DISTRIBUTION PATTERNS AND POPULATION SIZE OF THE ASHY STORM PETREL *OCEANODROMA HOMOCHROA*

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ABSTRACT

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The Ashy Storm Petrel (ASSP) *Oceanodroma homochroa* population has been surveyed intensively, both at sea within the California Current and on the adjacent breeding grounds. Nevertheless, colony-based estimates of breeding populations have significantly underestimated the species' abundance, especially in the northern portion of its range compared to the southern portion. The species has been described as abundant in central-northern waters, whereas it is considered rare or uncommon in the southern portion. We analyzed aerial and ship tracks from 1980 to 2017 (~497 000 km covering 91 267 km^2), to estimate total ASSP population size and at-sea distribution. Modeling the results of these formal surveys (7211 ASSPs seen) led to an estimated total population of about 13 445 ASSPs (95% confidence interval = 10 128–27 820), with 62% of the population frequenting the northern portion of the range, i.e., north of Point Conception (especially Monterey Bay north through the Gulf of the Farallones to Cordell Bank), compared with 38% in the south (especially waters around the northern Channel Islands). Based on over a thousand well-organized bird-watching surveys, almost the entire population can occur in a single flock in the northern portion during the California Current's autumn Oceanic Period. These flocks occur in trophic hotspots: areas where submarine canyons cut into the shelf. Such large "molting flocks" have been shifting north from Monterey Bay to Cordell Bank since about 2007, but reasons for the northward shift remain a mystery. The apparent mismatch in at-sea vs. colony-based population sizes likely involves the non-breeding portion, which is especially difficult to estimate because it includes immature individuals as well as "floating" individuals: adults capable of breeding but denied access to breeding sites, which are limited by intraspecific competition.

Key words: at-sea aerial surveys, California Current, hotspots, seabird rafts, at-sea vessel surveys, world population size

INTRODUCTION

The Ashy Storm Petrel (ASSP) *Oceanodroma homochroa* is endemic to the central and southern portions of the California Current System (CCS), where it is found year-round. It breeds on coastal rocks and offshore islands within that portion of the CCS having a Mediterranean climate, that is, from north-central California, USA to central Baja California, Mexico (Carter *et al.* 2008, Howell 2012, Carter *et al*. 2016a, Ainley *et al.* 2019). The IUCN has listed ASSP as an endangered species whose population is decreasing, and the California Department of Fish & Wildlife lists it as a Species of Special Concern based on several factors: 1) relatively small global population size, 2) restricted range, 3) purported (but unsubstantiated long-term) decreasing population trend, 4) vulnerability to at-sea pollution, 5) disturbance at some breeding colonies, and 6) predation by natural and alien predators introduced to breeding locations (Carter *et al.* 2008, 2016a). A petition to have ASSP listed under the US Endangered Species Act was submitted, but the US Fish & Wildlife Service (USFWS) determined that such a designation was not warranted because the species was widely distributed within its range and because most of the breeding sites were protected. According to them, neither a change in range nor any decreasing species-wide trends were evident, and various threats were mostly localized (USFWS 2013). The status of this species is under continuous discussion among agencies (e.g., Parker 2016, Nur *et al.* 2019).

The ASSP range is divided into five regions, most of which are in California. From north to south: Region 1 covers Cape Mendocino to Point Año Nuevo, Region 2 covers Point Año Nuevo to Point Conception, Region 3 covers the northern Channel Islands, and Region 4 covers the southern Channel Islands. Region 5 is in Mexico and covers Coronado to the San Martin islands (Fig. 1). The total world breeding population of ASSP is concentrated in the center of the species' range, at the northern Channel Islands and the Farallon Islands (i.e., Point Conception in Region 3 northward to Bodega Bay in the southern portion of Region 1; see Fig. 1 and Table 1). The total breeding population has been estimated to be ~8200 birds, with a range of 3000–13 250 birds as of 2015 (Carter *et al*. 1992, 2008, 2016a; Table 1), though the USFWS puts the total at 7559 birds (USFWS 2009). Arriving at these estimates has taken several decades and studies.

Population estimates from colony counts indicate that a near-equal proportion of the population currently breeds in the southern portion of their range at the Channel Islands, compared to the northern portions of their range, at the Farallon Islands. Based on surveys during 1979–1980, Sowls *et al.* (1980) initially estimated 5187 breeding birds for California, with ~4000 (77%) at the Farallon Islands (Region 1; Ainley & Lewis 1974) and most of the remainder at the Channel Islands (Region 3; Hunt *et al.* 1981). After additional surveys, Carter *et al.* (1992) estimated 7209 breeding birds for California, adding to the much earlier estimate of ~4000 breeding birds (55%) for the South Farallon Islands and reasoning that earlier counts at the Channel Islands should be elevated. Most recently, colony-based estimates for the Channel Islands have further increased to 6375 breeding birds (Carter *et al.* 2016a; Table 1). There are no colony-based data to indicate whether the size of ASSP breeding population at the Channel Island colonies have changed since this most recent estimate. In contrast, multiple population estimates derived from colony counts have been published for the Farallon Islands. In 1992, Sydeman *et al.* (1998) estimated that the Farallon breeding population had shrunk to ~2600 breeding birds, though the estimate was likely negatively affected by anomalous ocean conditions during their year of study, specifically the El Niño-Southern Oscillation. During this time, higher numbers of birds were reported at sea (Ainley & Boekelheide 1990, Ainley & Hyrenbach 2010), in accordance with reduced breeding incidence and presence on the island. Therefore, there was likely no such change, as reported by Sydeman *et al*. (1998). Most recently in 2012, Nur *et al.* (2013) estimated 5768 "resident" ASSP at the Farallon Islands, an estimate that included both breeders and established non-breeders. (Residency was defined as being captured at least twice within a year or in multiple years.) Nur *et al.* further noted that the population had increased between 2000 and 2005–2006, followed by a decrease to about one third of the peak by 2012. Consistent with that increase was an increase in number of ASSP observed at sea (Ainley & Hyrenbach 2010).

Fig. 1. Known breeding locations (black dots) of the Ashy Storm Petrel *Oceanodroma homochroa* in California, USA and Baja California, Mexico (updated from Carter *et al.* 1992, 2008; map altered from Carter *et al.* 2016a). The five regions are described in Table 1; Region 1 begins with northernmost colony and Region 5 ends with southernmost colony. Note, the current paper questions the validity of population sizes among the northern Channel Islands.

A different picture of ASSP abundance has been derived from scientific at-sea surveys, which reveal that ASSP are relatively sparse south of Point Conception, including in the vicinity of the Channel Islands. Summarizing available information, Howell (2012: pp. 417–418) deemed the species to be "fairly common to locally abundant year-round over continental slope and adjacent offshore waters… in central California," but "uncommon to rare off southernmost California and Baja California." Briggs *et al.* (1987), who repeatedly surveyed the coastal waters off California by air during 1976–1983, encountered at most 1400 ASSP individuals in waters south of Morro Bay/Point Conception (i.e., 175 birds encountered per year). Similarly, during repeated and intensive ship-based surveys of waters south of Pt. Conception, as part of the California Cooperative Oceanic Fisheries Investigations (Cal-COFI) program during 1987–2006, only 1026 ASSP individuals were encountered (i.e., 51 birds per year). An aerial survey south of Point Conception (1999–2001; Mason *et al.* 2007) also found few ASSPs (density range: 0.02–0.20 birds/km^2, depending on season). Therefore, the scientific at-sea counts of ASSP do not appear to match the colony data reported for south of Point Conception (Regions 3–5 in Fig. 1). Moreover, during 1987–1998,

TABLE 1
Frequency of known Ashy Storm Petrel *Oceanodroma homochroa* breeding sites[a] by size and estimates of the number of breeding birds by region[b], as of 2015 (updated from Carter *et al.* 1992, 2008, 2016a)

	Colony size range						Number breeding birds		
	1–25	26–100	101–500	501–1000	1001–5000+	Total sites	Minimum	Middle	Maximum
Region 1	5	8			1	14	1 214	3 570	5 925
Region 2	5					5	5	65	125
Region 3	5	6	7	1		19	1 369	3 297	5 225
Region 4	6		2			8	208	679	1 150
Region 5	1	3	1			5	180	503	825
Total	22	17	10	1	1	51	2 976	8 114	13 125

[a] "Breeding site" is defined as a distinct geographic location. Some of these could be clumped enough to constitute a "colony," but given evidence of Ashy Storm Petrel intercolony movement (Ainley *et al.* 2019), we used the term "breeding site" instead.

[b] Region 1 – Cape Mendocino to Point Año Nuevo; Region 2 – Point Año Nuevo to Point Conception; Region 3 – northern Channel Islands; Region 4 – southern Channel Islands; Region 5 – Coronado to San Martin islands (see Fig. 1).

no trend in observed ASSP numbers was detected during Cal-COFI cruises. In contrast, the three other storm petrel species regularly frequenting those waters—Leach's *Oceanodroma leucorhoa*, Black *O. melania*, and Least *O. microsoma*—did exhibit changing decadal trends relative to marine climate (Hyrenbach & Veit 2003).

Extensive at-sea counts for northern and central California, on the other hand, are in accord with Howell's (2012) description and better match both colony counts and at-sea scientific counts in that region; i.e. there are more ASSP in the north compared to the south. Aerial surveys by Briggs *et al.* (1987) estimated 5600 to 11 200 individuals encountered off northern/central California, depending on the season (i.e. 700–1400 birds encountered per year). These numbers are corroborated by ship-board surveys during 1986–2006 (4339 individuals were encountered between 1980 and 2001 in a smaller portion of the region, i.e. 207 birds per year; NOAA 2003). These counts are consistent with at-sea surveys during 1980–1995, as well as with extrapolations about the proportion of observed birds that are non-breeders, which totals 7300 breeding birds (Spear & Ainley 2007). Also, areas where ASSP concentrate at sea (i.e., hotspots; *sensu* Santora *et al.* 2017, 2018) have been fairly well-established for central California, where rafting flocks of up to 13 000 individuals have been regularly observed in slope waters from Monterey Bay to the northern Gulf of the Farallones and especially over submarine canyons (densities reaching > 100 birds/km^2; NOAA 2003 and Results section below). Those flocks are generally encountered in the autumn, contain many molting individuals, and may include birds from the entire range (see Adams & Takekawa 2008). An insignificant decreasing trend in at-sea results from spring surveys in central California (1985–2006) was noted by Ainley & Hyrenbach (2010), while a slightly increasing trend was evident at the Farallones (Warzybok *et al.* 2015).

TABLE 2
A summary of aerial and ship-based surveys providing data for this study; all are strip censuses. Data are from all oceanographic seasons, though some months are missing from some data sets. Most surveys contributed to estimates for areas both north and south of 35.1°N (Fig. 2) and include data for the entire year range given.

Years covered	No. of years	Agency[a]	Ship/Air	No. ASSP
1980–1983	4	CNCA (MMS)	Air	1606
1995–1997	3	MMS	Air	9
1999–2002	4	USGS	Air	254
1994–2016	22	OSPR	Air	785
1985–2015	29	Various	Ship	941
1987–2016	30	Cal-COFI	Ship	1363
1993–1995	8	EPOCS (NSF)	Ship	71
1993–2014	6	ORCAWALE[b] (NMFS)	Ship	475
1996–2001	7	SF-DODS	Ship	1707

[a] Cal-COFI = California Cooperative Oceanic Fisheries Investigations (funded/supported by the California and National Science Foundation); CNCA = Central and Northern California Aerial survey; EPOCS = Equatorial Pacific Ocean Climate Studies, cruises that departed/returned to US ports (funded by the National Science Foundation); MMS = Minerals Management Service; NMFS = National Marine Fisheries Service; NSF = National Science Foundation; OSPR = Office of Spill Prevention and Response (California Department of Fish and Wildlife); SF-DODS = San Francisco Deep Ocean Disposal Site (US Army Corps of Engineers); USGS = US Geological Survey; Various = Point Reyes Bird Observatory and HT Harvey & Associates on NMFS Rockfish Assessment cruises.

[b] ORCAWALE (NMFS, i.e., Oregon, California and Washington Line Transect Expedition = 1996, 2001, 2008) is a combination of several sequential projects: PONDS (Populations of Northern *Delphinus* Stocks = 1993), CSCAPE (Collaborative Survey of Cetacean Abundance and the Pelagic Ecosystem = 2005), and CalCurCEAS (California Current Cetacean & Ecosystem Assessment Surveys = 2014).

Given the varying levels of agreement between at-sea counts and colony counts, a summary and analysis of the existing at-sea data was needed. While existing colony-based data have been recently summarized (Table 1, Fig. 1), this is not the case for at-sea data. Overall, data from at-sea surveys might provide the best insights into the population size of this burrow-nesting, nocturnal (at colonies) species; Rayner *et al.* (2020) also reached this conclusion for the New Zealand Storm Petrel *Fregetta maoriana*. These natural history characteristics complicate colony-based abundance estimates. Clarke *et al.* (2003) successfully ground-truthed an analysis of population estimates of at-sea data using Generalized Additive Models (GAMs) for three surface-nesting seabird species, two from the Farallon Islands and one from the Galápagos. Another at-sea population estimate was verified by radar studies of burrow-nesting seabirds in Hawaii (*cf.* Spear *et al.* 1995, Day *et al.* 2003, Joyce 2016). The key is to have intensive surveys covering an appreciable portion of the foraging range or at-sea range of the species in question over an appreciable time period, to avoid the problems encountered by MacLean *et al.* (2013): very small spatial scale and just a few years of data. No other seabird in the world has had its marine distribution as extensively surveyed as that of the ASSP from 1976 to 2017. Herein we summarize and analyze existing at-sea data, from both formal surveys (aboard oceanographic research ships and aircraft) and from birding boat trips, to estimate the world population of ASSP and to detect hotspots where the species concentrates.

METHODS

Large-scale surveys—formal aerial/ship-based transects

Data sources

Our estimates of the ASSP world population are based on a compilation of nearly all systematic aerial and ship-based surveys of seabirds that have been conducted offshore of California during the 1980–2017 period (Table 2). The CCS has three general oceanographic seasons or "periods": Upwelling, Relaxation (or Oceanic), and Winter Storm (or Davidson Current; Bolin & Abbott 1963). Most surveys were done during summer (late Upwelling Period), which are also chick-rearing periods when both parents are at sea. We did not parse data by year to look at trends, because this would have reduced sample sizes to levels that would have added much more uncertainty to our statistical analyses and because colony-based estimates are independent of year, differing among colonies by as much as a decade. These efforts used continuous-strip surveys conducted with a strip width of 50–150 m for aerial surveys and 200–300 m for ship-based surveys (e.g., Clarke *et al.* 2003). Most cases involved at least two observers (see Spear *et al.* 2004; Fig. 2). The initial strip width for aerial surveys was 50 m until 1998, when it was increased to 150 m to accommodate a change in aircraft for Oil Spill Prevention and Response (OSPR) surveys. At that time, it became standard to use two observers instead of one, whenever glare conditions allowed. Within some ship-based surveys, strip width varied because of reduced visibility.

We counted all ASSP that occurred within strips, both flying and on the water. Given that storm petrels travel so slowly compared to speed of the survey ship/aircraft, they were effectively perceived as stationary. We therefore considered aerial and ship-based detections to be equivalent and did not require adjustment to factor in the relative speed and direction of either the survey platform or the storm petrels (see Clarke *et al.* 2003). Such a strategy was confirmed by our results.

Data standardization

All survey data were standardized to a common format and organized by survey, date, and time. Each sample represented either a position fix (latitude and longitude) or an observation of one or more birds.

We assumed that continuous sampling occurred along a given line unless the "IFGAP" field was true, which indicated a break in continuous sampling. Breaks in sampling occurred for various reasons, such as the observers going offline, the survey aircraft returning to base, or the survey ship moving to a new location overnight.

Creation of data snippets and association with predictor variables

The snippet database was intended to simplify the survey data, which were collected using a variety of survey protocols, by using a standard format based on a standard sampling unit. This was possible because, in spite of varying protocols, all studies were based on continuous-strip transects. For the ship surveys, data were binned *a priori* into transects based on time (e.g., 30-min segments; except for Joyce 2016). Latitude, longitude, and environmental variables were recorded at the start of each transect/segment. For analysis, we divided the survey track lines into smaller units (i.e., snippets), such that the area searched for each snippet was at least 0.95 km^2. Smaller areas would inject more samples with zero sightings, which is already a statistical issue for this species. By standardizing by minimum area surveyed, we accounted for varying strip widths (due to changes in the number of observers or in observation conditions) that sometimes occurred along the survey track. Since the exposure variable is the area searched, creating transects of equal area ensured that variance in the number of observations was equal across all snippets and did not vary among studies.

When a run of continuous sampling ended, the length of the last snippet created from that run was often less than the maximum allowable size of 1.0 km^2. For example, a run might be 107 km long with a strip width of 0.1 km. Small snippets, as noted, often result in zero sightings. Therefore, snippets that were > 0.95 km^2 in area were retained for analysis and smaller ones were discarded. Our final database consisted of a set of snippets in which each one represented 0.95–1.00 km^2 of searcher effort. Once a snippet was specified, we

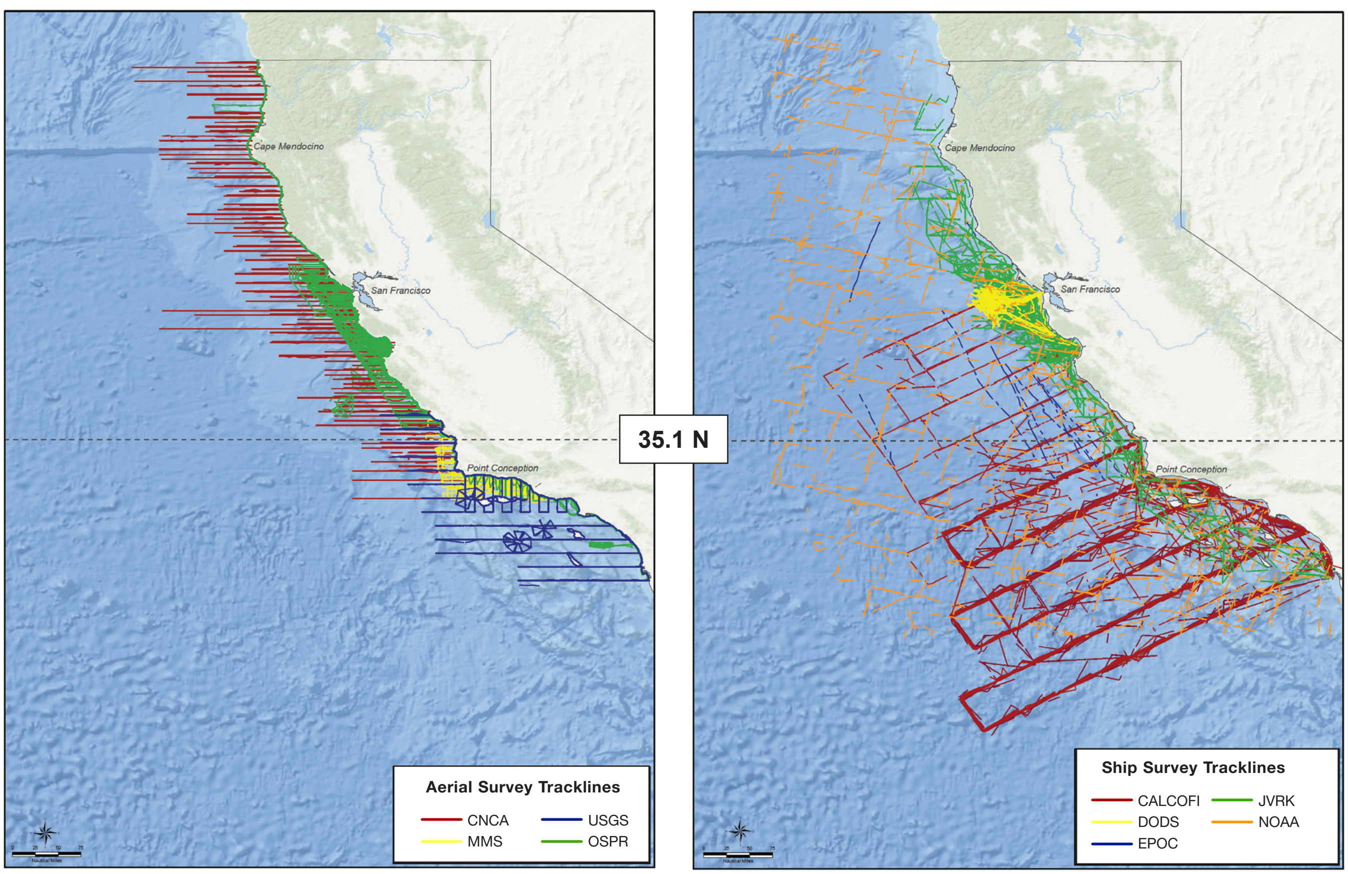

Fig. 2. Tracklines for aerial and ship-based surveys conducted off the coast of California, USA, 1980–2017. For definition of acronyms, see footnote to Table 2. JVRK = the Rockfish Assessment cruises of the National Marine Fisheries Service

calculated its midpoint, to which potential predictor variables were assigned. These variables included the factors listed in the Appendix.

A total of 97 867 snippets was created, 85 375 of which were > 0.95 km^2 (Table 3). Total survey length was similar for air and ship surveys (255 868 km and 240 607 km, respectively; Fig. 2), but ship-based surveys sampled more water area because of their greater strip width.

Small-scale surveys—birding boat trips

Somewhat constrained by available ports, birders have searched widely to find storm petrel flocks, even sometimes organizing overnight trips to expand the area searched, especially in the southern portion of the ASSP range. To quantify the very localized presence of autumn molting flocks and the change in hotspot location during the last few decades (see Results), we also report results from these birding boat trips (ecotourism) that were organized at frequent intervals, especially during July to November 1985–2015 (late Upwelling through Oceanic periods; Bolin & Abbott 1963), covering Monterey Bay (Monterey, Soquel, and Ascension canyons; n = 837 trips), waters off Halfmoon Bay (Pioneer Canyon; n = 61 trips, 2010–2015 only), and waters off Bodega Bay (Cordell Bank, Bodega Canyon; n = 152 trips; Fig. 3). We assessed the utility of similar trips conducted off Southern California into the waters around the Channel Islands but found them to be too infrequent (a few dozen over 20 years) for meaningful summary. Around Monterey Bay and Cordell Bank (i.e. the Monterey Bay and Gulf of the Farallones/Cordell Bank marine sanctuaries), surveys were done throughout the year, though most survey effort was concentrated in the Oceanic Period (Aug–Oct). During that season, winds are lightest, seas are calmest, and the diversity of seabirds in California waters is by far the highest, thus increasing the interest of participants (Ainley 1976, Stallcup 1976). These trips took place on ~30 m fishing vessels (i.e., "party boats") that were outfitted to allow two dozen or more passengers and typically lasted 8–12 h. Most trips sailed out of Monterey and lasted ~8 h (i.e., 07h30 to 15h30); those from Bodega and Halfmoon bays lasted 8–10 h and typically departed at 07h30. A small amount of chum (mostly fish-oil) was dribbled from the stern once well away from shore. The oil tended to attract larger petrels/albatross and gulls to the vessel. Storm petrels fly too slowly to be affected (i.e., they cannot keep up), other than when the vessel is stopped near a large flock or petrel "raft" for a long period. The chum then attracts storm petrels to the boat, enabling better identification of the several storm petrel species that might be in the flock.

Each trip usually had 2–5 leaders with many years of experience in observing and identifying seabirds, guiding 20–40 participants. Before each trip, leaders typically conferred with the captain to plan the potential route for the day, considering sea conditions, recent observations, patterns of sea-surface temperature (SST), and other factors. Otherwise, approximately the same routes were covered daily (Fig. 3), as finding storm petrel flocks became one of the usual goals. Once a storm petrel flock or a multi-species seabird foraging flock was spotted, the vessels moved closer to count birds and identify species. The leaders' primary responsibilities included spotting

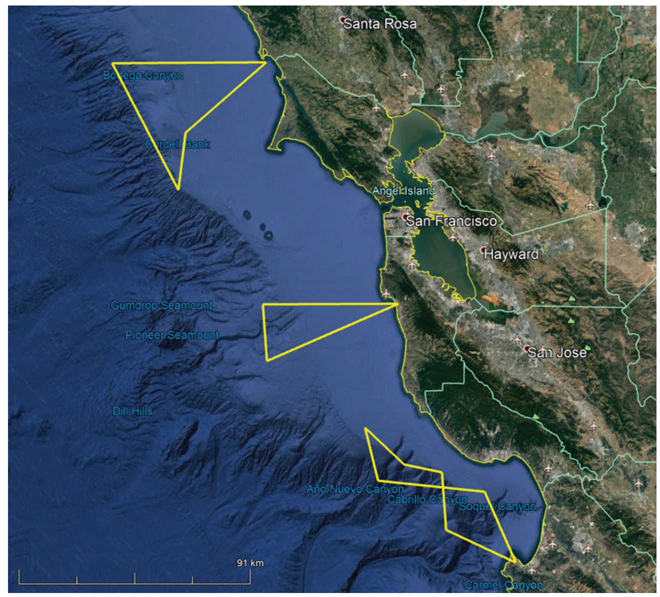

Fig. 3. Typical routes in the three areas for which pelagic birding surveys were analyzed in this paper. From north to south: Bodega Bay to waters overlying Bodega Canyon and Cordell Bank; Halfmoon Bay to waters overlying Pioneer Canyon; and Monterey to waters overlying Monterey, Soquel, and Ascension canyons.

TABLE 3
Number of snippets and area surveyed (km^2) by platform and study code

Years covered	Agency[a]	Ship/Air	All snippets		Snippets used in analysis[b]	
			Snippets	Area	Snippets	Area
1980–1983	CNCA (MMS)	Air	6 604	5 920.9	5 197	5 194.5
1994–2016	OSPR	Air	9 113	8 561.4	8 303	8 302.8
1995–1997	MMS	Air	1 003	955.5	908	907.8
1999–2002	USGS	Air	5 053	4 512.3	3 939	3 937.7
1985–2015	Various	Ship	13 798	12 783.7	11 821	11 818.4
1987–2016	Cal-COFI	Ship	52 161	49 466.2	47 030	47 023.6
1993–1995	EPOCS (NSF)	Ship	513	460.9	434	434.0
1993–2014	NOAA	Ship	5 202	4 570.7	4 027	4 025.3
1996–2001	SF-DODS	Ship	4 420	4 034.9	3 716	3 715.4

[a] See footnote to Table 2. NOAA = National Oceanic and Atmospheric Administration
[b] Only snippets representing > 0.95 km^2 were used in the subsequent analysis.

and identifying birds, showing them to participants, and recording counts of the seabirds, marine mammals, and other megafauna (sharks, turtles, etc.) encountered. Leaders were also responsible for documenting rare or unusual species and for recording relevant abiotic information associated with the observations. Leaders kept track of how many ASSP were seen throughout a trip; in recent years this has been done through implementation of the eBird "pelagic protocol", e.g., https://ebird.org/caribbean/news/pelagic-birding-with-ebird-caribbean. Trip leaders were usually situated at different positions on the boat, thus gazing at different sections of the ocean. Each eBird checklist started fresh hourly, so some birds may have been counted on more than one checklist, thus necessitating adjustments to daily totals. Leaders compared notes on the numbers of each species observed from the different areas that each viewed throughout the day, and they conferred again at the end of the trip to reach final consensus on its total numbers. There were no duplicate counts in the data that we analyzed in this paper.

Data analysis

Large-scale surveys—aerial and ship-based

The equivalency of ship and air surveys is supported by our GAMs, which found that platform type was not a useful predictor for the number of birds observed. Our goal was to develop a GAM that could predict ASSP abundance based on systematic ship and aerial surveys. We examined three different ways of modeling ASSP abundance, following the lead of Clarke *et al.* (2003), who developed the method of using GAMs to estimate population abundance of seabird species using at-sea surveys (see statistical models reviewed below, and Appendix). Clarke *et al*. then ground-truthed the models based on thorough colony-based counts for three species of surface-nesting seabirds: Waved Albatross *Phoebastria irrorata*, Western Gull *Larus occidentalis*, Common Murre *Uria aalge*. The data for two of the species came from surveys included in the present analysis.

Empirical method

We binned observation and effort data from all large-scale surveys into geographical cells measuring 5′ × 5′ (minutes of latitude × minutes of longitude). The size of these cells was influenced by survey protocols from the late 1970s and early 1980s, which were based on navigation by dead reckoning and were resolved to a positional accuracy of only 5′. In general, 5′ appears to be a good compromise between using larger blocks (thereby increasing the number of snippets that fall within a given cell but at the cost of decreasing spatial resolution) versus smaller cells (which results in fewer snippets per cell but improves spatial resolution). Multiple studies of bird populations in the California Current have also utilized cells of this size for analysis (e.g., Briggs *et al.* 1987, NOAA 2003, Mason *et al.* 2007).

In cases where the strip width was relatively small, such as aerial surveys during the early 1980s (width = 50 m), some snippets could be > 10 km in length and longer than the north-south range of a 5′ cell, which is about 9.3 km. Depending on their degree of convolution, these transects sometimes extended outside the relevant 5′ × 5′ block. Snippets that were ≥ 10 km long contributed 9.0% of all transects. In such cases, the correspondence between the 5′ grid and the values of the predictor variables was probably reduced, especially when the survey tracklines ran perpendicular to the coastline and shelf break; in these areas, variables such as depth or SST can change rapidly. The probable net effect of including these longer transects is a weakening of the relationship between the number of birds observed and the predictor variables. However, as noted above, by removing small extensions of snippets, there were still highly significant relationships between five of the covariates and the number of ASSP observed.

To maximize the spatial and temporal coverage of these data, we combined all seasons and years to estimate the total number of birds present in the study area, on average, during the years and months for which there were data. Within each cell, ASSP density (i.e., birds per km^2) was estimated by dividing the total number of birds observed in that cell by the total area sampled within that cell. The predicted number of birds within the cell was calculated as the surface area (ocean portion, if it included land) of the cell (in km^2) times the density. The total population of ASSP in the study area was thus equal to at least the sum of the number of estimated birds within all cells that were sampled.

This estimator did not account for the population within unsampled cells. About 51% of the cells in the study area were not sampled or were lightly sampled, although the majority of these were adjacent to cells in which the estimated density of ASSPs was very low or where they were never observed at all. A population estimate based on the empirical method is a minimum, since it does not include population estimates of unsampled cells. The treatment of unsampled cells is described in the *Hybrid model* section below.

Zero-inflated negative binomial model

We used a GAM as implemented in R version 3.4.1 using the "mgcv" package 1.8–28 to estimate the number of bird observations expected in searching 1 km^2 of ocean. Covariates used to estimate this number are listed in the Appendix.

While we initially intended to use the correlations (r) between the number of birds observed and the various predictor variables as a criterion for model selection, all the correlations were small (< 0.02 in absolute value). However, since the data set was very large, many of the coefficients on the predictors were still significantly different from zero, even for very small values of alpha ($P < 0.001$).

Since none of the explanatory variables was strongly correlated with the number of birds observed, we looked for a GAM in which the distribution of the expected number of birds observed best matched the distribution of the actual data. The distributions evaluated included the Poisson, the zero-inflated Poisson, the quasi Poisson, Poisson-inverse Gaussian, the zero-inflated Poisson-inverse Gaussian, the negative binomial, the zero-inflated negative binomial, and the generalized inverse Gaussian (Sichel). We selected the zero-inflated negative binomial model (ZINB) used for similar purposes by Joyce (2016), Welsh *et al.* (2000), and McGowan *et al.* (2014), among others. The ZINB model assumes that the number of birds observed is a result of two processes: (1) a logistic (0 or 1) function determining whether or not ASSP are present at all in a particular snippet, and (2) a function estimating how many ASSP are present, in the event that they are. ASSP distributions are sometimes highly clumped, and the small-scale surveys (e.g., birding boat trips) indicate that a large proportion of the population could be present in a single very large flock. In any case, the size of some flocks was equivalent to the total population, according to our models. Based on visual inspection, none of the models fit the observed distribution well for very large flock sizes. The best fit was the ZINB model, which may have tended to overestimate small counts and underestimate large counts. Almost all the apparently high-density areas were sampled and therefore are not affected by the structure of the ZINB model. GAM estimates of density were used in relatively empty portions of the ASSP range, especially seaward of the shelf, where densities are typically very low. Estimates by tallying cell by cell population size indicated that 92.7% of all cells each contained 1.0 bird or less. Overall, about 1527 (out of 13 445 birds) were added to the population estimate calculated using the empirical method, based on the ZINB estimates for unsampled cells. Thus, if the model did overestimate the population in those cells, the actual population would be smaller than our estimate, but that underestimate would be less than 1527 birds (see Results and Discussion for additional information).

We tested all the candidate explanatory variables (see Appendix for a complete list of variables) using a backwards selection procedure (Hastie *et al.* 2009). The decision to include or exclude explanatory variables in the final model was based on both significance levels and Akaike information criterion values; either method resulted in equivalent sets of variables. For the final model, we used only highly significant ($P < 0.001$) explanatory variables. These included distance to land, distance to 2000 m depth contour (lower slope), distance to colony, latitude for both portions of the model, distance to 200 m contour (shelf break), and average SST for the logistic portion.

Hybrid model

The empirical method resulted in a minimum estimate because it did not include birds that were present in unsampled cells. We estimated the populations in unsampled cells by prediction, using the ZINB model described above. To accomplish this, we laid a 5′ × 5′ grid over the study area and counted the number of birds observed from the midpoint of each of the unsampled cells using the values of the predictor variables for that point in space. We then used the ZINB model to estimate how many ASSP we would expect to count at that location based on the values of the explanatory variables, then multiplied the resultant value by the area of the cell. This yielded an estimate of the expected number of ASSP in the cell. The sum of the population estimates (empirical method) over all sampled cells plus the sum of the population estimates (ZINB model) for all unsampled cells is therefore our best population estimate within the study area. We placed 95% confidence limits on these estimates using a bootstrap procedure iterated 1000 times.

Small-scale surveys—birding boat trips

Data were summarized by dividing months in half for each year. Throughout the 1985–2015 study period, the number of ASSP seen was added among surveys available for a given half-month, and that total was then divided by the number of surveys in that half-month over the entire temporal span of the data set. We did this instead of taking an average (or the high count), because it was unknown whether the large flock known to exist in a given area was encountered on a particular trip. For instance, one trip might report a flock of a few thousand ASSP but a few days later, no birds or only a few would be encountered in the same location, then large numbers would be seen there on the next trip not long after. Therefore, it was very likely that the molting/rafting flock was present in the area during that intervening survey but was not encountered. These numbers were then plotted by half-month periods by year, and regional population trends conditional upon year and the 95% confidence interval (CI) about these trends were visualized using locally weighted smoothing (LOESS) in package "ggplot2" (Wickham 2016) in R version 3.6.1 (R Core Team 2019). In another analysis, we compared the high counts by half-month among the three birding boat trip survey areas shown in Fig. 3: Monterey Canyon, Pioneer Canyon, and Bodega Canyon.

RESULTS

Population size

GAM results were used to estimate the total number of ASSP within the study area and within the northern and southern parts of the study area separately. In our models, there was no influence of platform type, i.e. aircraft vs. ship, which supports our decision to not correct for flux (as in Clarke *et al.* 2003). Thus, ASSP fly slow enough that they are essentially stationary, contributing to the total just as much as those resting on the water. The northern sub-region (north of 35.1°N) consisted of 3212 cells and the southern sub-region consisted of 6321 cells (see Fig. 4 for the distribution depicted by each model). The hybrid model estimated a total ASSP population of 13 445 birds, the largest estimate of the three alternative methodologies (Table 4). Estimates for both the empirical method and the ZINB model are similar, at 11 633 and 11 918 birds, respectively. Likewise, the proportion of the population in the northern versus southern ranges is consistent, with the northern range accounting for roughly two thirds of the total population in all three cases. Although the 95% confidence limits are relatively large for the ZINB and the hybrid models, estimates based on the empirical method have a narrower range.

TABLE 4
Estimates of Ashy Storm Petrel *Oceanodroma homochroa* population size within the California Current System based on at-sea surveys

		Empirical method		ZINB model		Hybrid model	
Sub-region	**Number of cells**	**Estimate**	**Percent of total**	**Estimate**	**Percent of total**	**Estimate**	**Percent of total**
North	3 212	7 161	60	8 160	70	8 336	62
South	6 321	4 757	40	3 473	30	5 109	38
Totals	9 533	11 918		11 633		13 445	
95% CI[a]	-	[8 599–13 358]		[5 694–50 637]		[10 128–27 820]	
90% CI	-	[8 890–12 751]		[6 321–31 796]		[10 531–21 030]	

[a] Confidence interval

Large-scale distribution

Clearly, there are many more ASSPs frequenting waters to the north of Point Conception than to the south (Fig. 4). The pattern is the same regardless of survey platform used, with results from the three statistical models agreeing closely. The species generally occurs on the outer continental shelf (near the shelf break) and continental slope, especially around the Farallon Islands and the northern Channel Islands. Nightly colony arrival at darkness indicates that dispersion during the day, at least during breeding, is not extensive

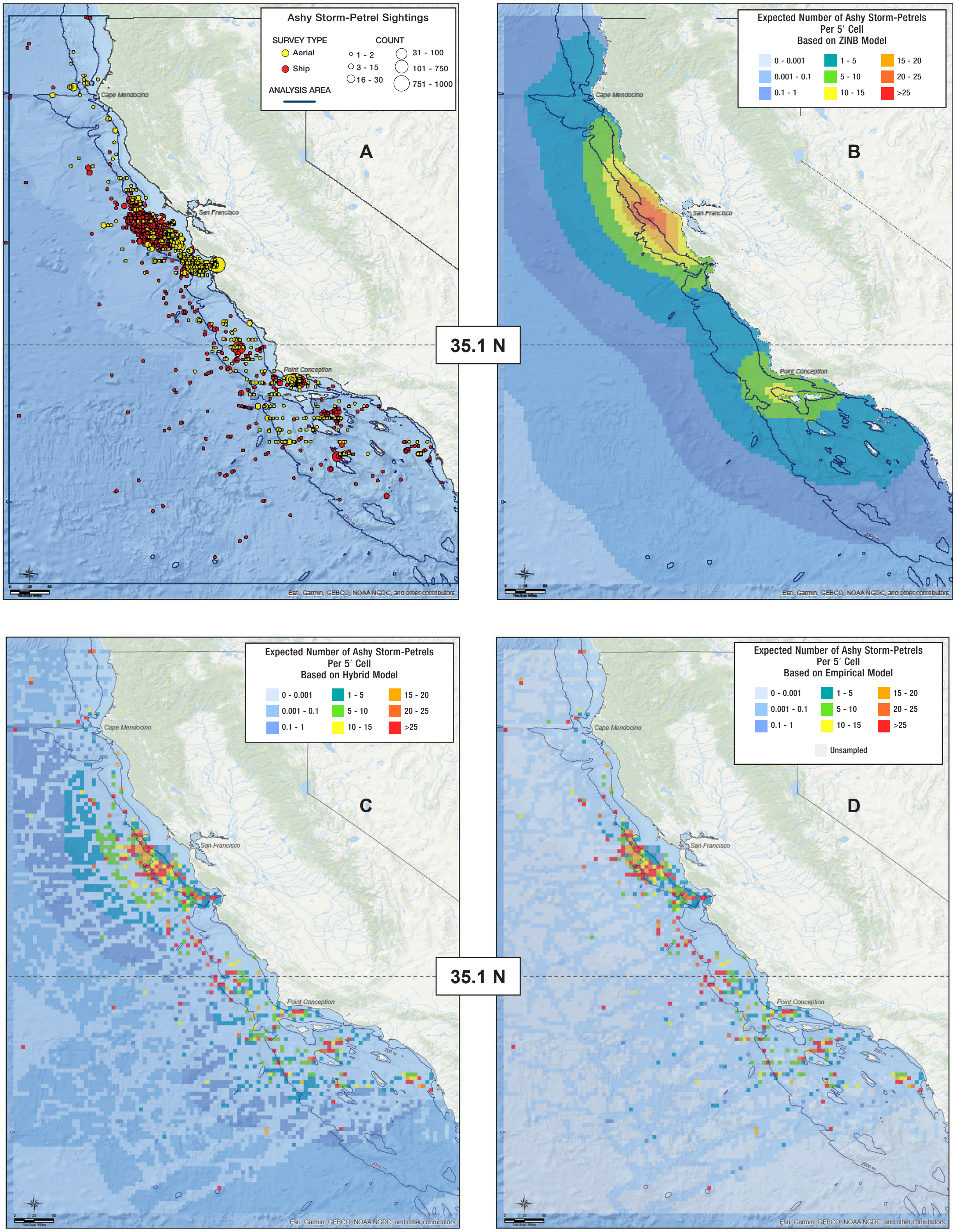

Fig. 4. Results of models depicting Ashy Storm Petrel *Oceanodroma homochroa* distribution: A) spread of individual sightings, 1980–2017; B) zero-inflated negative binomial model; C) hybrid model; and D) empirical model.

(see Ainley *et al.* 1975, Adams 2016). Sightings of single birds far offshore occur with very low but increasing frequency toward the south of the Channel Islands. However, these sightings may involve a higher frequency of incorrect identification, with confusion between ASSP and other dark *Oceanodroma* storm petrels. All these species nest in the southern Channel Islands and Mexican islands (see Howell 2012), thus possibly becoming problematic owing to increased prevalence in at-sea surveys. The dozen or so records of unidentified dark storm petrels were not included in our analysis.

Small-scale patterns—hotspots

Three major hotspots were detected by birders over the years, beginning with the first birding boat trips in the 1970s (e.g., Stallcup 1976). These were centered over submarine canyons that cut into the outer continental shelf of central-northern California, especially the Monterey/Soquel/Ascension and Bodega canyons (Figs. 3, 5). ASSP association with these submarine canyons is consistent with them being krill hotspots (Santora *et al.* 2017, 2018), and the storm petrels forage on small prey. Large flocks occurred, usually rafting on the water, and were dominated by molting individuals. Seasonally, numbers encountered on trips began to increase in the second half of June but were most prevalent from the second half of August to the second half of October (Oceanic Period). Birding boat trips conducted from ports in Southern California out to the Channel Islands and beyond during the past 30 years have failed to find flocks or numbers anywhere near to what has been observed in central California waters.

The largest flocks seen on trips in Monterey Bay, all during the Oceanic Period, included: 7000 birds in October 1992, 8400 in October 1999, 9000 in August/September 1988 and 2007, 10 700 in September 2008, and 13 000 in September 1986. From 1985 through 2011, in virtually every half-month of the Oceanic Period, counts exceeded at least 1000 birds. Numbers appeared to peak during 2006–2008, but dropped off dramatically thereafter (Figs. 6, 7). The highest numbers of ASSP in the vicinity of Bodega Canyon/Cordell Bank also occurred during the Oceanic Period, and during approximately the same array of months as in Monterey Bay (Fig. 5). The largest flocks encountered in this area included: 5000 in September 2004 and 2007, 6000 in August 2015, 6400 in August 1994, and 10 500 in September 2013. A flock of 5000 encountered in January 2012 was very unusual, as counts during that month (Davidson Current Period; Bolin & Abbott 1963) were typically no more than 100 birds. Clearly, numbers of ASSP in this area of the northern Gulf of the Farallones began to increase during the latter part of the study period, thus complementing the decrease seen in Monterey Bay (Figs. 6, 7).

Finally, as ASSP flocks became smaller in Monterey Bay, the birding community began to schedule their trips elsewhere to find them, assuming that no actual decrease in population size was happening. Besides Bodega Canyon, where it was known that numbers were increasing, repeated trips departed from Halfmoon Bay to access Pioneer Canyon, where large flocks indeed were found (Figs. 3, 8). Clearly, the size of flocks in Monterey Bay canyons during 2010–2015 had become far smaller than those at Pioneer and Bodega canyons. The complementarity of counts in Monterey Bay versus Bodega Canyon are evident in Fig. 5; i.e., when there are more birds in one area, there are fewer in the other. Several trips out of ports north of the Gulf of the Farallones, e.g., Fort Bragg near Cape Mendocino, found only a few ASSP: i.e., 68 in August 2011 but otherwise 30 or fewer birds on other trips (see also Howell 2012).

DISCUSSION

Compared to colony-based estimates of ASSP breeding populations, analysis of at-sea numbers indicates similar underestimates for both the northern sub-region (mostly in the Farallon Islands—5700 (Nur *et al.* 2013) vs. 8336 birds (this study)) and the southern sub-region (3200 (Carter *et al.* 2016a) vs. 5109 birds (this study)). The total is slightly higher than the maximum estimate of population size, based on surveys of all colonies (*cf.* Tables 1 and 4). Our results are similar to those obtained by Spear & Ainley (2007) for the northern sub-region during spring-summer; they used most of the ship-based (not aerial) data analyzed here. They used GAMs to generate their population estimate of 7287 birds (CI 4500–9070), which was corrected for flux. Their result is further evidence that we were justified here in considering ASSP to be stationary relative to ship/aircraft speed; i.e. there was no difference between flux corrected and uncorrected population estimates.

Our results may not be overestimates, as the colony-based surveys, according to the researchers involved, involve only breeding birds ("residents"; Nur *et al.* 2019), whereas the at-sea data include breeders, non-breeders, and "floaters," which includes breeding-capable adults that do not breed owing to a breeding cavity not being

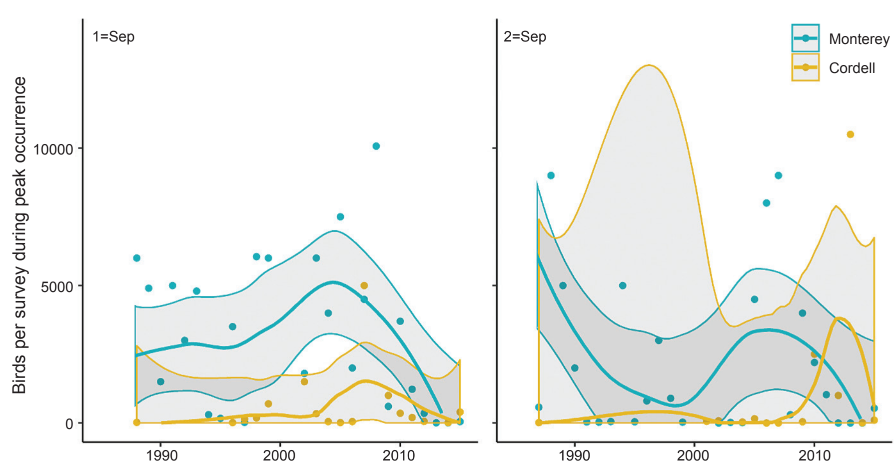

Fig. 5. The pattern of Ashy Storm Petrel *Oceanodroma homochroa* prevalence at submarine canyons in Monterey Bay and Cordell Bank, 1985–2015. Values shown are the total number of birds logged during each half-month (1985–2015) divided by the number of surveys conducted in each half-month period. The labels 1=Sep and 2=Sep refer to the first and second half of September.

available. Many of these might be included in what Nur *et al.* (2019) define as "transients." Indeed, Adams (2016) reported that ASSPs banded at one of the Channel Islands were recovered at multiple other islands, including one at the Farallones; if these were not transients, they were floaters. Nevertheless, floaters do visit colonies where they are caught in mist nets used to estimate colony size. Floaters, which are prospecting for nesting sites, cannot be distinguished from breeders, because both form incubation patches (regardless of whether they are incubating an egg). ASSP do not dig burrows but rely on natural cavities on the xeric, soil-deprived islands found in the Mediterranean climate of the southern CCS. A shortage of cavities results in floating populations of cavity-nesting birds, including seabirds, as noted both at Southeast Farallon and San Miguel islands (Ainley & Boekelheide 1990). Among other petrel species (almost all of which nest in burrows or cavities), the size of the non-breeding portion of colony populations (which would include floaters) has

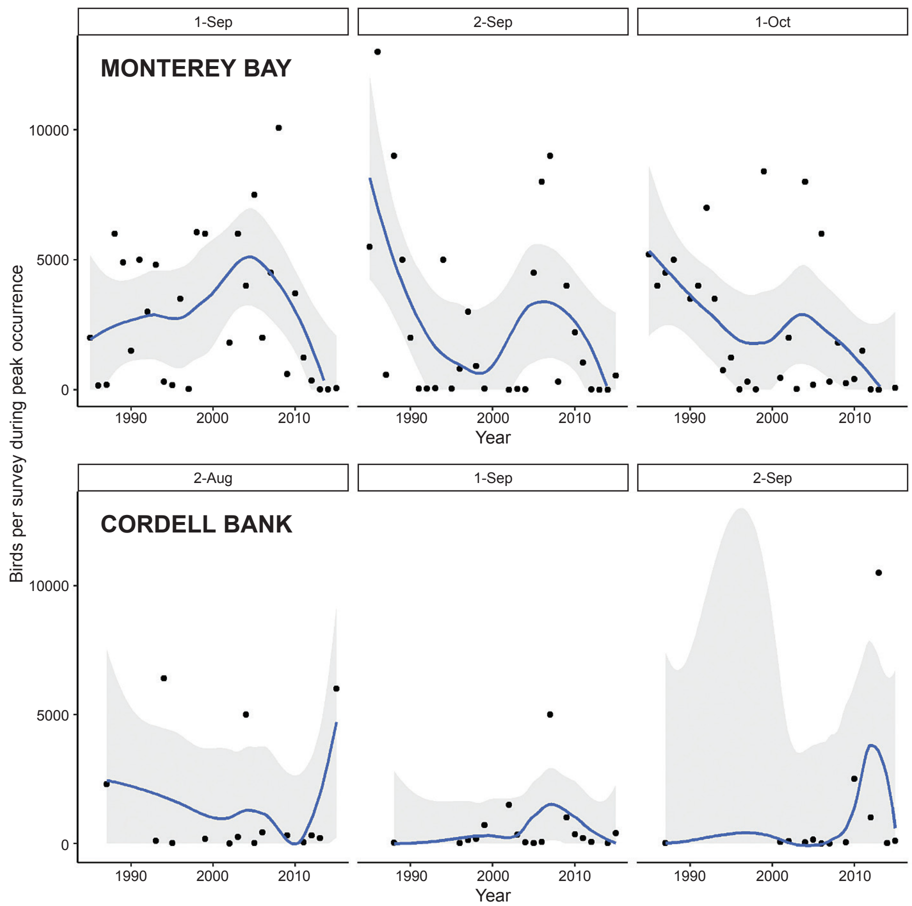

Fig. 6. Half-monthly high counts among the three periods of highest counts in Monterey Bay and Cordell Bank, 1985–2015, analyzed using Generalized Additive Models (line, with 95% confidence intervals in gray). On the x-axis, 1 and 2 refer to the first and second half of each month.

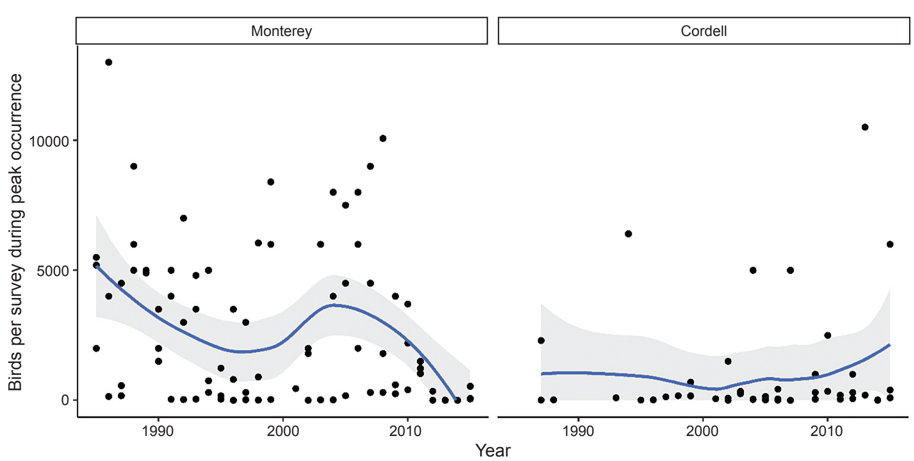

Fig. 7. Counts in Monterey Bay and Cordell Bank, 1985–2015, analyzed on an annual basis using Generalized Additive Models (line, with 95% confidence intervals in gray).

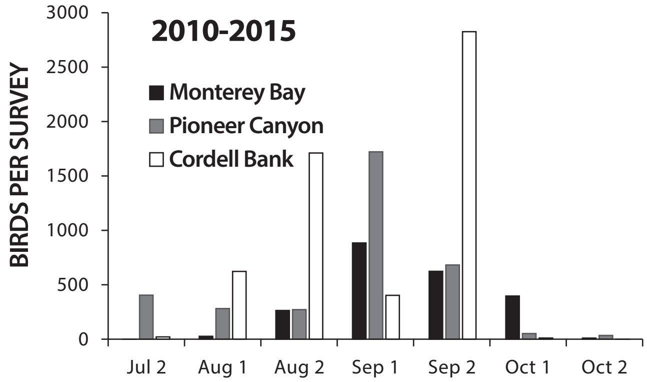

Fig. 8. Numbers of Ashy Storm Petrel *Oceanodroma homochroa* seen per survey, compared among Monterey Bay, Pioneer Canyon, and Cordell Bank, 2010–2015. (Regularly scheduled Pioneer trips began in 2010.) On the x-axis, 1 and 2 refer to the first and second half of each month. Sightings during each half-month were totaled then divided by the number of surveys during the five-year period.

been found to be a significant portion of the total number of birds that frequent the colonies (reviewed by Warham 1996: pp. 39–45). Our results indicate a pattern like that determined for the New Zealand Storm Petrel (Rayner *et al.* 2020), in which the at-sea population estimate is higher than the colony-based estimate.

Another issue with past estimates of breeding population size at the Channel Islands is that supposed ASSPs breeding at Santa Catalina Island were recently inspected more closely and identified as Leach's Storm Petrels (LESP; Carter *et al.* 2016b). The body size of LESP and other hydrobatid species decreases latitudinally, becoming more similar to ASSP toward the south (*cf.* measurements in Ainley 1980, Ainley *et al.* 2019). The problem originated from sightings of only the heads of petrels in cavities, and subsequent incorrect identification based only on the gray head of the southern LESP populations in California. Rump color is also required for accurate determination. Since then, closer inspections of birds at other localities on those islands have not been done to verify the colony-based estimates. It is possible that in the southern portion of the ASSP range, identification of storm petrels at sea judged to be ASSP, could also have included dark-rumped LESP (and related species). In that area, a few sightings of birds that could not be identified by species were not included in our analysis.

Therefore, it appears from at-sea surveys that there are more ASSP than previously thought, based on colony estimates, although a large portion of the difference may be among non-breeding individuals. Regardless, it has been confirmed that the entire population or almost all of it can occur together in just one flock during the Oceanic Period (e.g., a flock of 10000 to 13000ASSP). Why these mega-flocks, which include a large proportion of molting individuals, appear to have moved north from Monterey Bay to Pioneer Canyon and Cordell Bank/Trough in the northern Gulf of the Farallones remains a mystery. It is worth investigating whether some unknown decadal and spatial changes in the food web are involved, or whether it is merely birds avoiding disturbance by the ever-increasing numbers of baleen whales (see Ainley & Hyrenbach 2010), especially in the Monterey Bay area. There may also be some level of interference competition if ASSP and whales are foraging on the same prey, but there are no data on ASSP diet. It could just be that the ASSP in their "molting flocks" shifted to avoid continual disturbance by surfacing whales and boat traffic.

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