LONG-TERM DYNAMICS OF SEABIRD SPECIES COMPOSITION ACROSS THE DRAKE PASSAGE

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ABSTRACT

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We present standardized, quantitative information on the avifauna of the Drake Passage obtained during six crossings between Patagonia and the South Shetland Islands during the summer–autumn period, 1998–2020. We compare inter-annual and seasonal patterns of species occurrence, adding to previous, published surveys, and we discuss species association with the different zones and water masses of the region.

Key words: Drake Passage, ocean climate, seabirds, species composition

INTRODUCTION

The Drake Passage, one of the most dynamic stretches of ocean on the planet, is a narrow passage through which waters of the Southern, Atlantic, and Pacific oceans compete for space and prominence. Within its 820 km width is one of the highest spatial ‘densities’ of major frontal zones: the Subtropical (STF), Subantarctic (SAF), and Antarctic Polar (APF) fronts, as well as the Southern Boundary of the Antarctic Circumpolar Current (SBACC; Orsi *et al*. 1995). Other oceanographic boundaries include the shelf break fronts of Patagonia and the South Shetland Islands. The frontal jets in Drake Passage separate four biogeographic zones (Pollard *et al*. 2002, Force *et al*. 2015): waters north of the SAF belong to the Sub-Antarctic Zone (SAZ); the Polar Frontal Zone (PFZ) located between the SAF and APF; the Antarctic Zone (AZ) located between the APF and SBACC; and south, the Continental Zone (CZ) is characterized by coastal water properties. Simultaneously, the PFZ and AZ are located in the central part of the Drake Passage (CDZ), and the SAF and CZ are located near the coast of South America and Antarctica, respectively (Fig. 1). Thus, within short distances, distinctly different water masses, with their associated biota, are crossed. Given that seabirds are sensitive to variability in marine ecosystems (Rajpar *et al*. 2018), it may be instructive to consider changes in the avifauna as one crosses the Drake Passage to better understand avifaunal occurrence patterns in the context of ocean climate. The subject has been considered previously (Starck & Wyrzykowski 1982, Hunt *et al*. 1990, Ribic *et al*. 2011, Force *et al*. 2015, Sheets 2017). Indeed, seabirds are easily detected and identified, occur near the top levels of food webs and thus act to integrate processes at lower levels, have distributions constrained by ocean climate boundaries, and respond quickly to changes in respective habitat conditions. Herein, we add to this body of work with the aim to further understand the inter-annual and seasonal biotic dynamics of the Drake Passage through changes in avian species composition and abundance.

METHODS

Data acquisition

Information was collected on cruises through the Drake Passage during the summer–autumn period: March 1998 – Olexander Peklo (Peklo 2001); February 2006 – Ihor Dykyy; March 2007 – Vladlen Trokhymets; March 2009 and March 2019 – Ihor Dykyy; and February and April 2020 – Vladlen Trokhymets, Ihor Dykyy, Olexander Salganskiy, and Anatolii Chernov.

Cruises passed between the ports of Punta Arenas (Chile) or Ushuaia (Argentina) and the South Shetland Islands (Fig. 1). Average annual temperature ranged from 5 °C in the north to –3 °C in the south, and surface water temperatures during cruises ranged from 6 °C in the north to −1 °C in the south.

Survey design

Conventional approaches were used to collect avifaunal information (Franeker 1994, Hunt *et al*. 1994, Spear *et al*. 1992, Veit 1995). Observations were made from the stern of the ship assisted with Greenkat 10 × 50 KENT binoculars and a Panasonic Lumix DMC-ZS5 12.1 MPM camera. Standardized band transects were used (Tasker *et al*. 1984). The recordings were gathered by two observers using the vector method (Spear *et al*. 2004). This made it possible to accurately calculate of the number of birds by species, including those of all sizes. The width of the count strip for large species (albatrosses, giant petrels) was 500 m and for all others it was 300 m (Boldac & Fifield 2017).

Reaction to the movement of the vessel was also assessed. First, all birds seen from the stern in a 180° radius were registered, and then counts of all birds forward of this zone allowed adjustment for those individuals overtaken as the ship progressed. After recording,

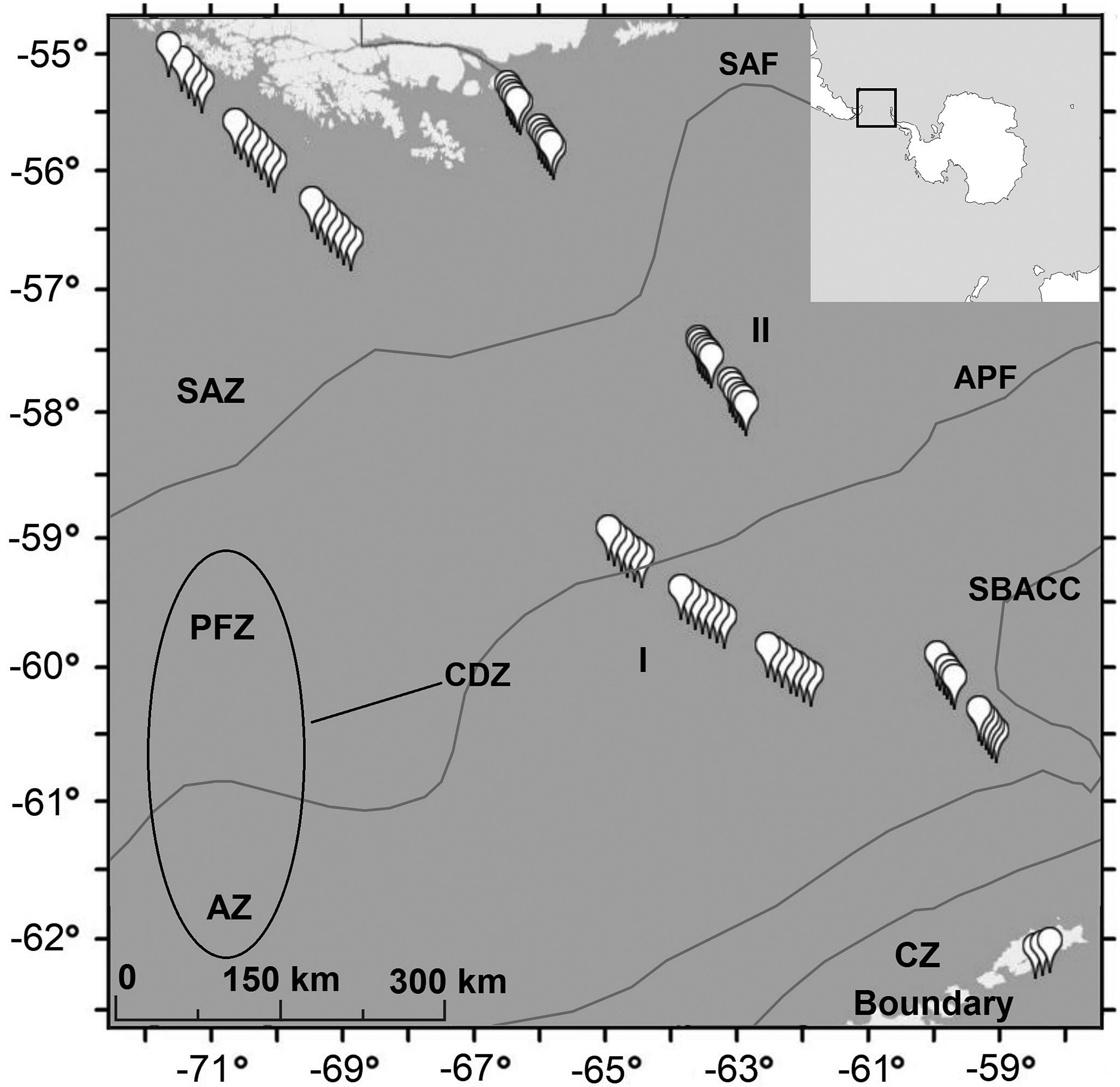

Fig. 1. Map showing bird registration points in the Drake Passage using the example of 2020 (I, February; II, April), which corresponds to the standard route of long-term monitoring of seabirds by Ukrainian researchers. Abbreviations: SAZ – Sub-Antarctic Zone, PFZ – Polar Frontal Zone, AZ – Antarctic Zone, CDZ – central part of Drake Passage (Polar Frontal Zone and Antarctic Zone), CZ – Continental Zone, SAF – Sub-Antarctic Front, APF – Antarctic Polar Front, SACCF – Southern Antarctic Circumpolar Front, Boundary – Southern Boundary.

a specific bird was not registered again with the number of birds following the ship, which was estimated at regular intervals; only new individuals who joined the group were added (Gjerdrum *et al*. 2012). Counts were performed every 20 min during daylight from 09h00 to 13h00 and from 14h00 to 18h00. Species identification was based on Lowen (2011) and Onley & Bartle (1999).

The similarity of bird species composition among ocean zones was determined using the Sorenson index, which is calculated by the following formula: $S = 2C/A + B$, where A and B are the number of species in samples A and B, respectively, and C is the number of species common to the two samples (Murguía & Villaseñor 2003).

Box and whisker plots, one-way analysis of variance (ANOVA), and multivariate factor analysis were used to determine the influence of habitat factors on species presence. We used R3.6.2 language and environment for statistical computing with RStudio 1.2.5033 interface (R Core Team, 2019).

RESULTS AND DISCUSSION

Species composition

Thirty-eight species of seabirds were identified across all end-of-summer and autumn passages (Table 1). Species richness

TABLE 1
Species composition of avifauna within the typical route through the Drake Passage to the Vernadsky Research Base (generalized for summer–autumn 1998, 2006, 2007, 2009, 2019, and 2020), combined with information from Ainley *et al*. (1994, autumn 1986*) and Force *et al*. (2015, summer–autumn 1994–2009)**

	Bird species	SAZ[a]	CDZ[a]	CZ[a]	1*	2**
	I. Order Charadriiformes I.1. Family Laridae					
1	Kelp Gull *Larus dominicanus*	+	-	+	+	+
2	Dolphin Gull *Leucophaeus scoresbii*	+	-	-	-	+
3	South American Tern *Sterna hirundinacea*	+	-	+	-	+
4	Arctic Tern *Sterna paradisaea*	-	-	-	+	+
5	Antarctic Tern *Sterna vittate*	-	-	+	+	+
	I.2. Family Stercorariidae					
6	Brown Skua *Stercorarius antarcticus*	-	-	+	+	+
7	Chilean Skua *Stercorarius chilensis*	-	-	-	-	+
8	South Polar Skua *Stercorarius maccormicki*	+	-	+	+	+
	I.3. Family Chionidae					
9	Snowy Sheathbill *Chionis alba*	-	+	+	+	+
	II. Order Procellariiformes II.1. Family Procellariidae					
10	Southern Giant Petrel *Macronectes giganteus*	+	+	+	+	+
11	Northern Giant Petrel *Macronectes halli*	-	+	-	-	+
12	Southern Fulmar *Fulmarus glacialoides*	+	+	+	+	+
13	Antarctic Petrel *Thalassoica antarctica*	-	+	-	+	-
14	Cape Petrel *Daption capense*	+	+	+	+	+
15	Snow Petrel *Pagodroma nivea*	-	-	-	+	+
16	Blue Petrel *Halobaena caerulea*	+	+	+	+	+
17	Antarctic Prion *Pachyptila desolata*	+	+	-	+	+
18	Slender-billed Prion *Pachyptila belcheri*	-	-	-	-	+
19	Fairy Prion *Pachyptila turtur*	-	-	-	+	+
20	White-chinned Petrel *Procellaria aequinoctialis*	+	+	-	+	+
21	Westland Petrel *Procellaria westlandica*	-	-	-	-	+
22	Little Shearwater *Puffinus assimilis*	-	-	-	-	+
23	Pink-footed Shearwater *Ardenna creatopus*	-	-	-	-	+
24	Great Shearwater *Ardenna gravis*	+	-	-	-	+
25	Sooty Shearwater *Ardenna grisea*	+	+	-	-	+
26	Manx Shearwater *Puffinus puffinus*	-	-	-	-	+
27	South Georgia Diving Petrel *Pelecanoides georgicus*	-	-	-	-	+
28	Magellanic Diving Petrel *Pelecanoides magellani*	+	+	-	-	+
29	Common Diving Petrel *Pelecanoides urinatrix*	-	-	-	+	+
30	Kerguelen Petrel *Aphrodroma brevirostris*	+	+	+	+	+
31	Atlantic Petrel *Pterodroma incerta*	-	-	-	-	+
32	Mottled Petrel *Pterodroma inexpectata*	-	-	-	-	+
33	White-headed Petrel *Pterodroma lessonii*	-	-	+	-	+
34	Stejneger's Petrel *Pterodroma longirostris*	-	-	-	-	+
35	Soft-plumaged Petrel *Pterodroma mollis*	-	+	-	+	+

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	Bird species	**SAZ[a]**	**CDZ[a]**	**CZ[a]**	**1***	**2****
	II.2. Family Diomedeidae					
36	Yellow-nosed Albatross *Thalassarche chlororhynchos*	+	-	-	-	-
37	Southern Royal Albatross *Diomedea epomophora*	+	+	+	-	+
38	Wandering Albatross *Diomedea exulans*	+	+	-	+	+
39	Shy Albatross *Thalassarche cauta*	-	+	-	-	+
40	Grey-headed Albatross *Thalassarche chrysostoma*	+	+	+	+	+
41	Black-browed Albatross *Thalassarche melanophris*	+	+	+	+	+
42	Sooty Albatross *Phoebetria fusca*	-	+	-	-	-
43	Light-mantled Albatross *Phoebetria palpebrata*	-	+	-	+	+
	II.3. Family Oceanitidae					
44	Wilson's Storm Petrel *Oceanites oceanicus*	+	+	+	+	+
45	Gray-backed Storm Petrel *Garrodia nereis*	-	-	-	-	+
46	Black-bellied Storm Petrel *Fregetta tropica*	+	+	+	+	+
	III. Order Sphenisciformes III.1. Family Spheniscidae					
47	King Penguin *Aptenodytes patagonicus*	-	-	-	+	+
48	Emperor Penguin *Aptenodytes forsteri*	-	-	+	+	-
49	Macaroni Penguin *Eudyptes chrysolophus*	-	-	-	+	+
50	Southern Rockhopper Penguin *Eudyptes chrysocome*	-	-	-	+	+
51	Adelie Penguin *Pygoscelis adeliae*	-	-	+	+	-
52	Chinstrap Penguin *Pygoscelis antarcticus*	-	-	+	+	+
53	Gentoo Penguin *Pygoscelis papua*	-	-	+	-	+
54	Magellanic Penguin *Spheniscus magellanicus*	+	-	-	-	+
	IV. Order Suliformes IV.1. Family Phalacrocoracidae					
55	Imperial Shag *Leucocarbo atriceps*	+	-	-	-	+
56	Antarctic Shag *Leucocarbo bransfieldensis*	-	-	+	-	-
	The total number of species	23	22	22	30	50
	The total number of species of different investigation		38		30	50

[a] Abbreviations: SAZ – Sub-Antarctic Zone; CDZ – central part of Drake Passage (Polar Frontal Zone and Antarctic Zone); CZ – Continental Zone

and composition differed as expected depending on ocean characteristics, i.e., water masses bounded by fronts. Overall, our findings were consistent with previous reports. In March 1986, 30 species of seabirds were recorded across the Drake Passage (Ainley *et al*. 1994), and in January–March 1994–2009, a much broader time series, 50 seabird species were recorded (Force *et al*. 2015; Table 1). The Sorensen Index was similar among surveys: (i) between our results and those of Ainley *et al*. (1994), $S = 0.68$; (ii) between our results and those of Force *et al*. (2015), $S = 0.67$; and (iii) between the results of Ainley *et al*. (1994) and Force *et al*. (2015), $S = 0.68$. The lower species representation in Ainley *et al*. (1994) is likely related to their one-year effort and the availability of data only for autumn. In contrast, it is likely that our results are more closely aligned with those of Force *et al*. (2015) because the efforts in both studies were multi-year and covered a broader seasonal period.

Within the SAZ, 23 species were recorded, five of which were not seen in other zones: Dolphin Gull *Leucophaeus scoresbii,* Great Shearwater *Ardenna gravis*, Atlantic Yellow-nosed Albatross *Thalassarche chlororhynchos*, Magellanic Penguin *Spheniscus magellanicus*, and Imperial Shag *Leucocarbo atriceps*. Species seen in the SAZ were dominated by Procellariformes: 17 species or 68.0 % of the total, 10 of which were in the family Procellariidae. There were fewer representatives of the families Diomedeidae and Oceanitidae: five and two species, respectively. We also encountered four species of Charadriiformes and one species each of Sphenisciformes and Suliformes. The domination of Procellariiformes was consistent with previous findings (Ainley *et al*. 1994, Hunt *et al*. 1994, Force *et al*. 2015).

Within the CDZ, 22 species were recorded, seven of which were not seen in other Zones: Northern Giant Petrel *Macronectes* *halli*, Antarctic Petrel *Thalassoica antarctica*, Antarctic Prion *Pachyptila desolata*, Soft-plumaged Petrel *Pterodroma mollis*, Shy Albatross *Thalassarche cauta*, Sooty Albatross *Phoebetria fusc*a, and Light-mantled Albatross *Phoebetria palpebrata*. A number of Procellariiformes were observed: 21 species, or 95.5 % of the total, again dominated by the family Procellariidae, represented by 12 species. Diomedeidae and Oceanitidae were also present: seven and two species, respectively. Charadriiformes was represented by one species. Similar avifaunal patterns in these waters have been recorded by previous studies (Brown *et al*. 1975, Starck & Wyrzykowski 1982, Hunt *et al*. 1990, Hunt *et al*. 1994, Force *et al*. 2015, Sheets 2017).

Within the CZ, 22 species were registered, seven of which were not seen in zones to the north: Antarctic Tern *Sterna vittata*, Brown Skua *Stercorarius skua*, White-headed Petrel *Pterodroma lessonii*, Emperor Penguin *Aptenodytes forsteri*, Adelie Penguin *Pygoscelis adeliae*, Chinstrap Penguin *Pygoscelis antarcticus*, and Gentoo Penguin *Pygoscelis papua*. Clearly, this represents an Antarctic avifauna, among which the representation of penguins was much greater than in northern zones (from one to four species). Procellariformes also predominated, although their share decreased significantly compared to that of northern areas: 11 species, or 50.0 % of the total. Again, the family Procellariidae dominated: six species, with three and two species, respectively, of Diomedeidae and Oceanitidae. Charadriiformes, Sphenisciformes, and Suliformes were represented by six species, four species, and one species, respectively. Thus, this zone exhibited reduced representation of Procellariiformes and increased representation of Charadriiformes and Sphenisciformes, similar to the findings of other studies (Starck & Wyrzykowski 1982, Hunt *et al*. 1990, Hunt *et al*. 1994, Force *et al*. 2015, Sheets 2017).

Using the Sorenson Index, we compared the species lists of the major zones crossed. There was high avifaunal similarity between the SAZ and other areas, and low similarity between the CDZ and CZ: (i) SAZ with CDZ, S = 0.67; (ii) SAZ with CZ, S = 0.58; and (iii) CDZ with CZ, S = 0.50. This can be explained by the contribution of South American nesting species to the Drake Passage avifauna, because many Procellariiformes species nest on its coast and adjacent islands and archipelagos. In addition, for the SAZ and CZ, a number of respective, common coastal species occur in the adjacent ocean areas during seasonal migrations. These include a number of *Larus*, *Sterna*, and *Skua* species. Moreover, the CZ is characterized by significantly lower species richness of Procellariiformes and higher numbers of Sphenisciformes and Charadriiformes than other zones.

When comparing the species lists in different areas of the Drake Passage in different years (Table 2), similarities between zones was lower: (i) SAZ with CDZ, S = 0.58 (0.4–0.71); (ii) SAZ with CZ, S = 0.43 (0.38–0.48); (iii) CDZ and CZ, S = 0.49 (0.36–0.57) (Table 3).

For most inter-year pairwise comparisons in every zone, a high degree of similarity was found for the CDZ (S = 0.69 [0.54–0.82]) and CZ (S = 0.62 [0.4–0.86]), but there was low similarity for the SAZ (S = 0.49 [0.36–0.71]). Thus, we conclude that avifaunal composition has been stable in recent decades within the oceanic area of the Drake Passage, in agreement with other studies (Ainley *et al*. 1994, Force *et al*. 2015). Species composition was less stable within the coastal areas of the Drake Passage, especially along the South American coast and islands where several species nest. Therefore, the species richness of seabird faunas is essentially formed from two groups: the South American and Antarctic

TABLE 2
Species composition of avifauna and the number of seabirds in different areas of the Drake Passage in end-summer and autumn of 1998 (Peklo 2001), 2006, 2007, 2009, 2019, and 2020 (original data)[a]

Species of birds	Region	1998 March	2006 February	2007 March	2009 March	2019 March	2020 February	2020 April
Kelp Gull	SAZ	0	0.4(0–1)	0	11(5–17)	—	0	0
Larus dominicanus	CDZ	0	0	0	0	0	0	0
	CZ	2(0–6)	0.1(0–2)	1.2(0–4)	—	0	1.6(0–5)	3.7(0–11)
Dolphin Gull	SAZ	0	0	0	0.3(0–2)	—	0	0
Leucophaeus scoresbii	CDZ	0	0	0	0	0	0	0
	CZ	0	0	0	—	0	0	0
South American Tern	SAZ	0	1.8(0–5)	0	1.2(0–3)	—	0	0
Sterna hirundinacea	CDZ	0	0	0	0	0	0	0
	CZ	0	0.2(0–2)	0	—	0	0	0
Antarctic Tern	SAZ	0	0	0	0	—	0	0
Sterna vittata	CDZ	0	0	0	0	0	0	0
	CZ	0	1.2(0–3)	1(0–2)	—	0.3(0–2)	0.8(0–3)	0
South Polar Skua	SAZ	0	0	0	1.7(1–2)	—	0.2(0–3)	0
Stercorarius	CDZ	0	0	0	0	0	0	0
maccormicki	CZ	1.3(0–3)	2.6(0–7)	2(0–6)	—	0	0.3(0–5)	0.3(0–1)
Great Skua	SAZ	0	0	0	0	—	0	0
Stercorarius skua	CDZ	0	0	0	0	0	0	0
	CZ	0	0.2(0–2)	0	—	0	0	0

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Species of birds	**Region**	**1998 March**	**2006 February**	**2007 March**	**2009 March**	**2019 March**	**2020 February**	**2020 April**
Snowy Sheathbill	SAZ	0	0	0	0	—	0	0
Chionis alba	CDZ	0	0	0	0	2.6(0–7)	0	0
	CZ	0	0	0	—	0	0.2(0–2)	0.7(0–1)
Southern Giant Petrel	SAZ	4.7(2–8)	0.2(0–1)	2.4(0–5)	2(1–3)	—	11.4(4–25)	6.3(1–13)
Macronectes giganteus	CDZ	1.2(0–5)	0.1(0–1)	1.9(0–3)	0.4(0–1)	2.9(0–7)	3(0–6)	1.3(0–4)
	CZ	4(4)	0.6(0–3)	2.6(0–5)	—	1.5(0–2)	0.8(0–3)	0.7(0–1)
Northern Giant Petrel	SAZ	0	0	0	0	—	0	
Macronectes halli	CDZ	0	0.1(0–1)	0	0	0.3(0–3)	0	
	CZ	0	0	0	—	0	0	
Southern Fulmar	SAZ	0	0	0	0	—	0	2.7(1–6)
Fulmarus glacialoides	CDZ	0.1(0–2)	0	0	0.6(0–2)	2.8(1–5)	1.8(0–5)	2(0–4)
	CZ	10(7–15)	0	0	—	9.5(7–10)	2.2(0–6)	3.3(0–6)
Antarctic Petrel	SAZ	0	0	0	0	—	0	0
Thalassoica antarctica	CDZ	0	0	0	0	0	0	1.1(0–3)
	CZ	0	0	0	—	0	0	0
Cape Petrel	SAZ	0.1(0–1)	0	0	0	—	0	11.1(2–41)
Daption capense	CDZ	1.4(0–20)	0.6(0–1)	2.5(0–8)	1.4(0–4)	4.1(0–10)	0.4(0–2)	5.3(1–10)
	CZ	10.7(6–14)	0.8(0–12)	7.4(4–15)	—	11.5(10–12)	5.6(1–12)	5.3(0–13)
Blue Petrel	SAZ	0	0	0	0	—	0	0.2(0–1)
Halobaena caerulea	CDZ	0	0	0	0	0.1(0–1)	0	0.1(0–1)
	CZ	0	0	0	—	0.3(0–1)	0	0
Antarctic Prion	SAZ	0	0	0	0	—	0	0.3(0–2)
Pachyptila desolata	CDZ	0.4(0–7)	0.1(0–2)	0.7(0–3)	0.8(0–4)	0	3.9(0–8)	1.2(0–4)
	CZ	0	0	0	—	0	0	0
White-chinned Petrel	SAZ	0.4(0–2)	0.6(0–1)	0	0	—	0.1(0–1)	2.4(0–4)
Procellaria	CDZ	0.1(0-1)	0.6(0–2)	0	0	1.6(0–2)	0.1(0–1)	0.6(0–2)
aequinoctialis	CZ	0	0	0	—	0	0	0
Great Shearwater	SAZ	0.1(0–1)	0	0	0	—	0	0
Ardenna gravis	CDZ	0	0	0	0	0	0	0
	CZ	0	0	0	—	0	0	0
Sooty Shearwater	SAZ	2.4(0–16)	0	0	0.2(0–1)	—	0	0
Ardenna grisea	CDZ	0	0	0	0.4(0–1)	0	0	0
	CZ	0	0	0	—	0	0	0
Magellanic Diving	SAZ	0	0	0	0	—	0	0.1(0–1)
Petrel *Pelecanoides*	CDZ	0.1(0–2)	0	0	0	0	0	0
magellani	CZ	0	0	0	—	0	0	0
Kerguelen Petrel	SAZ	0	14(1–47)	0	0	—	0	0.1(0–1)
Aphrodroma	CDZ	0	0	0	0	0	0	0.1(0–2)
brevirostris	CZ	0	0	0	—	0.2(0–1)	0	0
White-headed Petrel	SAZ	0	0	0	0	—	0	0
Pterodroma lessonii	CDZ	0	0	0	0	0	0	0
	CZ	0	0.1(0–1)	0	—	0	0	0
Soft-plumaged Petrel	SAZ	0	0	0	0	—	0	0
Pterodroma mollis	CDZ	0.1(0–1)	0	0	0	0	0	0
	CZ	0	0	0	—	0	0	0
Yellow-nosed	SAZ	0	1.2(0–3)	0	0	—	0	0
Albatross *Thalassarche*	CDZ	0	0	0	0	0	0	0
chlororhynchos	CZ	0	0	0	—	0	0	0
Southern Royal	SAZ	0	0.4(0–1)	0.6(0–2)	0	—	1.2(0–3)	1.3(0–3)
Albatross *Diomedea*	CDZ	0	1(0–5)	1.4(0–4)	0	0.8(0–2)	0.1(0–1)	0.2(0–4)
epomophora	CZ	0	0.1(0–1)	0	—	0	0	0

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Species of birds	Region	1998 March	2006 February	2007 March	2009 March	2019 March	2020 February	2020 April
Wandering Albatross *Diomedea exulans*	SAZ	3(0–10)	0	0.8(0–3)	0	—	0.4(0–2)	0
	CDZ	0.8(0–3)	0.2(0–2)	1.1(0–4)	0	0.1(0–1)	0.1(0–1)	0
	CZ	0	0	0	—	0	0	0
Shy Albatross *Thalassarche cauta*	SAZ	0	0	0	0	—	0	0
	CDZ	0	0.1(0–1)	0	0	0	0	0
	CZ	0	0	0	—	0	0	0
Grey-headed Albatross *Thalassarche chrysostoma*	SAZ	0	0	0	1(0–3)	—	0.4(0–2)	2.9(0–12)
	CDZ	0.5(0–2)	0.1(0–1)	0.2(0–2)	0.5(0–3)	0.8(0–2)	0	0.5(0–2)
	CZ	0.3(0–1)	0	0	—	1(1)	0	0
Black-browed Albatross *Thalassarche melanophris*	SAZ	9.3(5–16)	6.8(0–20)	9(4–17)	5.4(1–30)	—	1.8(0–4)	15(2–37)
	CDZ	0.8(0–2)	4.1(0–13)	3.9(0–12)	0.3(0–1)	4.4(0–8)	2.6(0–4)	0.3(0–2)
	CZ	0.3(0–1)	1.5(0–7)	1(0–3)	—	1.3(1–2)	0.8(0–2)	0
Sooty Albatross *Phoebetria fusca*	SAZ	0	0	0	0	—	0	0
	CDZ	0	0.5(0–3)	0	0	0	0	0
	CZ	0	0	0	—	0	0	0
Light-mantled Albatross *Phoebetria palpebrata*	SAZ	0	0	0	0	—	0	0
	CDZ	0	0	0	0	0.1(0–1)	0	0
	CZ	0	0	0	—	0	0	0
Wilson's Storm Petrel *Oceanites oceanicus*	SAZ	1.4(0–6)	1.6(0–5)	2(1–5)	2.3(2–3)	—	4(1–10)	0.3(0–3)
	CDZ	4.1(0–11)	0.6(0–2)	2.3(0–8)	0.5(0–2)	9.9(0–30)	0.4(0–5)	0.2(0–1)
	CZ	6(5–8)	0.5(0–2)	2.6(1–6)	—	0	0.4(0–3)	0
Black-bellied Storm Petrel *Fregetta tropica*	SAZ	0	0.2(0–1)	0	0	—	0	0
	CDZ	1.7(0–11)	0	0	0.3(0–1)	0.1(0–2)	0	0
	CZ	0	0.1(0–1)	0	—	0.2(0–1)	0	0
Emperor Penguin *Aptenodytes forsteri*	SAZ	0	0	0	0	—	0	0
	CDZ	0	0	0	0	0	0	0
	CZ	0	0.1(0–1)	0	—	0	0	0
Adelie Penguin *Pygoscelis adeliae*	SAZ	0	0	0	0	—	0	0
	CDZ	0	0	0	0	0	0	0
	CZ	0	0	0.4(0–1)	—	0	0	0
Chinstrap Penguin *Pygoscelis antarcticus*	SAZ	0	0	0	0	—	0	0
	CDZ	0	0	0	0	0	0	0
	CZ	0	4(0–42)	0	—	0.3(0–2)	0	0
Magellanic Penguin *Spheniscus magellanicus*	SAZ	0	0.8(0–4)	0	8(0–60)	—	0	0
	CDZ	0	0	0	0	0	0	0
	CZ	0	0	0	—	0	0	0
Gentoo Penguin *Pygoscelis papua*	SAZ	0	0	0	0	—	0	0
	CDZ	0	0	0	0	0	0	0
	CZ	0	5.2(0–45)	9.6(3–28)	—	0	2.6(0–12)	0
Imperial Shag *Leucocarbo atriceps*	SAZ	0	0.6(0–1)	1(0–3)	0	—	0	0.9(0–5)
	CDZ	0	0	0	0	0	0	0
	CZ	0	0	0	—	0	0	0
Antarctic Shag *Leucocarbo bransfieldensis*	SAZ	0	0	0	0	—	0	0
	CDZ	0	0	0	0	0	0	0
	CZ	0.3(0–1)	0.1(0–1)	0.4(0–1)	—	0	0.3(0–2)	0
The total number of species	SAZ	8	12	6	10	—	8	13
	CDZ	12	12	8	9	14	9	12
	CZ	9	16	10	—	10	11	6
Number of birds (individuals) per one observation	SAZ	21.6	28.7	15.8	33.1	—	19.5	43.6
	CDZ	11.3	8.1	14	5.3	30.7	12.4	12.9
	CZ	34.9	17.4	28.2	—	26.1	15.6	14

[a] Quantitative data are presented in the form of arithmetic mean (μ), which is the sum of birds of a certain species detected during repeated observations, divided by the number of observations; the parentheses show the minimum and maximum number of birds. Abbreviations: SAZ – Sub-Antarctic Zone; CDZ – central part of Drake Passage (Polar Frontal Zone and Antarctic Zone); CZ – Continental Zone.

TABLE 3
Level of year-on-year similarity of species lists by Sorensen's Index recorded in different years in different Drake Passage zones

SAZ[a]	**1998 March**	**2006 February**	**2007 March**	**2009 March**	**2019 March**	**2020 February**
1998		0.36	0.53	0.42	—	0.59
2006	0.36		0.42	0.52	—	0.48
2007	0.53	0.42		0.36	—	0.71
2009	0.42	0.52	0.36		—	0.55
2019	—	—	—	—		—
2020	0.59	0.48	0.71	0.55	—	
CDZ[a]	**1998**	**2006**	**2007**	**2009**	**2019**	**2020**
1998		0.67	0.70	0.72	0.67	0.76
2006	0.67		0.80	0.54	0.67	0.76
2007	0.70	0.80		0.67	0.61	0.82
2009	0.72	0.54	0.67		0.64	0.63
2019	0.67	0.67	0.61	0.64		0.67
2020	0.76	0.76	0.82	0.63	0.67	
CZ[a]	**1998**	**2006**	**2007**	**2009**	**2019**	**2020**
1998		0.56	0.74	—	0.53	0.80
2006	0.56		0.69	—	0.46	0.67
2007	0.74	0.69		—	0.40	0.86
2009	—	—	—		—	—
2019	0.53	0.46	0.40	—		0.48
2020	0.80	0.67	0.86	—	0.48	

[a] Abbreviations: SAZ – Sub-Antarctic Zone; CDZ – central part of Drake Passage (Polar Frontal Zone and Antarctic Zone); CZ – Continental Zone

components. If various species are "inshore feeders," such as the Magellanic Diving Petrel *Pelecanoides magellani*, Imperial Shag *Leucocarbo atriceps*, and a number of other species, they are absent in waters of the major frontal zones.

Numbers of birds

During the austral summer and autumn, densities were relatively low within waters of the CDZ (Table 2). The arithmetic mean number of birds was M = 12.1 (*lim* = 5.3–21.7). In comparison, the mean number of birds in waters of the SAZ and CZ reached M = 23.7 (*lim* = 15.8–33.1) and M = 24.4 (*lim* = 15.6–34.9), respectively. Thus, the total number of seabirds in waters of the CDZ was two times lower than numbers within waters of the SAZ and CZ (see also Ainley *et al*. 1994, Hunt *et al*. 1994, Force *et al*. 2015). Force *et al*. (2015) noted high mean densities near the SAZ (~55°S), where seabird density was greater than six individuals per km^2, and at CZ (~61°S), where seabird density was greater than four individuals per km^2. In waters between 55.5°S and 60.0°S (the southern part of the Sub-Antarctic, Polar Front, and the Southern Boundary of the Antarctic Circumpolar Current), Force *et al*. (2015) reported an increase in bird density from less than one to greater than two individuals per km^2.

The analysis based on the box and whisker plot confirmed significant differences among the Drake Passage avifauna (Fig. 2). This can be explained by the fact that both pelagic and coastal birds occur off the coast of both South America and Antarctica.

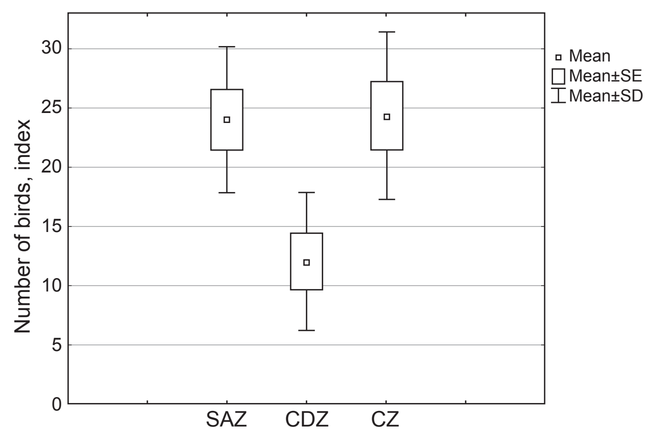

Fig. 2. Box and whisker plot comparing long-term dynamics of the seabird number in different regions of the Drake Passage. Abbreviations: SAZ – Sub-Antarctic Zone, CDZ – central part of Drake Passage (Polar Frontal Zone and Antarctic Zone), CZ – Continental Zone, SE – standard error, SD – standard deviation.

Any avifaunal changes were primarily due to the occurrence of dominant species in the relevant areas of the Drake Passage and their ethological features, i.e., the ability to form large flocks.

Black-browed Albatross *Thalassarche melanophris* and Southern Giant Petrel *Macronectes giganteus* are the dominant species in waters of the SAZ, with the additions of Kerguelen Petrel *Aphrodroma brevirostris* in 2006 and Kelp Gull *Larus dominicanus* in 2009. The dominant seabird species in waters of the CZ were Cape Petrel *Daption capense*, Northern Giant Petrel, with addition of the Gentoo Penguin in 2007. The high numbers of Cape Petrel and Northern Giant Petrel led to a predominance of the Southern Boundary ornithofauna in 1998 and Gentoo Penguin in 2007. The penguins formed flocks of up to 28 individuals. Similar trends in the formation of the dominant complex of seabird species are also characteristic of studies by other scientists conducted in the Drake Passage (Ainley *et al*. 1994, Hunt *et al*. 1994, Ribic *et al*. 2011, Force *et al*. 2015). For example, according to Force and colleagues, Black-browed Albatross was one of the dominant species of the SAZ (27.96–48.34 individuals/km^2), and the Cape Petrel was one of the dominant species of the CZ (6.04–10.91 individuals/km^2). Evidently, there has been significant variation in the dominant complexes of seabird species in the SAZ. It appears that the dominant species within these areas plays a crucial role in shaping the number of seabirds and the structure of their groups.

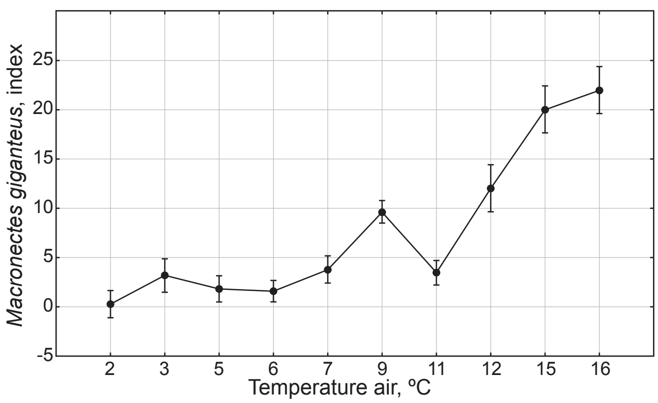

Fig. 3. Relationship between air temperature and the number of Southern Giant Petrels *Macronectes giganteus*; F (9.71) = 64.592, P < 0.001. Temperature data retrieved from www.britannica.com on 20 July 1998.

Seasonal dynamics

In 2020, we made observations of seabird species present in the Drake Passage in both summer (February) and autumn (April). In summer, 16 seabird species were observed in the Drake Passage (Table 2). Within waters of the SAZ, there were eight seabird species, and in waters of the CDZ and CZ there were nine species. Species richness was graded, increasing in richness from the coast of South America to the coast of Antarctica. This is because increasing air and water temperatures (and decreasing sea ice) in summer causes many species of birds to shift closer to the Antarctic coast to take advantage of enhanced prey availability (Ainley *et al*. 1994, Meyer *et al*. 2020). In autumn, 17 species of seabirds were observed in the Drake Passage, with 13 in the SAZ, 12 in the CDZ, and six in the CZ. Accordingly, the trend in autumn was opposite to that of summer, i.e., there was a marked increase in species richness from the coast of Antarctica to the coast of South America. This can be explained by the worsening weather conditions during this period and the migration of birds to warmer regions of the planet.

Our seasonal analysis of avifaunal composition also confirmed that the CDZ group remained the most stable across seasons. Birds begin to migrate northward to waters off the coast of South America with the onset of autumn. Bird numbers increased more than two-fold (from 19.5 to 43.6 individuals) between summer and autumn only within coastal South American waters, but in other zones, numbers remained stable. The same changes were evident within certain species: Cape Petrels (from 0 to 11.1 individuals) and Black-browed Albatross (from 1.8 to 15 individuals). In contrast, the number of Southern Giant Petrels *Macronectes giganteus* decreased (from 11.4 to 6.3 individuals).

Our statistical analysis using ANOVA revealed that wind speed, atmospheric pressure, and air temperature were the most important determinants of avifaunal composition. Air temperature was linked to seabird occurrence only for the Southern Giant Petrel and Wilson's Storm Petrel *Oceanites oceanicus* (Figs. 3, 4).

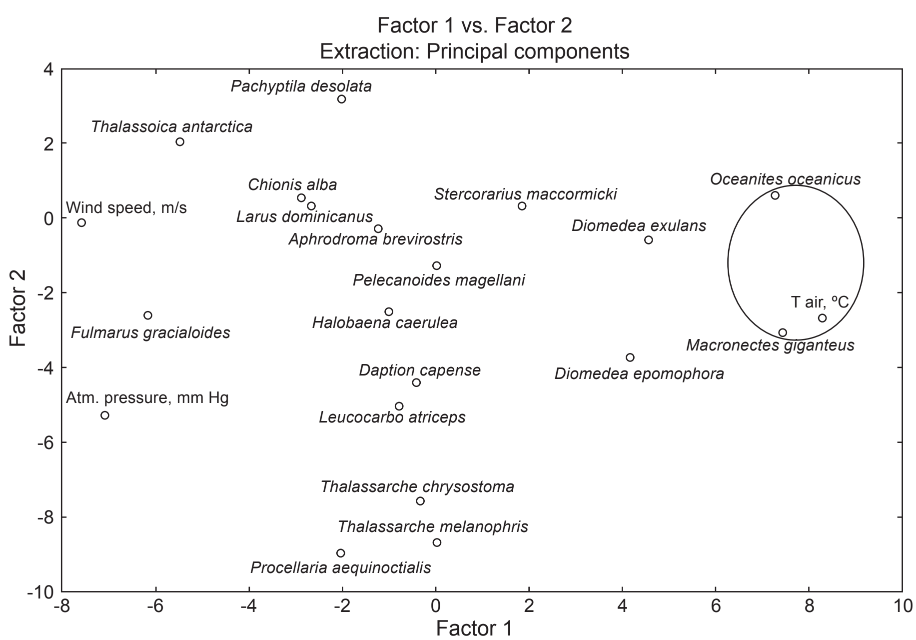

Fig. 4. Multifactor analysis of the influence of habitat factors on different seabird species in the Drake Passage.

CONCLUSION

Thirty-eight to fifty species of seabirds are now known to occur in the avifauna of the Drake Passage, depending on the temporal breadth of the data set. Species composition was highly similar in the SAZ compared to other zones (S = 0.67 and 0.58), and low similarity occurred between the CDZ and CZ (S = 0.50). The central part of the Drake Passage exhibits characteristics of a giant ecotone between two complex ecosystems, those of South America and Antarctica. This is indicated by the fact that all zones of the Drake Passage were characterized by only 10 of the total 38 species of birds. The number of birds in summer groups in the CDZ was lowest across all years of study. The dominant species complexes in the SAZ and CZ were completely different, and polydominance was inherent in the CDZ. Although seabird species composition was similar between summer and autumn, there was seasonal variation in the dominant species. Air temperature also significantly affected the occurrence of at least two species of seabirds—the Southern Giant Petrel and Wilson's Storm Petrel.

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