to provide spatially explicit variance measures for SWFSC summer and fall and CalCOFI winter and spring model predictions (Barlow et al. 2009; Becker et al. 2016, 2017, 2020; Forney et al. 2012). Miller et al. (2022) recently developed techniques for deriving more comprehensive measures of uncertainty in GAM predictions that account for the combined uncertainty from environmental variability, the GAM coefficients, *ESW*, and $g(0)$. These techniques include generating multiple daily density surfaces (for covariate rasters at each time slice) accounting for model parameter uncertainty (via posterior sampling from the model parameters) and providing a range of possible density estimates from which variance can be calculated. For this study, the Miller et al. (2022) methods were applied to estimate spatially explicit measures of variance that accounted for these combined sources of uncertainty.

The estimates of g(0) developed by Barlow (2015) and used for model development are based on segment-specific Beaufort sea state conditions, which are currently not compatible with the Miller et al. (2022) methods for estimating variance. Therefore, to incorporate the variance of g(0) into the pixel-specific estimates, an overall estimate of uncertainty in $g(0)$ was derived using the variance estimates for this parameter weighted by the proportion of survey effort conducted within each of the Beaufort sea state categories for the respective SWFSC summer and fall and CalCOFI winter and spring surveys, and estimated based on 10,000 bootstrap values. The Barlow (2015) g(0) estimate for Pacific white-sided dolphin was considered an outlier (i.e., 1 for all sea states), possibly because of small sample sizes, so for this species the g(0) estimates for common dolphins were used because they have similar sighting characteristics (Jefferson et al. 2015).

For short-beaked common dolphins, pixel-based uncertainty estimates were based on the group encounter rate model, which does not include uncertainty in group size estimates because the expected group size was incorporated into the density equation (Equation 2) as a constant based on the size bias regression method. Therefore, the pixel-based variance estimates for this species are under-estimated to a small degree. However, our analysis includes the dominant sources of uncertainty to a greater extent than previous similar studies (e.g., Becker et al. 2017, 2020).

2.3.6 | Model Comparison

Differences in the two sets of model-predicted spatial distribution and estimated species abundance in the study area were evaluated relative to current knowledge about species occurrence off the U.S. West Coast in the cool seasons. This included analyses of systematic survey data collected in different regions of the CCE study area between 1975 and 1992, including ship and aerial surveys conducted in the Southern California Bight (Dohl et al. 1978), aerial surveys conducted in nearshore waters off the California coast (Dohl et al. 1983; Forney and Barlow 1998), and ship and aerial surveys conducted off Oregon and Washington (Green et al. 1992). More recent data used to evaluate model performance included predictions of relative cetacean density off the coast of Washington based on multiple data sources (Menza et al. 2016), habitat suitability predictions for fin whale in the California Current based on tag data (Scales et al. 2017), and species distribution models for rorquals off Oregon (Derville et al. 2022). In addition, previous design- and model-based estimates of cetacean density based on the 2005 to 2015 CalCOFI ship surveys off southern and central California (Becker et al. 2017; Campbell et al. 2015) were also used for cross validation purposes.

For each species, the winter and spring model-based abundance estimates for the CCE study area were calculated as the sum of the individual grid cell abundance estimates, which were derived by multiplying the cell area (in km^2) by the predicted grid cell density, exclusive of any portions of the cells located outside the study area or on land. Area calculations were completed using the R packages *geosphere* and *gpclib* in R (version 2.15.0). Uncertainty for the CCE study area abundance estimates was estimated using the Miller et al. (2022) techniques described above and thus accounted for the combined uncertainty from environmental variability, the GAM coefficients, *ESW*, and $g(0)$. For short-beaked common dolphins, group size uncertainty from the size bias regression estimates was combined into the study area variance estimates using the delta method (Seber 1982).

3 | Results

A total of 89,279 km of on-effort survey data collected on 9 SWFSC surveys from July to November between 1991 and 2018 within the CCE study area was used to develop the summer and fall models. The number of sightings within the species-specific truncation distances and available for modeling ranged from 296 to 1034 (Table 3). A total of 33,995 km of on-effort data from 29 CalCOFI surveys conducted during January to April in 2005–2020 was used to develop the winter and spring models. The number of sightings used for modeling was much lower than those available from the summer and fall surveys, ranging from 39 to 256 (Table 3).

There were six additional species for which there were sightings in both sets of surveys but not enough sightings in the CalCOFI winter and spring dataset to support spatially extrapolated model development, including striped dolphin (*Stenella coeruleoalba*), long-beaked common dolphin (*Delphinus delphis bairdii*), common bottlenose dolphin (*Tursiops truncatus*), Risso's dolphin (*Grampus griseus*), northern right whale dolphin (*Lissodelphis borealis*), and minke whale (*Balaenoptera acutorostrata*). Seasonally extrapolated models were developed for these species from the SWFSC summer and fall models. For completeness, model results for these species are presented in the Supporting Information S.3.

The range of covariate values included in the SWFSC summer and fall modeling dataset was generally larger than that of the CalCOFI winter and spring dataset, which is not surprising given the much greater span of latitude included within the full SWFSC CCE study area (Table 4). However, the extent of extrapolation in the daily winter and spring prediction surfaces was generally greater for the SWFSC summer and fall modeling dataset, although only univariate extrapolation (vs. combinatorial extrapolation) was evident for both modeling datasets (Supporting Information S.1). To avoid extrapolation artifacts, pixels with covariates outside the range of the respective modeling datasets were discarded from the daily density surfaces prior to making predictions from the models. The percentage of pixels omitted across all years ranged from 3.4% (short-beaked

TABLE 4 | Covariate values used to develop the species distribution models based on the Southwest Fisheries Science Center (SWFSC) 1991–2018 summer and fall and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) 2005–2020 winter and spring shipboard surveys.

Variable		SWFSC summer and fall	CalCOFI winter and spring	Prediction surfaces
SST (°C)	Mean	16.76	14.68	12.81
	Min	9.96	9.17	6.39
	Max	23.18	18.92	22.41
SSH (cm)	Mean	0.13	0.14	0.13
	Min	−0.09	−0.07	−0.02
	Max	0.4	0.36	0.59
MLD (m)	Mean	22.46	46.91	46.1
	Min	0.21	0.42	0.18
	Max	102.67	170.8	315.11
SSTsd	Mean	0.21	0.18	0.14
	Min	0.006	0.01	0.0005
	Max	2.16	1.69	4.22
SSHsd	Mean	0.01	0.009	0.01
	Min	0.0003	0.0003	0.0000007
	Max	0.05	0.04	0.11
Depth (m)	Mean	−2914	−2783	−3187.97
	Min	−5036	−4787	−5060
	Max	−15	−13	0

Note: Values include the mean, minimum (min), and maximum (max) values observed during the respective surveys based on the Regional Ocean Modeling System (ROMS) values for all modeling segments from the respective surveys. Also shown are the covariate values for all of the ROMS-based daily surfaces used to make the full California Current Ecosystem study area winter and spring predictions (habitat covariates outside the space of the data used to build the respective models were eliminated prior to making the predictions). Covariates include sea surface temperature (SST), sea surface height (SSH), mixed layer depth (MLD), bathymetric depth (depth), and the standard deviation (sd) of both SST and SSH (see text for details).

common dolphin CalCOFI winter and spring model) to 14.7% (fin whale summer and fall SWFSC model) from a total of 10,942,021 potential pixel values across all years (12,011 pixels per density surface and 911 daily surfaces).

3.1 | Detection Functions

For the CalCOFI winter and spring data, a half-normal model with Beaufort sea state as a covariate provided the best fit to the perpendicular distance data for all four species. The truncation distance for common dolphins was 1.5 km, eliminating 18% of the most distant sightings. This is higher than the recommended percentage of 5%–15% (Buckland et al. 2001), but in passing mode the group size estimates decreased with increasing distance, suggesting estimation bias at larger distances. Excluding a greater percentage of sightings thus reduced the potential bias in group size estimation. Further, a size bias regression method was used to estimate the expected mean group size within this truncation distance. Truncation distances for the other species were 1.2 km for Pacific white-sided dolphin (eliminating 11% of the most distant sightings), 1.3 km for Dall's porpoise (eliminating 13% of the most distant sightings) and 3.6 km for large whales (eliminating 14% of the most distant sightings).

3.2 | Correction Factors

To account for unidentified animals on the 2018 SWFSC survey, correction factors for unidentified large whales were applied separately by Beaufort sea state category to the fin whale sightings, because the proportion of unidentified whales increased with increasing sea state. These correction factors were 1.04, 1.08, 1.10, 1.30, and 1.46 for sea states 0–1, 2, 3, 4, and 5, respectively. For the common dolphin group, larger multipliers were not associated with greater sea states, so a uniform correction factor of 1.71 was applied across all sea states for the 2018 survey sightings of short-beaked common dolphins.

Similar to the SWFSC CCE data, correction factors estimated from CalCOFI winter and spring data for fin whale varied by sea state, as the proportion of unidentified large whales increased with increasing sea state, resulting in correction factors of 1.09, 1.45, 1.54, 1.95, and 2.12 for Beaufort sea states 0–1, 2, 3, 4, and 5, respectively. For the common dolphin group, the multiplier was greater in lower sea states—likely because of a confounding effect of larger estimated group sizes in lower sea states when in passing mode; therefore, a uniform correction factor of 1.33 was used across all sea states.

3.3 | Model Metrics and Explanatory Performance

The expected group size for short-beaked common dolphins based on the size bias regression method and used in the respective density equations (see Equation 2) was 108.16 (CV = 0.061) for the SWFSC summer and fall data and 47.06 (CV = 0.076) for the CalCOFI winter and spring data.

Explanatory performance was similar to those of past SDMs developed for these species in the CCE study area (Becker et al. 2017, 2018, 2020), with explained deviance ranging from approximately 10% to 39%, AUC values from 0.66 to 0.87, TSS values from 0.24 to 0.58, and observed: predicted density ratios greater than 0.79, with the majority greater than 0.93, indicating that model-predicted absolute abundance estimates in the respective study areas were similar to values derived from design-based line-transect methods (Table 5). The key predictor variables (i.e., those with the most influence on the model) were similar for both sets of models, although the SWFSC summer and fall models consistently included more covariates than the CalCOFI winter and spring models (Table 5) because of the larger geographic range and greater sample sizes of the SWFSC surveys. The functional forms of the predictor variables were generally similar between datasets within the same range of covariate

TABLE 5 | Summary of the Southwest Fisheries Science Center (SWFSC) summer and fall and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) winter and spring species distribution models.

Species	Predictor variables	Expl. Dev.	AUC	TSS	Obs:Pred
Short-beaked common dolphin					
SWFSC	SST + depth + SSH + SSHsd	9.88	0.73	0.36	0.99
CalCOFI	SST + depth + MLD	10.80	0.71	0.35	0.98
Pacific white-sided dolphin					
SWFSC	Depth + SSH + SST + MLD + SSHsd	39.30	0.82	0.51	0.79
CalCOFI	MLD + SST + SSTsd	39.40	0.76	0.50	1.10
Dall's porpoise					
SWFSC	SSH + SST + depth + SSHsd + SSTsd	27.40	0.87	0.58	0.94
CalCOFI	SST + SSH + SSHsd	19.70	0.78	0.47	0.93
Fin whale					
SWFSC	SSH + SST + depth + MLD + SSTsd	13.20	0.66	0.24	0.87
CalCOFI	Depth + SSH + SST	20.10	0.84	0.57	1.03

Note: Variables are listed in the order of their significance, and abbreviations are as follows: depth, bathymetric depth; MLD, mixed layer depth; SSH, sea surface height; SSHsd, standard deviation of SSH; SST, sea surface temperature; SSTsd, standard deviation of SST. All models were corrected for effort with an offset for the effective area searched (see text for details). Comparative performance metrics included percentage of explained deviance (Exp.Dev.), the area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS), and the ratio of observed to predicted density for the study area (Obs:Pred).

values, with the exception of depth for short-beaked common dolphin and SSHsd for Dall's porpoise (Figure 2). In winter and spring, short-beaked common dolphins are associated with the deepest waters within the CalCOFI study area, while in summer and fall within the entire CCE study area, the functional form indicates a bimodal distribution, with the greatest number of dolphins found in waters approximately 500 m deep, or offshore in waters approximately 4000 m deep (Figure 2a). Based on the SWFSC summer and fall model, greater numbers of Dall's porpoise are found in waters with highest variability in SSH (i.e., frontal regions), while in the CalCOFI study area in winter and spring, Dall's porpoise are associated with waters with little to no variability in SSH (Figure 2c).

3.4 | Predictive Performance and Model Validation

Predictive performance varied by species and model type, and data available to validate the model predictions also varied by species and location within the CCE study area. Therefore, the models' ability to predict winter and spring distribution patterns and estimate absolute abundance for the CCE study area are discussed separately for each species below. In addition to previously published data that were used for cross validation, the 2017–2020 CalCOFI cool season data used to develop the spatially extrapolated models were also used to evaluate the seasonal extrapolation of the SWFSC summer and fall models within the CalCOFI study area. With the exception of short-beaked common dolphin, there were too few yearly sightings to provide a meaningful visual comparison of cool season observations to predicted density patterns from the seasonally extrapolated models, but the 2017–2020 yearly abundance estimates derived for the smaller CalCOFI region provided an additional cross validation dataset for this portion of the study area (Supporting Information S.2).

3.4.1 | Short-Beaked Common Dolphin

Abundance. The seasonally and spatially extrapolated models both yielded greater numbers of short-beaked common dolphins within the CCE study area during winter versus spring (Figure 3; Table 6), consistent with previous seasonal design-based estimates for waters off Southern California (Campbell et al. 2015). Both models also exhibited similar patterns of interannual variability in abundance. For example, both models predicted greatest winter and spring abundance in 2018 and substantial decreases in the numbers of short-beaked common dolphins present in the CCE study area in 2020 and 2021 (Figure 4, Table 6).

The winter and spring abundance estimates for short-beaked common dolphin predicted from the two models were quite different, however, as the spatially extrapolated 2017–2021 average estimates were about four times greater than those predicted by the seasonally extrapolated model for the full CCE study area (Table 6), and up to three times greater for the smaller CalCOFI study area (Supporting Information S.2). The short-beaked common dolphin is a warm temperate species whose distribution generally shifts northward into the CCE study area when ocean conditions are warm and southward into waters off Mexico when conditions are cool (Barlow 2016; Becker et al. 2014, 2018, 2022; Dohl et al. 1986; Forney and Barlow 1998; Heyning and Perrin 1994). Fewer short-beaked common dolphins are thus expected within the CCE study area during winter and spring than during summer and fall; however, the abundance predicted by the seasonally extrapolated model (121,114, CV = 0.439) was lower than a previous design-based winter estimate for Southern California waters only (225,949, CV = 0.32; Campbell et al. 2015), and less than one eighth of the model-based summer and fall abundance estimate of 1,056,308 (CV = 0.207) for the CCE study area

(Becker et al. 2020). Conversely, the average of the 2017–2021 winter and spring estimates from the spatially extrapolated model (365,744 dolphins; Table 6) was similar to an abundance estimate of 305,694 (CV = 0.340) common dolphins made for nearshore waters off California based on aerial survey data collected between February and April in 1991 and 1992

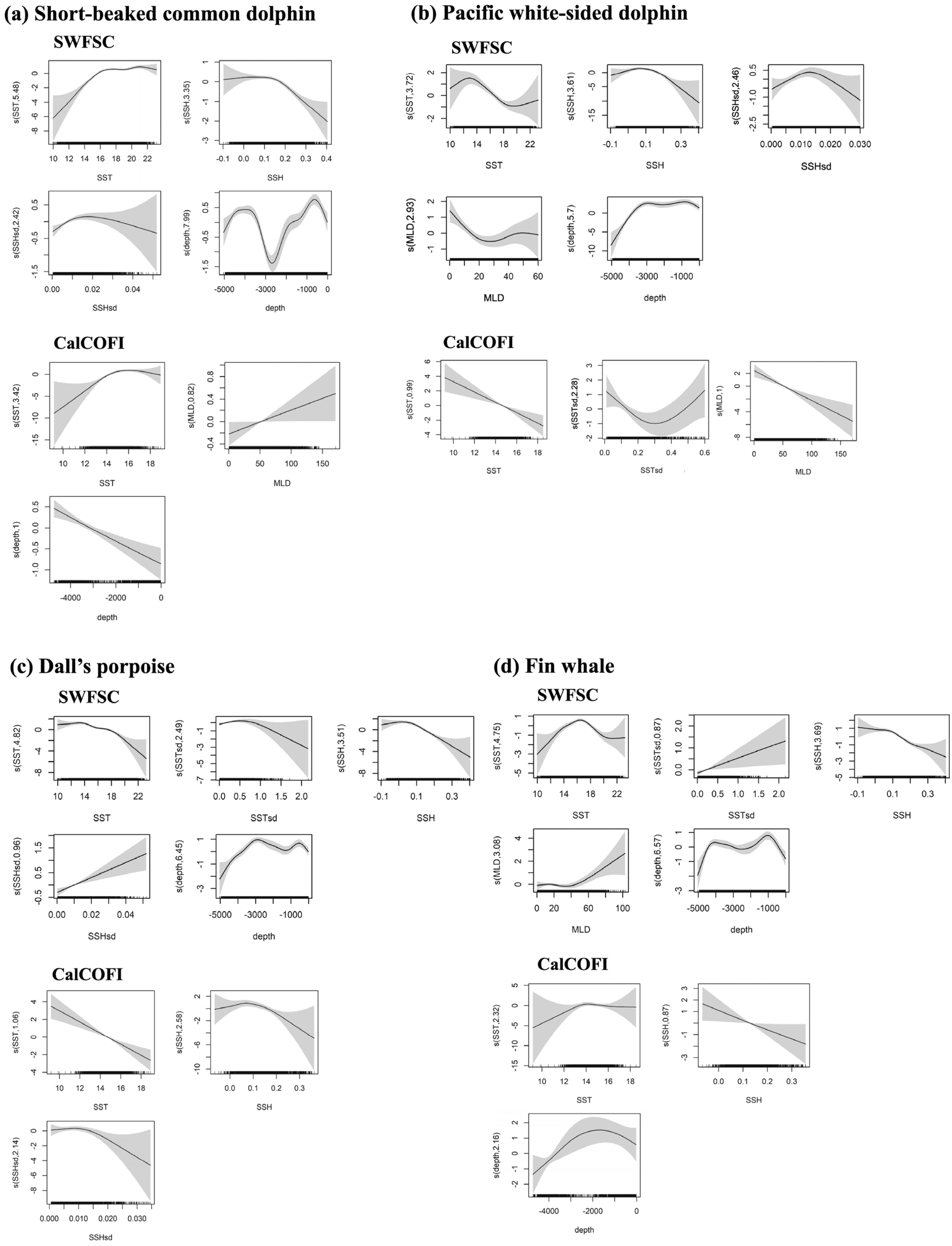

FIGURE 2 | Legend on next page.

FIGURE 2 | Functional forms for variables included in the final Southwest Fisheries Science Center (SWFSC) summer and fall and California Cooperative Oceanic Fisheries Investigations (CalCOFI) winter and spring species distribution models for (a) short-beaked common dolphin, (b) Pacific white-sided dolphin, (c) Dall's porpoise, and (d) fin whale. Predictor variables included: SST, sea surface temperature; SSTsd, standard deviation of SST; MLD, mixed layer depth; SSH, sea surface height; SSHsd, standard deviation of SSH; and depth, bathymetric depth. The y-axes represent the term's (linear or spline) function, with the degrees of freedom shown in parentheses on the y-axis (linear terms are represented by a single degree of freedom). Zero on the y-axes corresponds to no effect of the predictor variable on the estimated response variable. Scaling of y-axis varies among predictor variables to emphasize model fit. The shading reflects 2× standard error bands (i.e., 95% confidence interval); tick marks ('rug plot') above the X-axis show data values.

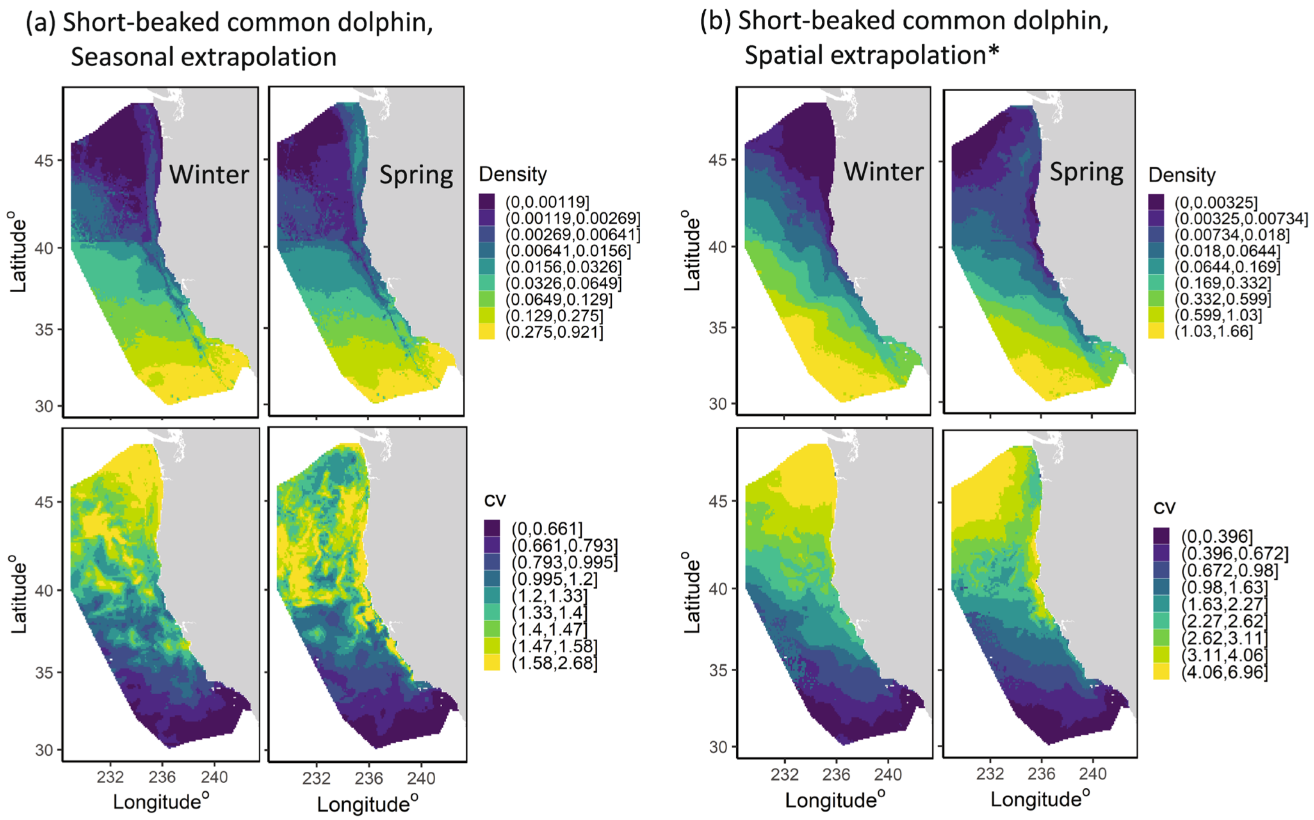

FIGURE 3 | Predicted short-beaked common dolphin winter and spring density (top panels) and coefficient of variation (CV; bottom panels) estimates from (a) the seasonally extrapolated Southwest Fisheries Science Center summer and fall species distribution model, and (b) the spatially extrapolated California Cooperative Oceanic Fisheries Investigations winter and spring species distribution model; the "*" indicates which model exhibited better performance. The density estimates are the multi-year average (2017–2021) values based on predicted daily cetacean species densities covering winter (December–February) and spring (March–May). Density ranges are presented in quantiles based on the combined winter and spring predictions for the respective models in order to show differences between seasons and years (see Figure 4). Predictions are shown for the California Current Ecosystem study area (1,141,800 km^2).

(Forney and Barlow 1998). Given the documented increase in the abundance of short-beaked common dolphins in the CCE during the last two decades (Barlow 2016; Becker et al. 2018), the spatially extrapolated model predictions appear to be more accurate than the seasonally extrapolated predictions.

Distribution. Both models predicted the greatest densities of short-beaked common dolphins within the southern portion of the study area during winter and spring (Figure 3), consistent with expected southern shifts during the cool water periods (Barlow 2016; Becker et al. 2014, 2018, 2022; Dohl et al. 1986; Forney and Barlow 1998; Heyning and Perrin 1994). The spatially extrapolated model identified a band of low densities extending southeast from Point Conception (34.45° N), separating high-density areas in the southwest portion of the study area from moderate density regions within the Southern California Bight (Figure 3b). This area is encompassed within the boundaries of the CalCOFI survey data used for model building (i.e., the model is not extrapolating in this region), and these distribution patterns were similar to those previously identified in other studies (Becker et al. 2017; Campbell et al. 2015; Forney and Barlow 1998).

The seasonally extrapolated model predicted high densities throughout much of the Southern California Bight and also captured a similar band of low density; however, densities near shore were predicted to be higher than documented during prior studies, which identified the greatest densities in offshore waters during the cool seasons (Becker et al. 2017; Campbell et al. 2015). Further, a comparison of the seasonally extrapolated predicted densities to actual sightings from the 2017–2020

TABLE 6 | Model-predicted yearly and average (2017–2021) mean estimates of abundance (Abund) within the CCE study area for winter (December–February) and spring (March–May), derived from the seasonally extrapolated summer and fall Southwest Fisheries Science Center (Seasonal) and the spatially extrapolated winter and spring California Cooperative Oceanic Fisheries Investigations (Spatial) species distribution models. Coefficient of variation (CV) estimates account for the combined uncertainty from environmental variability, the GAM coefficients, effective strip width, and g(0) (see text for details).

		2017		**2018**		**2019**		**2020**		**2021**		**2017–2021 Average**	
Species	**Extrapolation type**	**Abund**	**CV**	**Abund**	**CV**	**Abund**	**CV**	**Abund**	**CV**	**Abund**	**CV**	**Abund**	**CV**
Short-beaked common dolphin													
Winter	Seasonal	117,262	0.095	160,199	0.086	140,468	0.088	118,833	0.093	68,833	0.121	121,114	0.439
	Spatial	463,940	0.103	493,511	0.107	485,886	0.105	437,901	0.109	363,556	0.107	448,934	0.253
Spring	Seasonal	85,254	0.109	107,572	0.099	77,310	0.114	53,750	0.141	26,790	0.203	70,135	0.493
	Spatial	355,067	0.109	364,442	0.108	323,892	0.111	203,145	0.139	166,221	0.155	282,553	0.340
Pacific white-sided dolphin													
Winter	Seasonal	59,060	0.492	61,007	0.544	64,470	0.576	61,169	0.578	36,369	0.589	56,415	0.405
	Spatial	671,894	0.568	628,988	0.547	585,137	0.511	555,016	0.509	736,617	0.556	635,352	0.817
Spring	Seasonal	88,792	0.460	99,656	0.405	73,593	0.444	87,498	0.411	66,140	0.501	83,145	0.538
	Spatial	1,122,327	0.706	1,049,909	0.751	1,401,424	0.724	970,674	0.691	968,372	0.719	1,102,541	0.775
Dall's porpoise													
Winter	Seasonal	58,999	0.186	59,354	0.161	46,503	0.179	43,679	0.183	42,095	0.202	50,112	0.319
	Spatial	240,927	0.378	187,014	0.320	152,179	0.319	173,563	0.398	192,325	0.390	189,167	0.411
Spring	Seasonal	46,194	0.252	53,937	0.227	39,902	0.252	43,999	0.248	24,482	0.277	41,703	0.334
	Spatial	335,181	0.437	358,291	0.430	363,949	0.474	356,507	0.474	256,249	0.529	334,033	0.212
Fin whale													
Winter	Seasonal	5309	0.301	5838	0.240	4872	0.257	4293	0.241	2906	0.215	4643	0.324
	Spatial	1219	0.300	1566	0.288	1207	0.281	1048	0.278	924	0.269	1194	0.223
Spring	Seasonal	5238	0.392	6983	0.420	4533	0.364	4468	0.398	1743	0.301	4593	0.431
	Spatial	1515	0.300	1707	0.309	1399	0.271	1611	0.268	871	0.273	1422	0.273

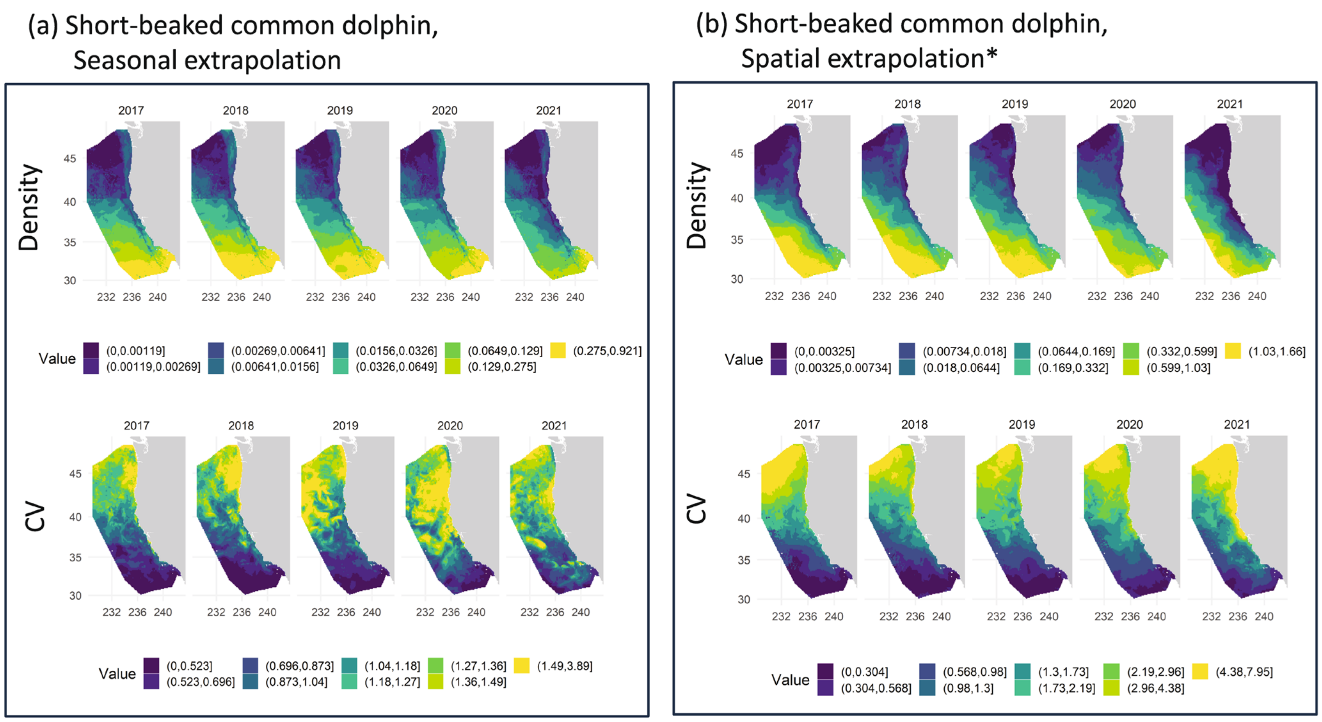

FIGURE 4 | Predicted short-beaked common dolphin annual 2017–2021 density (top panels) and coefficient of variation (CV; bottom panels) estimates from (a) the seasonally extrapolated Southwest Fisheries Science Center summer and fall species distribution model, and (b) the spatially extrapolated California Cooperative Oceanic Fisheries Investigations winter and spring species distribution model; the "*" indicates which model exhibited better performance. The annual density estimates reflect the combined cool season (December–May) averages from predicted daily cetacean species densities for each respective year. The density ranges are presented in quantiles based on the combined winter and spring predictions for the respective models to show differences between years and seasons (see Figure 3). Predictions are shown for the California Current Ecosystem study area (1,141,800 km^2).

CalCOFI cool season surveys shows the model underestimated density in the offshore areas where the majority of sightings occurred (Supporting Information S.2).

Based on the seasonally extrapolated model's apparent underestimation of abundance and failure to capture the offshore distribution shift of short-beaked common dolphins in the cool seasons, the spatially extrapolated model exhibited better performance in this study area.

3.4.2 | Pacific White-Sided Dolphin

Abundance. Both models predicted substantially greater numbers of Pacific white-sided dolphins in the CCE study area during spring versus winter (Figure 5, Table 6). These results are consistent with the seasonal design-based abundance estimates of Campbell et al. (2015), and with results from aerial surveys conducted off Oregon and Washington between April 1989 and September 1990 that documented the greatest densities during late spring and early summer and the lowest densities during winter (Green et al. 1992). Interannual variability in abundance was also apparent for both sets of models (Table 6).

There was, however, an order-of-magnitude difference in predicted abundance between the seasonally extrapolated and spatially extrapolated models (Table 6). The lowest spatially extrapolated model predictions for the entire CCE study area during winter and spring were 15 to 44 times higher than the previously published model-based summer and fall 2018 estimate of 39,999 (CV = 0.222; Becker et al. 2020). The abundance of this cool-temperate species is expected to increase in the CCE study area during cool seasons (Becker et al. 2014; Campbell et al. 2015; Forney and Barlow 1998; Green et al. 1992); however, the magnitude of the increase predicted by the spatially extrapolated model is much too large to be accounted for by distribution shifts or potential increases in population. The 2017–2021 average spring abundance estimate from the spatially extrapolated model was 1,102,541 (CV = 0.775), which is approximately 8% higher than a prior range-wide estimate of 931,000 (CV = 0.90) Pacific white-sided dolphins within the entire North Pacific (Buckland 1993). Abundance estimates derived from the spatially extrapolated model thus appear to be ecologically implausible.

The average 2017–2020 abundance estimate from both the seasonally extrapolated model and the spatially extrapolated model for the smaller CalCOFI study area (the area where the latter model is not extrapolating) compared well to the Campbell et al. (2015) design-based estimates for winter (16,718) and spring (23,983) for the southern portion of the CalCOFI study area (Supporting Information S.2). This suggests that the substantial CCE-wide abundance estimates derived from the spatially extrapolated model are primarily due to model extrapolation in the northern portion of the study area.

Distribution. Both models predicted greatest Pacific white-sided dolphin densities throughout waters off Washington and

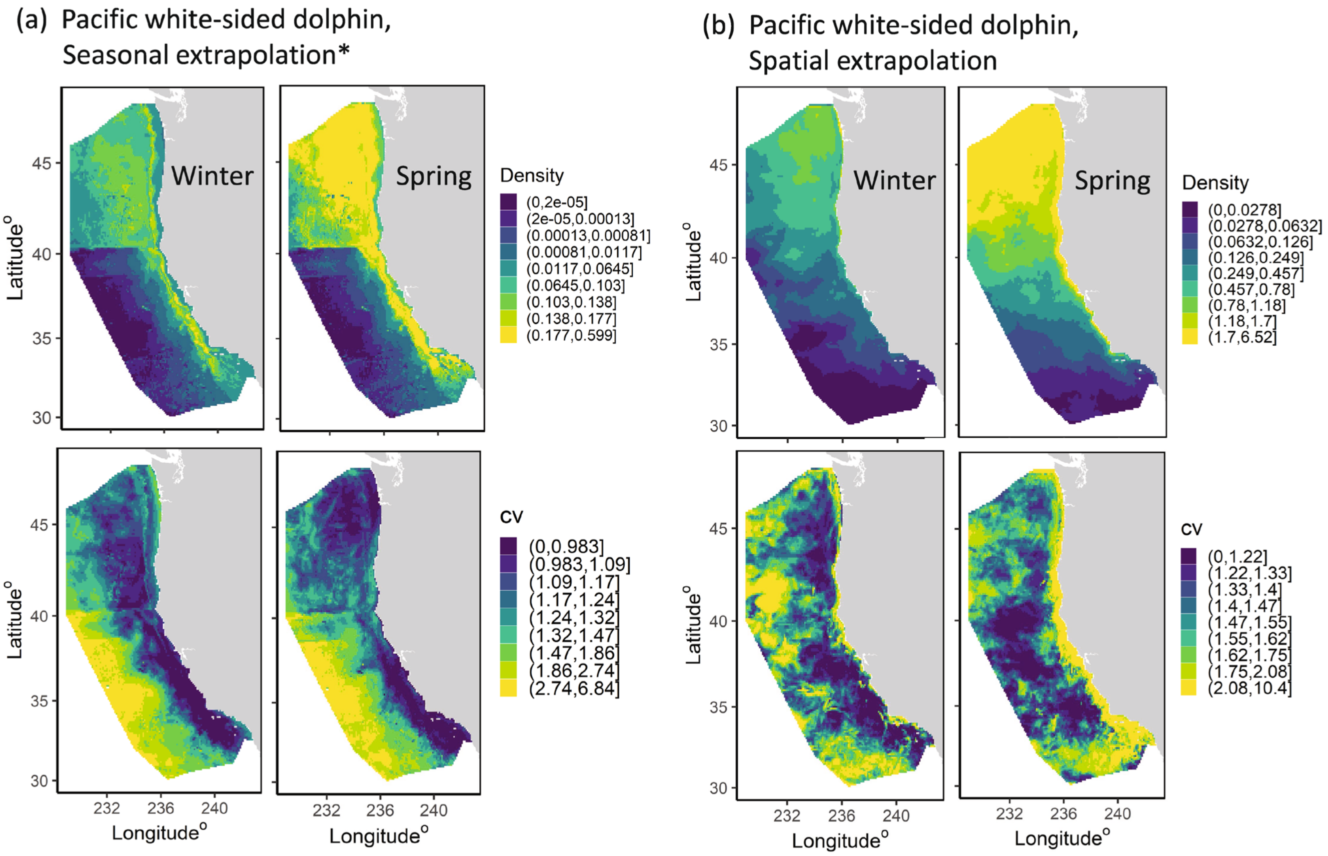

FIGURE 5 | Predicted Pacific white-sided dolphin winter and spring density (top panels) and coefficient of variation (CV; bottom panels) estimates from (a) the seasonally extrapolated Southwest Fisheries Science Center summer and fall species distribution model, and (b) the spatially extrapolated California Cooperative Oceanic Fisheries Investigations winter and spring species distribution model; the "*" indicates which model exhibited better performance. The density estimates are the multi-year average (2017–2021) values based on predicted daily cetacean species densities covering winter (December–February) and spring (March–May). Density ranges are presented in quantiles based on the combined winter and spring predictions for the respective models in order to show differences between seasons and years (see Figure 6). Predictions are shown for the California Current Ecosystem study area (1,141,800 km^2).

Oregon (i.e., north of 42° N) and extending southward along a narrow coast band to Point Conception (Figure 5). The seasonally extrapolated model predicted a distinct region of lower density along most of the U.S. West Coast, which is consistent with previous studies that documented most Pacific white-sided dolphins within slope and offshore waters rather than in shallower shelf waters (Forney and Barlow 1998; Green et al. 1992). These differences in coastal distribution patterns were also evident in the predicted annual 2017–2021 combined cool season distribution patterns (Figure 6). The seasonally extrapolated model also predicted relatively high to mid-range densities throughout the Southern California Bight, consistent with documented southerly movements and multiple sightings of this species in waters south of Point Conception in the cool seasons (Becker et al. 2014; Campbell et al. 2015; Forney and Barlow 1998; Green et al. 1992).

Based on the unrealistically high estimates of abundance predicted by the spatially extrapolated model, and the mismatch in predicted distribution patterns along the coast, we consider the seasonally extrapolated model to have exhibited better performance for Pacific white-sided dolphins in this study area.

3.4.3 | Dall's Porpoise

Abundance. Seasonal abundance results from the two Dall's porpoise models were inconsistent. The spatially extrapolated model indicated substantially greater numbers of Dall's porpoise within the CCE study area during spring than during winter, while the seasonally extrapolated model showed less variability between the winter and spring periods, although abundance was generally predicted to be greater in winter (Table 6). Similar to the results for Pacific white-sided dolphin, the model-based absolute abundance estimates for the entire CCE study area were substantially different between the two datasets, with the spatially extrapolated model predicting an order-of-magnitude more Dall's porpoise during winter and spring than the seasonally extrapolated model (Table 6). Based on previous studies that yielded abundance estimates of 16,498 (CV = 0.608) during summer and fall 2018 (Becker et al. 2020) and 26,111 (CV = 0.296) during winter and spring 1991–1992 (Forney and Barlow 1998), the spatially extrapolated total abundance estimate averaging 261,600 porpoises during winter and spring (Table 6) is likely biased high, particularly in the northern portion of the study area where density estimates were as high as 1.12 porpoises km^{-2} (Figure 7b).

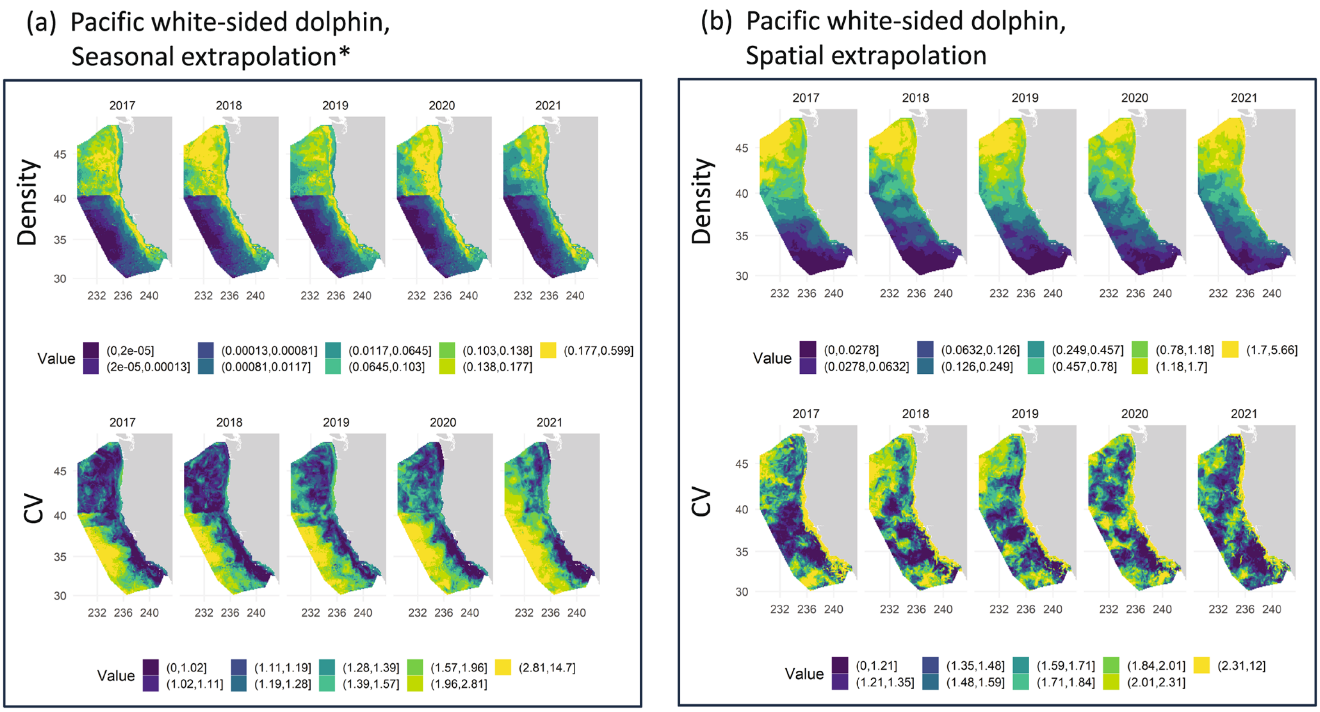

FIGURE 6 | Predicted Pacific white-sided dolphin annual 2017–2021 density (top panels) and coefficient of variation (CV; bottom panels) estimates from (a) the seasonally extrapolated Southwest Fisheries Science Center summer and fall species distribution model, and (b) the spatially extrapolated California Cooperative Oceanic Fisheries Investigations winter and spring species distribution model; the "*" indicates which model exhibited better performance. The annual density estimates reflect the combined cool season (December–May) averages from predicted daily cetacean species densities for each respective year. The density ranges are presented in quantiles based on the combined winter and spring predictions for the respective models to show differences between years and seasons (see Figure 5). Predictions are shown for the California Current Ecosystem study area (1,141,800 km^2).

The annual 2017–2020 abundance estimates for the smaller CalCOFI study area were similar for the seasonally extrapolated model and the spatially extrapolated model, with average estimates of 12,907 and 17,502 porpoises, respectively (Supporting Information S.2). Thus, the markedly greater CCE-wide estimate of abundance for the spatially-extrapolated model (Table 6) can be attributed to model extrapolation in the northern portion of the study area.

Distribution. The winter and spring distribution patterns predicted by the two models were generally similar, with greatest densities predicted for the northern portions of the study area and lowest densities in the southwest, with mid- to higher-level densities extending south along the nearshore regions into the Southern California Bight (Figure 7). Both models also showed lower density regions along the coast of Washington and Oregon, consistent with winter and spring sighting data and relative density model predictions that indicate that most Dall's porpoise are observed in slope and offshore waters, and fewest on the shelf (Green et al. 1992; Menza et al. 2016). Interestingly, the distribution patterns predicted by the seasonally extrapolated model for the study area south of 38° N were very similar to those derived from a previous winter and spring SDM developed with a subset of the CalCOFI sighting data used here (Becker et al. 2017).

The predicted annual 2017–2021 combined cool season distribution patterns for Dall's porpoise were similar to those described above, with interannual variability apparent for both sets of models (Figure 8). For the combined cool season, both models predict lowest numbers of Dall's porpoise present in the CCE study area during 2021 as compared to the previous 4 years (Figure 8, Table 6).

Based on the extreme abundance estimates predicted by the spatially extrapolated model, particularly in the northern portion of the study area, the seasonally extrapolated model appeared to exhibit better performance for Dall's porpoise in this study area.

3.4.4 | Fin Whale

Abundance. Fin whales occur year-round in the Southern California Bight, although they are significantly more abundant during summer and fall (Campbell et al. 2015; Carretta et al. 1995; Dohl et al. 1978, 1983; Forney and Barlow 1998). Both model-predicted abundance estimates were consistent with this seasonal pattern, as the winter and spring abundance estimates were substantially lower than a recent summer and fall fin whale abundance estimate of 11,065 whales for the CCE study area (Becker et al. 2020). However, the seasonally extrapolated model predicted three to four times greater numbers of fin whales in the CCE study area during the cool seasons than the spatially extrapolated model (Table 6), and about four times more fin whales within the CalCOFI study area (Supporting Information S.2). The average 2017–2020 abundance estimate of 980 fin whales derived from the spatially extrapolated model for

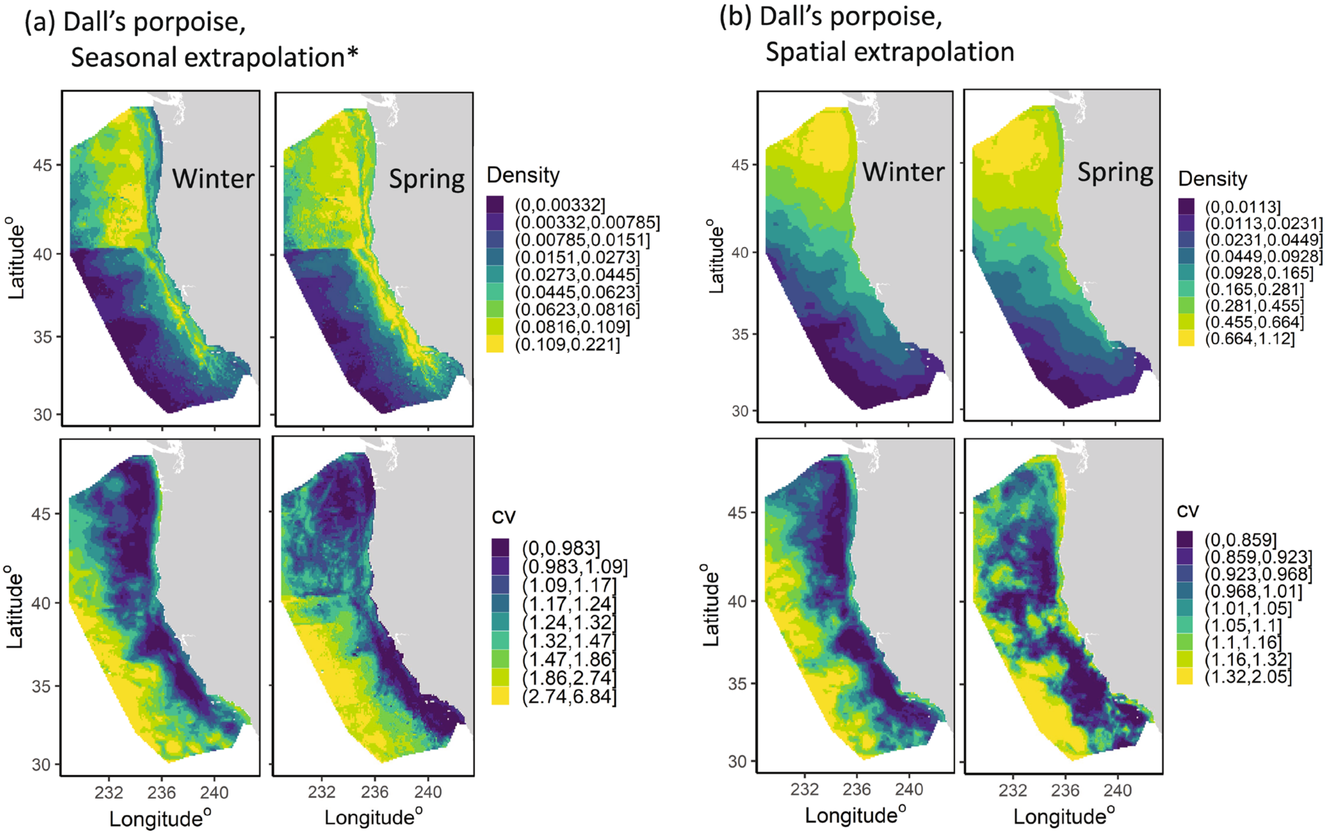

FIGURE 7 | Predicted Dall's porpoise winter and spring density (top panels) and coefficient of variation (CV; bottom panels) estimates from (a) the seasonally extrapolated Southwest Fisheries Science Center summer and fall species distribution model, and (b) the spatially extrapolated California Cooperative Oceanic Fisheries Investigations winter and spring species distribution model; the "*" indicates which model exhibited better performance. The density estimates are the multi-year average (2017–2021) values based on predicted daily cetacean species densities covering winter (December–February) and spring (March–May). Density ranges are presented in quantiles based on the combined winter and spring predictions for the respective models in order to show differences between seasons and years (see Figure 8). Predictions are shown for the California Current Ecosystem study area (1,141,800 km^2).

the CalCOFI study area (where there is no extrapolation) is more consistent with design-based estimates for the southern portion of the CalCOFI study area (155 for winter and 432 for spring; Campbell et al. 2015) than that derived from the seasonally extrapolated model (4031 fin whales). These comparisons suggest that the seasonally extrapolated model produced biased-high abundance estimates for the study area.

Distribution. Both models predicted highest fin whale densities south of Point Conception (34.45° N) during winter and spring, consistent with their established year-round residency patterns off Southern California (Figure 9; Campbell et al. 2015; Carretta et al. 1995; Dohl et al. 1978, 1983; Falcone et al. 2022; Forney and Barlow 1998). The distribution pattern predicted by the spatially extrapolated model more closely matched the occurrence patterns that have been described for this species in past studies, with the majority of winter and spring sightings in nearshore waters and over the continental shelf (Figure 9b; Campbell et al. 2015, Falcone et al. 2022; Forney and Barlow 1998; Scales et al. 2017). During summer and fall, fin whales tend to be more dispersed offshore and their distribution expands further north; however, high densities have not been documented for the southwest portion of the study area (Becker et al. 2020; Scales et al. 2017), where the seasonally extrapolated model predicted highest densities. Both models also predicted some moderate densities off Washington and Oregon, consistent with previous models of habitat suitability and other sighting data (Derville et al. 2022; Green et al. 1992; Scales et al. 2017).

Similar to the models for the other three species, the annual 2017–2021 combined cool season distribution patterns for fin whale were generally similar to those described above for the individual seasonal models, with interannual variability in abundance exhibited by both model predictions (Figure 10, Table 6). Both models predicted substantially fewer fin whales in the CCE study area in 2021, particularly off Washington and Oregon, and the greatest number of whales in 2018 (Figure 10, Table 6).

Based on the apparent biased-high abundance estimates derived from the seasonally extrapolated model, and the mismatch in predicted distribution patterns in the Southern California Bight, we consider the spatially extrapolated model to have exhibited better performance for fin whales in this study area.

4 | Discussion

The use of extrapolations for marine SDMs has been the topic of several studies that illustrated the challenges involved. Extrapolations

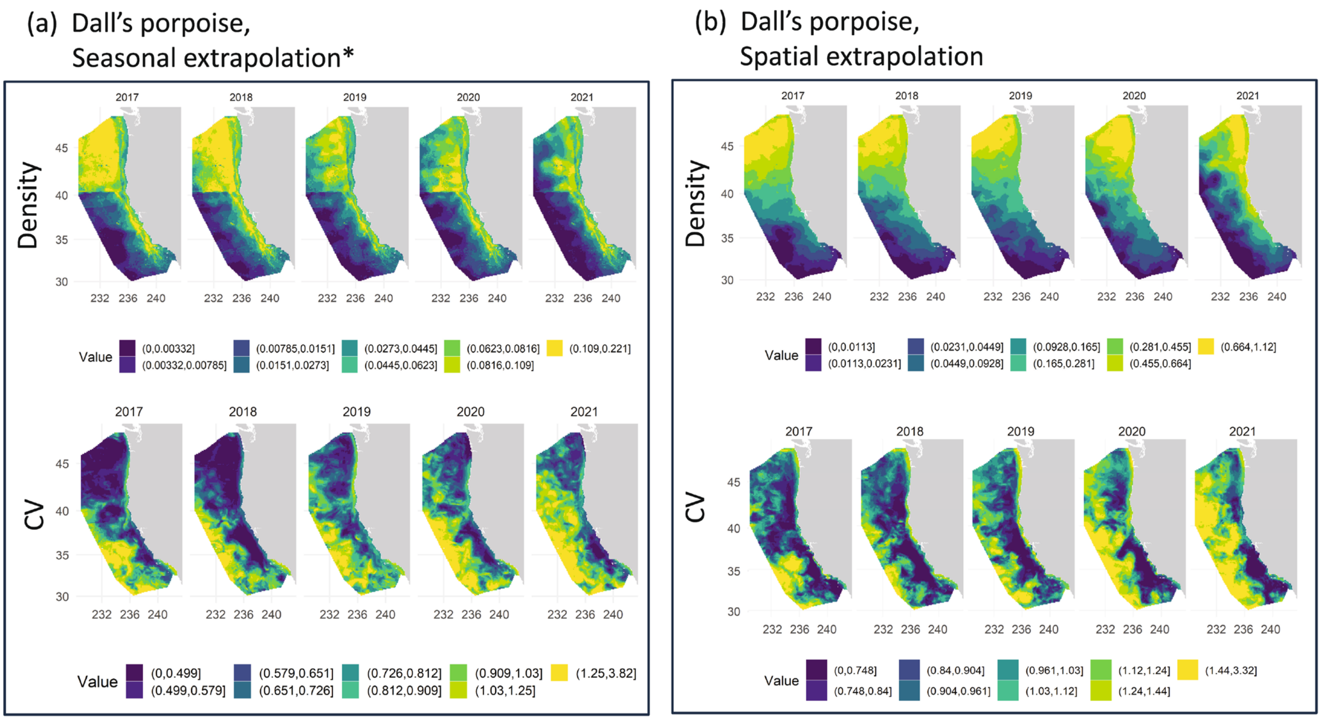

FIGURE 8 | Predicted Dall's porpoise annual 2017–2021 density (top panels) and coefficient of variation (CV; bottom panels) estimates from (a) the seasonally extrapolated Southwest Fisheries Science Center summer and fall species distribution model, and (b) the spatially extrapolated California Cooperative Oceanic Fisheries Investigations winter and spring species distribution model; the "*" indicates which model exhibited better performance. The annual density estimates reflect the combined cool season (December–May) averages from predicted daily cetacean species densities for each respective year. The density ranges are presented in quantiles based on the combined winter and spring predictions for the respective models to show differences between years and seasons (see Figure 7). Predictions are shown for the California Current Ecosystem study area (1,141,800 km^2).

may be inaccurate if they are done across ecosystems (Mannocci et al. 2020; Redfern et al. 2017), but when done with care and within similar ecoregions they can provide much-needed information for marine species management and conservation. When time and location-specific data are unavailable, careful extrapolations can inform management decisions that would otherwise be made in the absence of any information on species distribution and density (Mannocci et al. 2017). However, it is important to understand when and under what circumstances extrapolations are acceptable versus unacceptably biased, and which methods produce the most reliable results. In the present study we compared spatially extrapolated and seasonally extrapolated model predictions for four species within a highly dynamic ecosystem to increase our understanding and improve future application of extrapolated SDM predictions.

Given increasing demands to use SDMs to make predictions for insufficiently sampled geographic regions and during novel time periods, tools have been developed to assess the magnitude of the extrapolated predictions, reduce or eliminate extrapolation to the extent possible, cross-validate model predictions if data are available, and transparently present uncertainty in the predictions (Conn et al. 2015; Mannocci et al. 2017; Sequeira et al. 2018). In this study, a simple yet often effective avoidance measure was used to evaluate and discard any model predictions that were made outside the multivariate space of the data used to develop the original models (Bouchet et al. 2019). Model predictions were then cross-validated to the degree possible using available data within the study area, and uncertainty was characterized using recently developed techniques for deriving comprehensive measures of variance in GAM predictions (Miller et al. 2022).

A continuous year term was included as a covariate in previous SDMs developed using the same SWFSC CCE survey data, and successfully captured the population trends for both short-beaked common dolphin and fin whale whose abundance in summer and fall has increased substantially during the 1991 to 2018 time period. Year was specifically not offered to the models in this study because year can act as a proxy for a dynamic variable, which in this case could confound the spatial and seasonal extrapolations. The potential "noise" that a year term would introduce into the already complex extrapolation process was not considered appropriate for this analysis. For the two species with documented increases in population within the study area in summer and fall, if there have been similar increases in winter and spring, the resulting density estimates may be biased low.

To increase the predictive ability of SDMs, previous studies have combined disparate data sets to build a single combined model in an attempt to capture the strengths of the individual datasets (e.g., Redfern et al. 2017). This strategy was not considered appropriate in this case given the documented dynamic seasonal changes in cetacean abundance and distribution in the CCE, particularly within the Southern California Bight. Combining the summer and fall and winter and spring datasets inherently assumes that the functional forms of the habitat variables will be consistent between the SWFSC CCE-wide summer and fall and the CalCOFI Southern

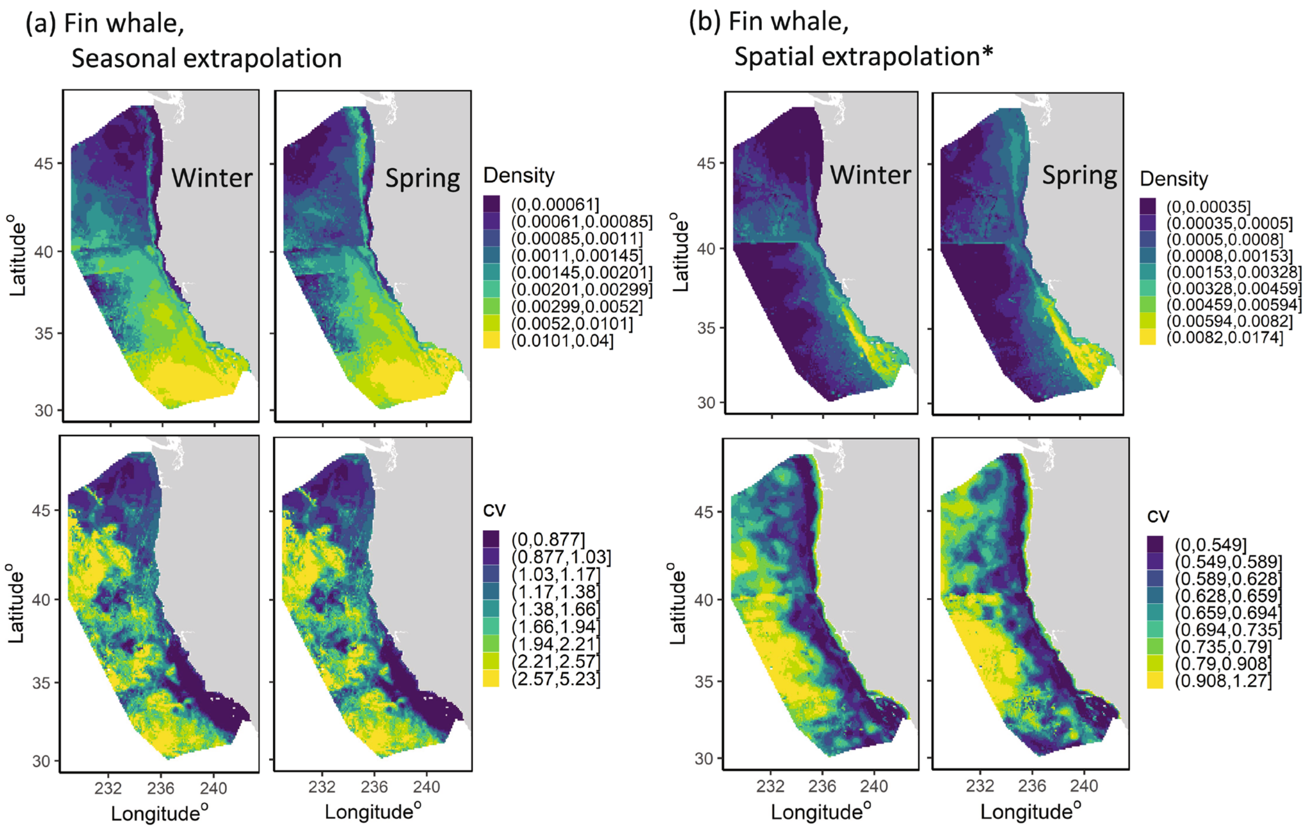

FIGURE 9 | Predicted fin whale winter and spring density (top panels) and coefficient of variation (CV; bottom panels) estimates from (a) the seasonally extrapolated Southwest Fisheries Science Center summer and fall species distribution model, and (b) the spatially extrapolated California Cooperative Oceanic Fisheries Investigations winter and spring species distribution model; the "*" indicates which model exhibited better performance. The density estimates are the multi-year average (2017–2021) values based on predicted daily cetacean species densities covering winter (December–February) and spring (March–May). Density ranges are presented in quantiles based on the combined winter and spring predictions for the respective models in order to show differences between seasons and years (see Figure 10). Predictions are shown for the California Current Ecosystem study area (1,141,800 km^2).

California-specific winter and spring datasets (which as shown for both short-beaked common dolphin and fin whale, were very different for the depth variable). In addition, the SWFSC data have substantially more sightings and would dominate the signal in the models. Pedersen et al. (2019) present an integrated hierarchical modeling approach that could, in theory, allow the SWFSC summer and fall and CalCOFI winter and spring surveys to be included in a single model. However, this approach was not deemed appropriate for our analyses because this would increase model complexity beyond what is supported by the limited sample sizes during the CalCOFI surveys. Further, there are marked oceanographic and ecological differences between the CalCOFI study area and the broader CCE (e.g., Daily et al. 1993; Miller 2023) that could confound such an approach. Finally, combining the datasets would not allow for a comparison of seasonal versus spatial extrapolation.

Based on our analysis, spatially-extrapolated predictions were better for short-beaked common dolphin and fin whale, while seasonally-extrapolated model predictions were better for Pacific white-sided dolphin and Dall's porpoise. Given the variability in these results, it is important to consider what species-specific or study-area specific characteristics may have affected this outcome. Two main factors were apparent: (1) the degree to which a model captures the species core habitat, that is, whether the functional curves of the covariates capture a peak; and (2) the effect of static predictors (e.g., depth, distance to shore, distance to an isobath, etc.) anchoring a species in geographic space and preventing the identification of distribution shifts in the novel space or time period. These are described in more detail below.

4.1 | Core Habitat

Core habitat for both short-beaked common dolphin and fin whale within the CCE study area is the Southern California Bight (Becker et al. 2022; Scales et al. 2017), which is well-sampled by the CalCOFI surveys. Conversely, the core distribution of both the cool temperate Pacific white-sided dolphin and Dall's porpoise is well north of the CalCOFI survey area, with the southern California Current Ecosystem representing their southern range limit within the eastern North Pacific (see e.g., Hamilton et al. 2009). The CalCOFI models for these two cool-temperate species are thus based on the southern portion of their habitat, with the functional forms reflecting only a small part of their larger habitat range (i.e., the tails of each species' optimum habitat). For example, the SST functional form in the CalCOFI models for both Pacific white-sided dolphin and Dall's porpoise was negative linear, with highest numbers of dolphins/porpoises

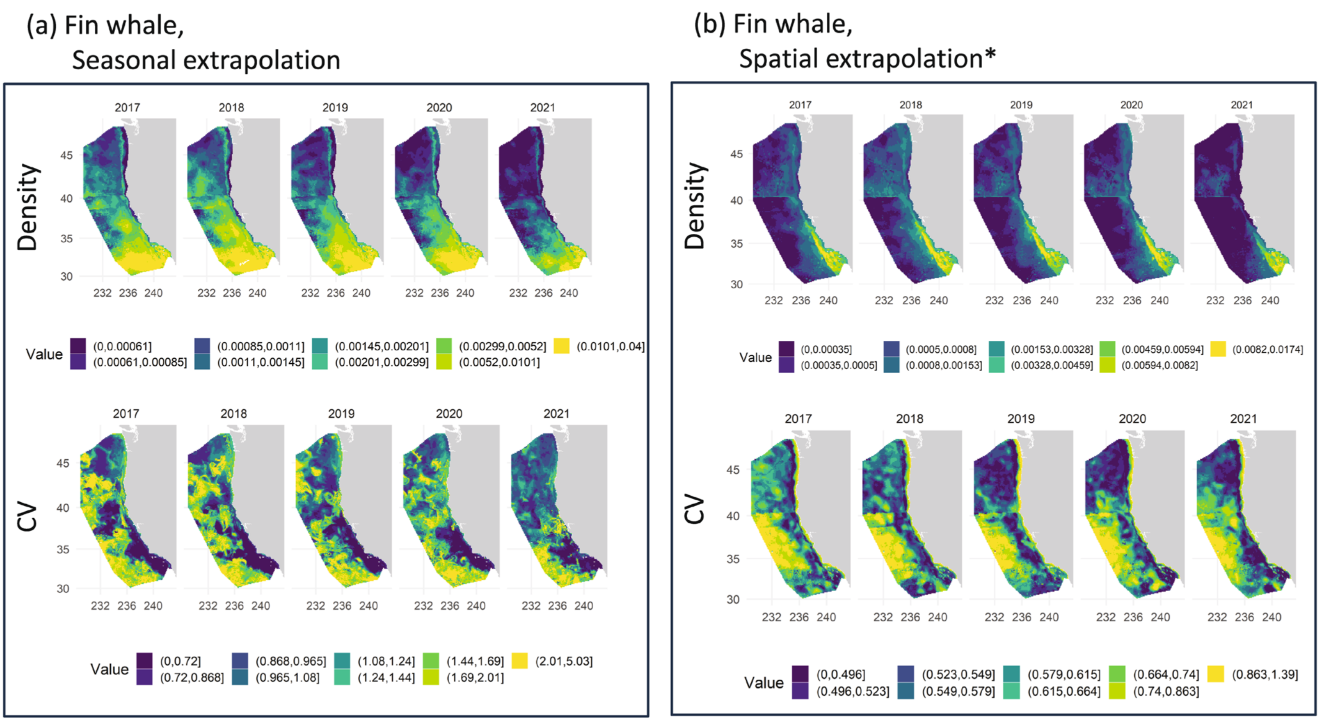

FIGURE 10 | Predicted fin whale annual 2017–2021 density (top panels) and coefficient of variation (CV; bottom panels) estimates from (a) the seasonally extrapolated Southwest Fisheries Science Center summer and fall species distribution model, and (b) the spatially extrapolated California Cooperative Oceanic Fisheries Investigations winter and spring species distribution model; the "*" indicates which model exhibited better performance. The annual density estimates reflect the combined cool season (December–May) averages from predicted daily cetacean species densities for each respective year. The density ranges are presented in quantiles based on the combined winter and spring predictions for the respective models to show differences between years and seasons (see Figure 9). Predictions are shown for the California Current Ecosystem study area (1,141,800 km^2).

found in the coolest waters of the study area (Figure 2b,c). When these models were used to predict on winter and spring conditions throughout the CCE study area, the widespread occurrence of cold water off Washington and Oregon likely caused the extreme density predictions in the northern portion of the study area (Figures 5b and 7b). The linear effect reflected only the portion of the functional plot from ~10°C to 18°C, rather than the unimodal relationship captured by the SWFSC summer and fall models that included temperatures from ~10°C to 23°C.

The SWFSC models included the core habitat for Pacific white-sided dolphin and Dall's porpoise in the northern waters of the study area, albeit in summer and fall, but the dataset had sufficient samples in the coolest waters for these seasons and the functional curves for SST showed a decrease (Pacific white-sided dolphin) and monotonic response (Dall's porpoise) in density within waters cooler than about 13°C (Figure 2b,c). The lowest SST values sampled were not substantially different between the two datasets (9.96°C for the SWFSC model versus 9.17°C for the CalCOFI model; Table 4), and both were warmer than the coolest waters typically encountered off Washington in the winter (e.g., approximately 8°C, given interannual variability; Legaard et al. 2006; Venegas et al. 2008). However, although the CalCOFI dataset included cooler SST values than the SWFSC dataset, the more unimodal relationships captured by the SWFSC summer and fall models were able to better define the SST-species habitat relationships in these species core habitat within the CCE study area. The seasonally extrapolated predictions for both these species produced reasonable abundance estimates and spatial distribution patterns that were consistent with those documented for these species in the cool seasons (Forney and Barlow 1998; Green et al. 1992; Menza et al. 2016).

This result powerfully illustrates that, even when using truncation as the primary method for eliminating or reducing the potential for extrapolation artifacts, resulting predictions can be extremely biased. The avoidance method used in this study discarded predictions made outside of the covariate ranges used to develop the CalCOFI models (i.e., in the above example any pixels with water temperatures < 9.17°C were not used; Table 4); however, the resulting density estimates from the spatially extrapolated models for both Pacific white-sided dolphin and Dall's porpoise were still substantially biased-high.

4.2 | Static Predictors

Bathymetry has proven to be an effective predictor in cetacean SDMs in the CCE study area (Abrahms et al. 2019; Becker et al. 2016, 2020; Forney 2000; Forney et al. 2012, Hazen et al. 2017), and depth was offered as a potential covariate in this study, similar to the approach taken by Mannocci et al. (2017). Depth was also included in previous SDMs (Becker et al. 2018) for eight cetacean species (including the four species addressed in this study) that were successfully used to predict substantial distribution shifts during a novel anomalously warm year in the CCE study area. This approach assumes that a species' preferred "depth habitat" will remain fairly constant over time and space.

As demonstrated here, however, the inclusion of depth can hinder novel predictions if a species shifts distribution to waters with notably different bathymetry in the novel space or time period. For both short-beaked common dolphin and fin whale, the functional form of depth in the SWFSC summer and fall models resulted in some mismatched distribution patterns predicted for winter and spring, particularly in their core habitat within the Southern California Bight, an area characterized by complex bathymetry (Hickey 1979).

In summer and fall within the CCE study area, short-beaked common dolphins exhibit a bimodal depth distribution, with highest densities occurring in relatively shallow waters throughout the Southern California Bight and also in deep waters (approximately 4000 m deep) off central and northern California (Becker et al. 2016, 2018, 2020). A significant southerly shift in short-beaked common dolphin distribution occurs in winter and spring, which was successfully captured by the SWFSC model predictions (Figure 3a). In the Southern California Bight, there is also a distinct shift in short-beaked common dolphin distribution offshore to pelagic waters in the southwestern portion of the CCE study area (Becker et al. 2017; Campbell et al. 2015). The shift away from waters over the continental shelf was not captured in the winter and spring predictions from the SWFSC summer and fall model, likely due to the inclusion of the bimodal depth function that resulted in higher predictions nearshore (Figure 2a).

A similar situation occurred for fin whale, a species that occurs year-round in the Southern California Bight but has a more widespread distribution in summer and fall (Becker et al. 2022; Forney and Barlow 1998; Scales et al. 2017). Similar to short-beaked common dolphin, the SWFSC summer and fall model included a bimodal depth function (Figure 2d), which resulted in high density predictions offshore for winter and spring, inconsistent with their cool season distribution in nearshore waters over the continental shelf (Campbell et al. 2015; Falcone et al. 2022; Forney and Barlow 1998; Scales et al. 2017).

4.3 | Seasonally Extrapolated vs. Spatially Extrapolated Models

Based on the results of this study, the best winter and spring predictions were generated by the spatially extrapolated models for short-beaked common dolphin and fin whale, and by the seasonally extrapolated models for Pacific white-sided dolphin and Dall's porpoise. These model predictions were able to capture seasonally variable differences in abundance and distribution that are consistent with known or suspected patterns. The selected model predictions for these four species provide spatially explicit density predictions that are quite different from summer and fall, and can inform management needs for cool seasons in the CCE study area. Despite greater uncertainty, these models are preferable to the alternative of using the summer and fall models to reflect annual abundance and distribution patterns. Until cool season specific SDMs can be developed, and with application of caution, these models provide a tool for assessing risk and developing mitigation measures for these species in the CCE study area in winter and spring.

4.4 | Future Studies

In order to reduce potential bias from extrapolations, we used truncation, that is, we discarded any model predictions that were made outside the multivariate space of the data used to develop the original models (Bouchet et al. 2019). This approach was selected because previous modeling studies using a subset of the SWFSC CCE data resulted in unreasonably high predictions from unconstrained predictions (Becker et al. 2012). Further, since the goal of this study was to compare seasonal versus spatial extrapolation, we wanted to use a consistent method that could be applied to both sets of models rather than applying model-specific approaches that could confound the results.

The truncation method eliminates pixels from the final average density surfaces, and thus the averages are based only on the other, in-range time slices. Depending on the percentage of pixels eliminated and the extent to which they are grouped together spatially or temporally, this could introduce bias in the predictions. Alternative methods for dealing with extrapolation in SDM predictions include "clamping" or "bounding" the covariate values to their sampled extremes (Bouchet et al. 2019), which would retain all the prediction pixels. However, the clamping or bounding approach is dependent on assessing the directionality of each response curve at the truncation point (Guevara et al. 2018), and would complicate the interpretation of results in this study introduced by using variable model-specific extrapolation approaches. The best method for dealing with extrapolation likely depends on how much of a (presumed) unimodal relationship has been captured. For linear relationships, this likely is only one side of a unimodal curve, so clamping may be better; however, if the functional plot captures the majority of a unimodal relationship, then allowing the extrapolation may be better (e.g., Guevara et al. 2018). Evaluating alternative methods for dealing with extrapolation, such as clamping, will be the focus of future analyses in this study area.

5 | Conclusions

SDMs are now firmly established as effective conservation and management tools, and the use of extrapolated model predictions for data-poor regions and time periods is expected to increase in the future. This study has shown that there are species-specific and study-area-specific factors to consider when making extrapolated model predictions. First, spatial extrapolation is likely to produce extremely biased predictions when the SDMs are developed outside of core habitat areas (i.e., at the tails of a species optimum covariate values). Even when limiting predictions to the univariate and multivariate space used to build the models, patterns can be exaggerated in core habitat. When a species is known or suspected to exhibit temporal shifts in distribution, static variables should be carefully evaluated prior to model inclusion. In all cases, extrapolations should always be interpreted with caution, even when methods have been used to control predictions. As additional data are collected within this study area during the cool seasons, more comprehensive cross-validation should be performed to provide additional insight into the future use and application of extrapolated SDM predictions.

Author Contributions

Elizabeth A. Becker: conceptualization, data curation, formal analysis, investigation, writing – original draft, writing – review and editing. **Karin A. Forney:** conceptualization, data curation, formal analysis, investigation, writing – review and editing. **Bruce J. Thayre:** data curation, software, writing – review and editing. **Katherine Whitaker:** data curation. **Ryan Hoopes:** visualization. **Joshua M. Jones:** data curation, writing – review and editing. **John A. Hildebrand:** data curation, writing – review and editing. **Jeff Moore:** conceptualization, data curation, writing – review and editing.

Acknowledgments

We are especially thankful for the hard work and dedication of all the marine mammal observers who collected the SWFSC and CalCOFI survey data used in this study. Chief Scientists for the SWFSC ship surveys included Lisa Ballance, Jay Barlow, Tim Gerrodette, Susan Chivers, and two of the co-authors (J.M., and K.A.F.). We thank the UCSC Ocean Modeling group for providing ROMS output. The ROMS near real-time system is supported by NOAA through a grant to the CeNCOOS Regional Association. The methods used to derive uncertainty estimates were developed as part of "DenMod: Working Group for the Advancement of Marine Species Density Surface Modeling" funded by OPNAV N45 and the SURTASS LFA Settlement Agreement, and managed by the U.S. Navy's Living Marine Resources (LMR) program under Contract No. N39430-17-C-1982. This modeling project was funded by the Navy, Commander, U.S. Pacific Fleet (U.S. Navy) and by the National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS), Southwest Fisheries Science Center (SWFSC). This manuscript was improved by the thoughtful reviews of Alexandra Curtis and Jason Roberts.

Conflicts of Interest

The authors declare no conflicts of interest.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.