

1 **A review of methods used to analyse albatross diets – assessing priorities across their range**

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36 **Abstract**

37 Many seabird populations are threatened by interactions with commercial fisheries, and climate
38 change. Understanding their prey requirements and dietary flexibility in this context is important for
39 effective conservation and management. However, changes in the methods used to assess diet, as
40 well as the spatial and temporal coverage of monitoring schemes, may reduce our ability to detect
41 and monitor these marine threats. To help assess conservation priorities linked to diet, we carried
42 out a systematic review of 109 albatross diet papers published between 1950 and 2016, which
43 corresponded to 296 studies when stratified by sampling year, breeding site and species. We
44 assessed the methods used, changes over time, and spatial and temporal sampling coverage by
45 species and island group. Most albatross studies have focused on chick-rearing, and diet during
46 other breeding phases is comparatively poorly-known. Furthermore, chicks are more commonly
47 sampled than adults and very rarely immature birds, all of which may differ in diet composition.
48 There was a pronounced shift over time in the preferred method of characterising diet, from the
49 morphological examination of prey remains to stable isotope analysis (SIA) of tissue. This shift has
50 reduced the volume of detailed taxonomic information available from morphological studies. This
51 difference in resolution hinders the ability to detect changes in prey species, with implications for
52 management of threatened albatrosses and for monitoring broader changes in marine ecosystems.
53 In a knowledge gap analysis for important breeding colonies (with >5% of global population), we
54 identified key sites where existing monitoring has provided a foundation for robust longitudinal diet
55 studies. Maintaining and augmenting these long-term research programmes will enable analyses of
56 the impacts of changing climate and fishing practices on seabird populations, and facilitate the
57 timely identification and implementation of management options.

58 **Introduction**

59 Two of the greatest marine threats facing seabird populations are interactions with commercial
60 fisheries and global environmental change (Croxall et al., 2002; Chambers et al., 2011). Commercial
61 fisheries often overlap spatially and temporally with seabird foraging areas, and incidental mortality
62 (bycatch) may occur when birds are attracted to vessels to feed on discards or bait (Brothers et al.,
63 1999). These interactions can be major drivers of population change, and bycatch has been linked to
64 substantial declines in some seabird species (Weimerskirch and Jouventin, 1987; Nel et al., 2002).

65

66 Environmental change, primarily driven by anthropogenic carbon emissions, are causing oceans to
67 warm and become more acidic (Feely et al., 2009). These changes affect food-webs and drive spatial
68 and temporal changes in prey abundance and availability, with some prey species predicted to move
69 to cooler waters or alter breeding phenology (Constable, 2014). Top predators depend on prey that
70 may be patchily distributed or show seasonal variation. As such, ocean warming may negatively
71 impact predator breeding success if they have insufficient plasticity to adapt to change (Grémillet
72 and Boulinier, 2009). Changes in prey availability or distribution can cause prey switching, increase
73 foraging duration, or alter breeding phenology to match seasonal peaks in prey abundance
74 (Gjerdrum et al., 2003; Le Bohec et al., 2008; Xavier et al., 2013). Environmental change may also
75 cause changes to fisheries, including their target species (Barbraud et al., 2012).

76

77 Seabirds are highly susceptible to changes in marine ecosystems due to their high trophic position
78 and the predominantly bottom-up control of most food webs (Frederiksen et al., 2006). Changes in
79 prey availability can influence a variety of seabird demographic parameters including breeding
80 success, recruitment and survival. Monitoring of these top predators is therefore important not only
81 for their conservation and management, but also provides indicators of the status of the broader
82 marine ecosystem (Cairns, 1987). Collection of dietary data from top predators is an important
83 component of monitoring strategies for many management bodies. For example, in the Southern

84 Ocean, the Commission for the Conservation of Marine Living Resources (CCAMLR) has an Ecosystem
85 Monitoring Program (CEMP) with the principal objective of determining the resource requirements
86 of key top predators (e.g. Adélie penguins (*Pygoscelis adeliae*) and black-browed albatross
87 (*Thalassarche melanophris*)) (SC-CCAMLR, 1997). Similarly, the Southern Ocean Observing System
88 (SOOS) was established to monitor changes in physical and biochemical properties of ocean
89 variables in relation to climate change, including monitoring of albatrosses and other land based
90 predators (Rintoul et al., 2012).

91

92 Different types of dietary analysis provide alternative datasets for assessing environmental and
93 fisheries-related changes in marine systems. Seabird diet studies fall into two main categories: those
94 employing morphological analysis to identify remains of prey items from physical attributes, and
95 those using biochemical analyses of tissue samples. Morphological analyses can provide high-level
96 taxonomic identification of prey items, including size estimates. Material for this can be obtained
97 from stomach contents of dead birds by dissection, from live birds by spontaneous regurgitation or
98 stomach lavage, or from pellets (which include indigestible prey remains) or remains of food
99 dropped in the colony (Barrett et al., 2007). Analysis of pellets (also termed boluses) identifies only
100 prey which have indigestible hard parts, primarily cephalopod beaks and fish otoliths, allowing
101 detailed information on species and size class of specific dietary components only (Xavier et al.,
102 2005). Biochemical methods primarily include stable isotope analysis and fatty acids; with
103 techniques such as DNA-based dietary analysis and compound-specific stable isotope in
104 development (Pompanon et al., 2012; Bradley et al., 2014). Stable isotope analysis (SIA) is the main
105 biochemical method used in seabirds and measures ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ (occasionally
106 $^{34}\text{S}/^{32}\text{S}$) in feathers, blood or other tissues from the target animal, which reflects those in their prey.
107 These measurements integrate the isotopic composition of food consumed during tissue formation,
108 allowing comparisons of habitat use based on environmental gradients in SI ratios, or of trophic
109 level, over periods of days or weeks (Phillips et al., 2009; Cherel et al., 2013). Fatty acid analysis

110 identifies the fatty acid signatures within the adipose tissue of predators and provides information
111 on individual prey groups and species (Budge et al., 2006). Morphological and biochemical analysis
112 convey complementary diet information. Morphological studies identify prey ingested over a short
113 timescale to a high level of taxonomic resolution, which is useful for studying prey selection or
114 consumption of fishery discards. SIA and fatty analysis studies are less labour intensive and provide
115 dietary information derived from prey consumed over a long period of time, which makes them
116 suitable for studying very broad dietary differences at a population scale (Karnovsky et al., 2012).

117

118 Albatrosses are one of the most threatened seabird groups, with 16 of 22 species currently on the
119 International Union for Conservation of Nature (IUCN) Global Red List and the other six species
120 classified as Near-threatened (IUCN, 2015). Current conservation efforts, coordinated through
121 bodies such as the Agreement for the Conservation of Albatross and Petrels (ACAP) and Birdlife
122 International, are focused on mitigation of known threats to albatross populations, which include
123 fisheries and climate change. Albatross feed on fish, cephalopods, and, in some species, crustaceans
124 and carrion (Cherel and Klages, 1998). This paper reviews the methods used to-date to investigate
125 albatross diet and summarises the spatial, taxonomic and temporal coverage of existing studies, with
126 the aim of identifying gaps in knowledge. Using this threatened group as a case study for other
127 seabirds, we develop a monitoring framework that should allow the detection of dietary responses
128 to changes in the wider environment, including fishing practices, with recommendations for future
129 research and management.

130

131 **Methods**

132 We conducted a literature search in February 2016 using Web of Science, Scopus and Google
133 Scholar. Search terms were 'albatross' combined with: 'prey', 'food', 'diet', 'stomach', 'bolus',
134 'isotope', or 'fatty acid' in any field. Articles were included if they were published in a peer-reviewed
135 journal from 1950 onwards and reported empirical albatross dietary data. Articles were excluded if

136 the title and abstract were not related to albatross or diet analysis, or were based on samples
137 already described in another article. Reference lists of articles, including reviews identified in the
138 literature search, were checked for additional studies.

139

140 *Dietary Database*

141 We extracted the data from each paper for entry into our database as follows: 1) albatross species
142 studied, 2) year of the study, 3) breeding site (island/peninsula), 4) breeding population (island
143 group), 5) stage in annual cycle, 6) sample type, 7) methodology (morphological or biochemical), 8)
144 age class, and 9) sample size (see table 1 for definitions). A study was defined as that in which diet
145 was analysed during a specific breeding or non-breeding season for a species at a site. For example if
146 a paper reported on samples collected from two species over three seasons at one colony, that was
147 considered as six studies. For each study, the conservation status according to the IUCN Red List
148 (IUCN, 2015) of each species was included and the approximate population size at that breeding site
149 was derived from published papers, ACAP species assessments
150 (<http://www.acap.aq/en/resources/acap-species2>) and the Birdlife International online database
151 (<http://www.birdlife.org/datazone/species/search>).

152

153 *Synthesis*

154 We reviewed the dataset for spatial and taxonomic gaps in diet sampling, focussing on breeding sites
155 (an individual island or peninsula) that are known to hold >5% of the global population (ACAP, 2015),
156 hereafter termed “IBS” (Important Breeding Sites), and for breeding populations (island groups or
157 mainland areas) that held >5% of the breeding population, hereafter termed “IBPs” (Important
158 Breeding Populations). Key dietary monitoring sites (KDMS) for each species were identified to
159 enable ongoing monitoring for the detection of changes over time. Sites were selected where there
160 had been full taxonomic coverage of prey in morphological studies of at least two sets of diet
161 samples.

162

163 **Results**

164 *Search results*

165 Of the 828 papers identified during the literature search, 109 quantified albatross diet in sufficient
166 detail to meet the selection criteria. Of these, 18 papers reported on samples described in more
167 detail elsewhere, therefore the final database included 91 original papers (Supplementary Table 1).
168 When stratified by sampling year, breeding site and species, these 85 papers reported on 306 diet
169 studies. Ten were excluded from subsequent analysis as they involved ≤ 3 samples. One study
170 conducted at sea was included even though the sample size was low, because it was the only study
171 for that species. These samples were pooled together as one study (7 samples over 6 years). The 296
172 studies in the final synthesis were conducted between the late 1940s and 2012 and published
173 between 1950 and 2016.

174

175 *Dietary Analysis Techniques*

176 Overall, 65.9% (n=195) of studies used morphological techniques to identify prey, 33.1% used
177 biochemical techniques (n=98), and three studies (1.0%) involved both techniques. Specifically, the
178 studies were: morphological analyses of stomach contents obtained as regurgitates (45.6%), from
179 dead birds (6.1%), by stomach flushing/lavage (3.4%) or using an unspecified method (2.7%); pellets
180 collected from around nest sites, usually regurgitated by chicks shortly before fledging (17.6%), and,
181 biochemical analyses either of stable isotope ratios (34.1%) or of fatty acids (0.3%). The majority of
182 all studies used one method; however, 9.1% of studies (n=27) used a combination, mostly
183 morphological analyses of regurgitates in combination with either pellets (n=12), stomach contents
184 of dead birds (n=5) or stomach flushing (n=5).

185

186 *Temporal span*

187 The use of morphological diet studies peaked in the 1970s with an average of 7.0 studies per year.
188 By the 2000s, the number of studies reduced substantially to an average of 1.3 per year from 2001-
189 2012. The first biochemical study of albatross samples using SIA was published in 1997 (on samples
190 collected in 1991), and the first (only) study involving fatty acids was published in 2010 (on samples
191 collected in 2006); the use of SI studies remains high, with an average of 8.8 per year from 2001-
192 2012 (Fig. 1).

193

194 Most studies collected samples during chick-rearing (67.9%), some during the non-breeding period
195 (23.1 %) and more rarely, during incubation (1.0 %) and brood guard (2.2%). In 5.7% of studies, the
196 breeding stage was not specified (Fig. 2). Considering all breeding stages, samples were obtained
197 from adults (37.1%), chicks (33.6%), juveniles (0.6%) or multiple age classes (14.9%). The majority of
198 combined studies comprised adults and chicks (13%), four studies of adults and juveniles (1.6%), and
199 two of adults, chicks and juveniles (0.6%). The ages of birds sampled were un-specified in 14.0% of
200 studies (Fig. 2). Biochemical techniques (almost exclusively SIA) were used more often in adults
201 (77.4%) than chicks (21.5%), and rarely in juveniles (2.9%), whereas morphological techniques were
202 more frequent for chicks (58.2%) than adults (38.9%) and again, rarely in juveniles (2.3%)(Fig. 2).
203 Samples from both adults and chicks were collected for the same time period in 42 studies;
204 however, only seven studies compared results from the two age classes.

205

206 *Species representation*

207 The diet of all 22 currently recognised albatross species has been studied on at least one occasion
208 (Table 2). However, morphological data on prey are entirely lacking for Amsterdam (*Diomedea*
209 *amsterdamensis*), Chatham (*Thalassarche eremita*), Salvin's (*T. salvini*), and white-capped (*T. steadi*)
210 albatrosses, and are limited for short-tailed albatross (*Phoebastria albatrus*) (only 7 samples over 6
211 years) and Tristan albatross (*D. Dabbenena* -pellets only). Of the 18 species with morphological diet
212 data available, only in six species were these samples collected within the last 10 years (Table 2).

213

214 *Spatial coverage*

215 Diet analyses have been carried-out at 38 breeding locations, corresponding to 65 separate albatross
216 species-site combinations (Fig. 3). However, many of these studies were at breeding sites that held
217 relatively few birds (Supplementary Table 2). There were 67 IBS for which we are able to quantify
218 sampling coverage. A further three island groups are estimated to hold >5% of the global population
219 of light-mantled albatross (*Phoebastria palpebrata*), but lack reliable counts for the individual islands.
220 Overall, dietary studies have been carried out at 58.2% of IBS (n=39). These include morphological
221 studies at 50.7% of sites (n=34), although only 8.9% (n=6) in the last ten years, and biochemical
222 studies (mostly SIA) at 37.3% of sites (n=25), all but two in the last ten years. There has been at least
223 one diet study at all of the IBS of nine species, less than half the IBS of four species, and at neither of
224 the two IBS of one species (short-tailed albatross) (Table 2). Including those for light-mantled
225 albatross (see above), there are 49 important albatross breeding populations (island groups with
226 separate species-site combinations that hold >5% of the population). There has been at least one
227 diet study on 91.8% of these important breeding populations (n=45); 75.5% have had morphological
228 studies (n=37) and 61.2% have had biochemical studies (n=30).

229

230 There have been two full morphological studies of diet for 13 species across 16 sites (28 species/site
231 combinations), and more than two such studies for 8 species across 9 sites (16 species/site
232 combinations), only a minority of which (for four species across five breeding sites; 9 species/site
233 combinations) included at least two sets of samples collected in the last 35 years. These sites are
234 proposed as key dietary monitoring sites (Table 3, Fig. 3).

235

236 **Discussion**

237 ***Species, spatial and temporal dietary information gaps***

238 Many dietary studies of albatrosses have been carried out over the last 40 years, but major gaps still
239 exist in terms of taxonomic, spatial and temporal coverage. The diets of five albatross species have
240 never been studied using morphological methods, or the methods applied provided data with low
241 taxonomic resolution. In addition, only seven samples have been collected over six years from the
242 short-tailed albatross. There are no data on the prey of the critically endangered Amsterdam
243 albatross, and although this gap is recognised in the recovery plan for this species, sampling of
244 stomach contents by induced regurgitation or stomach lavage is currently considered too invasive
245 (Delord et al., 2011). Other species with no prey information breed in remote locations without
246 permanent research bases and are difficult to access for logistical or political reasons. This includes
247 the Salvin's and white-capped albatrosses breeding on the Bounty and Disappointment islands
248 respectively, Chatham albatross on the privately-owned Pyramid Rock (Robertson et al., 2003), and
249 short-tailed albatross on volcanically-active Torishima Island and the disputed Minami-kojima islands
250 (Supplementary Table 3).

251

252 The majority of published studies are restricted to the chick-rearing period, largely because chick
253 regurgitations can be collected more easily, less invasively and with less impact than those of adults
254 (Phillips 2006). This has resulted in a major bias in our dietary knowledge towards a single age class
255 and breeding stage. The diet and distribution of adults, and their energy requirements, are known to
256 change with breeding stage (Prince et al., 1994; Bevan et al., 1995). In some species, the availability
257 of specific prey resources at certain times may be critical for successful breeding (Arata and Xavier,
258 2003), and extended foraging trip durations in poor food years can lead to reduced breeding success
259 (Fernandez et al., 2001). Only two studies have investigated diet during incubation, and eight during
260 brood guard, yet in one of the few comparisons between breeding stages, there was a clear seasonal
261 change in prey species composition (Hedd and Gales, 2001). Breeding success, and the decision
262 whether or not to breed by albatrosses, have been linked to environmental processes, with potential
263 carryover effects between the breeding and non-breeding seasons (Cuthbert et al., 2003; Rolland et

264 al., 2010). Long-lived species such as albatrosses are expected to prioritise their own survival over
265 that of their offspring when resources are limited, and hence adults that experience poor foraging
266 success are likely to abandon breeding rather than jeopardise their future reproductive potential
267 (Williams, 1966). Hence, improved knowledge of how fluctuations in availability of particular prey
268 influence the distribution, breeding success and survival of albatrosses is required to better
269 understand the impacts of ongoing and widespread changes in the marine environment.

270

271 The last diet review for albatrosses, published >15 years ago, highlighted the paucity of diet data for
272 the non-breeding period (Cherel and Klages, 1998). Since then, SIA has greatly increased our
273 knowledge of trophic level and habitat use during this period, with data now published for 18
274 species (Phillips et al., 2009; Cherel et al., 2013; Jaeger et al., 2013). Fisheries activity that poses a
275 threat for survival occurs throughout the year, so there remains a conservation imperative for
276 detailed dietary information during the non-breeding season, particularly morphological studies
277 which provide the most reliable indication of reliance on discards. The difficulty is that most
278 albatrosses do not return to land during the non-breeding period, and although samples can be
279 obtained from birds obtained as fisheries bycatch (Gould et al., 1997; Colabuono and Vooren, 2007),
280 these will be biased to ship-following individuals. An alternative is to obtain samples from adults
281 that have returned to colonies (Alvito et al., 2015), and potentially use SI ratios in feathers, natural
282 prey and discards, to distinguish the fisheries contribution to the diet using stable isotope mixing
283 models (Granadeiro et al., 2013) (Bugoni et al., 2010;). Understanding the diet and distribution of
284 juveniles is also important, as survival is at its lowest between fledging and returning to breed
285 (Terauds et al., 2006; Alderman et al., 2010). To date, only one study has presented a morphological
286 diet breakdown for juveniles (Colabuono and Vooren, 2007), and although samples from juveniles
287 were collected in five other studies, these were pooled with other age classes (West and Imber,
288 1986). Comparison of juvenile and adult foraging ecology in wandering albatrosses was recently
289 carried out using SIA (Jaeger et al., 2014). Juveniles and non-breeding birds fed in sub-tropical

290 waters, similar to breeding females, with males switching to colder waters during breeding. This
291 study provides an important insight into juvenile behaviour and the different life history strategies of
292 different age, sex and breeding classes that lead to diet variation.

293

294 Our analysis of the spatial and taxonomic coverage of dietary studies identified 28 IBS that are data-
295 deficient. For many of these important colonies, there is no information on diet composition,
296 including the largest breeding populations of grey-headed, shy, Buller's and northern royal
297 albatrosses. In some cases, there are data for another breeding site in close proximity. For example,
298 diets of grey-headed albatross at the IBS at the Paryadin Peninsula (South Georgia) and Isla
299 Bartolome (Islas Diego Ramirez) are unknown, but there have been studies at Bird Island and Isla
300 Gonzalo, respectively, which are within the same island groups. It is difficult to quantify the spatial
301 scale at which diet variation occurs, given many confounding effects such as breeding stage, season,
302 age, sex and resource availability. Diet can differ considerably between islands within relatively close
303 proximity (Thompson, 1992); thus, any breeding site or island group that holds a substantial
304 proportion of the global population is potentially an important target for a diet study, as is any site
305 considered to be a conservation or management priority. By using tracking studies and SIA, it would
306 be useful to identify IBS where birds have substantially different foraging distributions or feed at
307 distinct trophic levels. The former could be distinguished using the Seabird Tracking Database of
308 Birdlife International (<http://www.seabirdtracking.org/index.php>), and the latter using existing SI
309 data.

310

311 ***Diet analyses***

312 Each method of dietary analysis has advantages and disadvantages (for a reviews see (Barrett et al.,
313 2007; Karnovsky et al., 2012). There is no single method that identifies all the ages, size classes and
314 species of prey that an animal ingests. Some seabird studies have tried to achieve this by
315 incorporating a variety of methods and models (e.g. Chiaradia et al., 2014), yet it remains difficult to

316 characterise the true diet of top predators. The relative importance of certain prey in stomach
317 contents can be biased by differential rates of digestion, leading to under-estimation of soft-bodied
318 prey and over-representation of prey with hard parts, particularly squid, that tend to be retained for
319 long periods (Furness et al., 1984). More recent studies tend to analyse fresh and old squid beaks
320 separately to compare species composition over the short- or long-term (Cherel et al., 2000);
321 however, underestimation of soft-bodied prey is still an issue. Pellets only include prey that have
322 indigestible hard parts, primarily squid (Xavier et al., 2005), and large beaks (from large species and
323 individuals) are often over-represented, as small beaks tend to degrade (Brooke and Klages, 1986).
324 Stable isotope and fatty acid analysis does not suffer from the same issue of prey retention and
325 provides a less biased view of prey components. Rodhouse et al. (2013), reviewed a number of
326 studies where SIA and fatty acids have highlighted the importance of fish prey for predators that had
327 been assumed to eat mainly squid due to the retention of beaks in stomachs. Although these
328 biochemical techniques avoid biases from prey retention, taxonomic resolution is typically very poor
329 because SI ratios and lipid information for many prey species are unavailable, or overlapping (Inger
330 and Bearhop, 2008).

331

332 DNA-based approaches to diet analysis and compound-specific SIA are new techniques that may
333 allow some of the knowledge gaps identified in this review to be filled, potentially overcoming some
334 of the limitations of stomach contents analysis. DNA-based dietary analysis is a non-invasive means
335 of identifying individual prey species in the diet by detecting the genetic sequences in the predator's
336 faeces (Pompanon et al., 2012; Bowser et al., 2013; Jarman et al., 2013). This method can be used
337 during all breeding and life-history stages when scats can be collected (Bowser et al., 2013). As no
338 handling of birds is required, it provides an ideal method of assessing the diet of sensitive species.
339 The limitations are that prey age, size class and mass cannot be assessed. Scats must also be
340 available, so the approach is not feasible for determining diet during the non-breeding period for
341 species that remain far from land. Compound-specific SIA methods have the potential to provide

342 more detailed taxonomic identifications than standard SIA, but these methods are new and their
343 utility is still being explored (Bradley et al., 2014).

344

345 To determine the most suitable dietary method is a balance between method limitations,
346 disturbance and the information required (Table 4). To identify prey specific overlaps between
347 albatrosses and fisheries, analysis of stomach contents is ideal as the majority of target prey (fish
348 and squid) have identifiable hard-parts (Arata and Xavier, 2003). However fish prey can still be
349 difficult to identify when no hard parts remain (e.g. Ridoux, 1994). In contrast, SIA is also very useful
350 for identifying reliance on fisheries waste, particularly where discards from demersal or pelagic
351 fisheries differ isotopically from natural prey (Bugoni et al., 2010). When identifying changes in diet
352 over time due to environmental conditions, SIA and fatty acids can again highlight broad trophic
353 changes, but would ideally be complemented with information on all prey components. Although
354 pellets and stomach contents can identify changes in cephalopod and some other prey components,
355 no dietary method currently used for albatrosses can reliably quantify the contribution of soft-
356 bodied prey. This information will be important as the abundance of gelatinous prey is likely to
357 increase with warming oceans (Attrill et al., 2007). DNA-based dietary analysis may be the ideal
358 method to complement SIA in the future to enable detection of soft-bodied prey (McInnes et al.,
359 2016); however, hard-part analysis will be required if changes in prey size classes are to be
360 investigated

361

362 ***A synoptic strategy for albatross dietary studies***

363 This review provides a framework for prioritising global monitoring of albatross diets. To enable the
364 detection of prey changes resulting from climate change or fisheries practices, two key
365 improvements are necessary: 1) an increase in the collection of taxonomically-detailed prey
366 information and 2) maintenance and expansion of the network of long-term monitoring sites.

367

368 *Increase the collection of prey information*

369 Comprehensive morphological studies are either entirely lacking, or have not been conducted in the
370 last 35 years, for one third of albatross species, including three Critically Endangered species (Table
371 2). Furthermore, in the last decade, there has been a morphological study of the diet of only six
372 species. This general trend away from morphological techniques may reflect the more labour-
373 intensive nature of identifying individual prey and lack of sufficient taxonomic skills, or concerns
374 about biases associated with greater retention of hard parts and slower digestion of soft-bodied
375 prey (Barrett et al., 2007). The number of diet studies involving stomach contents has also declined,
376 possibly because of the perceived detrimental effects on chick survival. Although sampling in this
377 way had minimal impact on chick condition or breeding success (Phillips, 2006), the associated
378 disturbance and loss of a meal may be discouraging its wider use. Indeed, the management plans for
379 several albatross species state specifically that diet information is lacking due to the invasive nature
380 of current techniques (Delord et al., 2011; DSEWPC, 2011).

381

382 The observed shift away from morphological analysis of diet has reduced our ability to detect all but
383 major prey shifts, and yet has occurred against a background of major perturbations in marine
384 ecosystems, driven by a range of climate-related processes (Constable, 2014). These will continue to
385 influence the availability of food resources for albatrosses and their prey (Hays et al., 2005).

386 Environmental changes also alter the operation of fisheries, either by a decline or shift in distribution
387 of target stocks. Monitoring the impacts of these changes on albatross diet would ideally involve
388 complementary approaches: SIA to identify broad shifts in diet, and morphological analyses to
389 provide taxonomic detail to address more targeted questions, such as the effects of changes in
390 distribution or abundance of particular prey, or proposed changes in fisheries practices. In time, it is
391 hoped the development of new methods e.g. DNA-based dietary analysis, may help fill this gap in
392 taxonomic resolution, but in the meantime, resumed collection of morphological data is important
393 to detect any prey changes.

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418

Maintain and expand the network of long-term monitoring sites

Ongoing monitoring of key sites where there are existing time-series of robust diet data is imperative for detecting dietary shifts and identifying links between prey abundance and albatross demography. Long-term diet data is invaluable for enabling management and protection of species and their prey resources, and for observing changes to the wider marine system. The CCAMLR Ecosystem Monitoring Program (CEMP) (SC-CCAMLR, 1997) uses top predators such as the black-browed albatross as indicator species to monitor change in the marine environment, particularly in relation to competition with the fishery for Antarctic krill (*Euphausia superba*), and requires predator diet information in order to estimate consumption. The ongoing CEMP diet sampling programme of black-browed albatross at Bird Island (South Georgia) has provided one of the longest diet time-series for any site (>15 years; Supplementary Table 3). However, there are very few long-term dietary projects for albatrosses; only at five sites are there more than two full dietary studies published in the last 35 years. This makes it difficult to detect diet shifts, and even harder to attribute these to fishing activity or other changes in the environment. For these reasons, the implementation of a wider diet monitoring framework for albatrosses should be encouraged by international agreements such as ACAP and CCAMLR, or NGOs, including BirdLife International, and incorporated into national plans of action and recovery plans.

The proposed KDMS are a recommended starting point for establishing long-term monitoring sites as they allow comparison with existing dietary data. However, they should not be interpreted as the only sites, as there may well be others that are biogeographic, conservation or other management priorities. This network of sites identified here should be refined in the future, by using fisheries, environmental and tracking data to determine the pressures that affect different IBs and IBPs.

419 Further linkages between diet studies and other research avenues should be strengthened. Several
420 studies have linked diet composition to foraging location using tracking data (e.g.Xavier et al., 2003),
421 and to breeding success (e.g. Arata et al., 2004). Further work integrating longitudinal tracking and
422 diet studies would allow assessment of changes in important foraging areas or food resources, and
423 how this may affect breeding success. This will be important to identify projected environmental
424 changes and how species may adapt under different climate change scenarios or fishing impacts.
425 Furthermore, by linking tracking to diet, we can continue to identify geographic overlaps with
426 fisheries (Xavier et al., 2004) as well as likely location of prey (Xavier et al., 2006)

427

428 An open-access database of prey and SI information would assist in establishing distributions of prey
429 species and monitoring spatial and temporal changes. A centralised approach would ensure
430 uniformity in data collection and reporting, and enable collaboration and coordination between
431 management authorities. One such database has been established for the Southern Ocean
432 (Raymond et al. 2011) and at the time of writing, the Expert Group on Birds and Marine Mammals
433 within the Scientific Committee on Antarctic Research, are extending this database into a Southern
434 Ocean community resource with expanded coverage of SI and other diet data (including the data
435 compiled for the current study). Companion efforts would, ideally, broaden the database coverage
436 to include albatross breeding sites elsewhere. An updated dietary database would provide the
437 foundation for a thorough synthesis of prey and SI data, including a meta-analysis identifying the
438 important prey components for each species, and spatial and temporal variation.

439

440 **Conclusion**

441 On the basis of the gaps and trends identified in this review, we have outlined key recommendations
442 for future dietary work (Table 5). These are made specifically in the context of albatross
443 conservation management; however, they are likely to be applicable across many other seabird
444 groups. Our work highlights the pressing need for dietary studies both of highly threatened species

445 and major breeding sites in general. Taxonomic, spatial and temporal gaps exist in baseline sampling
446 coverage, particularly with regard to poorly-known stages of the breeding season, the non-breeding
447 period, juveniles and immature birds. The development of new non-invasive techniques with high
448 taxonomic resolution may assist in this process, and will be particularly useful for sensitive species
449 where disturbance is a major concern. Collecting information on seabird dietary requirements is
450 fundamental to enable monitoring of their prey, and should be designed to detect diet shifts over
451 short and long time-scales. Understanding how these prey changes affect breeding and non-
452 breeding birds will be crucial for gauging the threat these changing processes pose to seabird
453 populations. Ongoing diet monitoring across a network of key sites should be seen as a high priority
454 for conservation and management bodies, as should the continued collection of prey information to
455 complement SIA and enable detection of fine-scale differences in abundance and utilisation of key
456 individual taxa. The key findings, recommendations and proposed actions identified in this paper
457 (Table 5), will hopefully enable the detection and attribution of the impacts of climate or fisheries
458 processes on albatross populations and facilitate the timely implementation of responsive
459 management.

460

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464

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633

634 **Table 1:** Parameters used to categorise diet studies included within the database.

Category	Definition
Scientific name	Based on the 22 species recognised currently by ACAP, BirdLife International and IUCN.
Common name	
Analysis year	The nonbreeding or breeding period that the samples represent. Austral summers were categorised according to the year in which the chicks fledge (e.g. the 2002/2003 season was recorded as 2003). Feathers collected from adults at colonies were assumed to represent the preceding nonbreeding period.
Breeding site	An island with breeding pairs, or in a few cases, a peninsula/clearly disjunct piece of land on the same island.
Breeding population	An island group with pairs breeding, may contain numerous breeding sites
Stage (in annual cycle)	incubation, brood-guard, chick-rearing or nonbreeding period
Sample type	stomach contents (regurgitation, stomach lavage, whole stomach), pellet/bolus/cast, stable isotope (SIA), fatty acid (FAA)
Methodology	morphological, biochemical
Age class	adult, chick or juvenile
Sample size	number of samples analysed (studies with $n \leq 3$ were excluded from analysis). A sample was defined as either a bolus, blood collection, feather or stomach content taken from an individual bird.
IUCN Status	IUCN conservation status, February 2016.
Population size	number of pairs at the breeding site (ACAP 2015).
Reference	

635

636 **Table 2:** Gap analysis of dietary studies using morphological and biochemical approaches for each albatross species. IBS - important breeding sites (an island
637 or peninsula with >5% of the population), IBP - important breeding populations (an island group with >5% of the population). The latest study for each
638 technique is the year the study was carried out.

Species	IUCN Status ^a	Latest morphological Study (year)	No. Morphological studies	Latest biochemical study (year)	No. Biochemical studies	No. IBS	No. IBS with Morphological data	No. IBS with Biochemical data	% IBS with Morphological data	% IBS with Biochemical data	No. IBP	No. IBP with Morphological data	No. IBP with Biochemical data	% IBP with Morphological data	% IBP with Biochemical data
Amsterdam (<i>Diomedea amsterdamensis</i>)	CR		0	2007	2	1	0	1	0	100	1	0	1	0	100
Antipodean (<i>Diomedea antipodensis</i>)	VU	2001	4	2004	2	2	2	2	100	100	2	2	2	100	100
Atlantic yellow-nosed (<i>Thalassarche chlororhynchos</i>)	EN	2004 ^d	2	2007	5	3	1	1	33	33	2	1	1	50	50
Black-browed (<i>Thalassarche melanophris</i>)	NT	2009	30 ^e	2012	21 ^e	4	2	1	50	25	4	3	2	75	50
Black-footed (<i>Phoebastria nigripes</i>)	NT	1991	13	2006	4	4	3	0	75	0	1	1	0	100	0
Buller's (<i>Thalassarche bulleri</i>)	NT	1997	7	2009	2	3	2	1	67	33	3	3	2	100	67
Campbell (<i>Thalassarche impavida</i>)	VU	1997	1	1997	1	1	1	1	100	100	1	1	1	100	100
Chatham (<i>Thalassarche eremita</i>)	VU	-	0	2008	1	1	0	1	0	100	1	0	1	0	100

Grey-headed (<i>Thalassarche chrysostoma</i>)	EN	2009	35 ^e	2005	8 ^e	9	5	3	56	33	6	6	3	100	50
Indian yellow-nosed (<i>Thalassarche carteri</i>)	EN	2001	8	2008	3	3	3	2	100	67	3	3	2	100	67
Laysan (<i>Phoebastria immutabilis</i>)	NT	2000	14	2007	7	2	2	1	100	50	1	1	0	100	100
Light-mantled (<i>Phoebetria palpebrata</i>)	NT	2009	13	2007	9	4 ^b	3	1	75	25	7 ^c	5	3	63	38
Northern royal (<i>Diomedea sanfordi</i>)	EN	1993	10	2009	1	3	1	0	33	0	1	1	0	100	0
Salvin's (<i>Thalassarche salvini</i>)	VU	-	0	2008	2	8	0	1	0	13	1	0	1	0	100
Short-tailed (<i>Phoebastria albatrus</i>)	VU	2014 ^d	1	2006	2	2	0	0	0	0	2	0	0	0	0
Shy (<i>Thalassarche cauta</i>)	NT	1998	5	2009	1	2	1	1	50	50	1	1	1	100	100
Sooty (<i>Phoebetria fusca</i>)	EN	2009	9	2006	5	5	2	2	40	40	4	3	3	75	75
Southern royal (<i>Diomedea epomophora</i>)	VU	1996	7	2004	1	1	1	0	100	0	1	1	0	100	0
Tristan (<i>Diomedea dabbenena</i>)	CR	1979	1	2006	3	1	1	1	100	100	1	1	1	100	100
Wandering (<i>Diomedea exulans</i>)	VU	2009	36 ^e	2009	19 ^e	5	3	3	60	60	4	3	4	75	100
Waved (<i>Phoebastria irrorata</i>)	CR	1971	2	2004	1	1	1	1	100	100	1	1	1	100	100
White-capped (<i>Thalassarche steadi</i>)	NT	-	0	2008	1	2	0	1	0	50	1	0	1	0	100
Overall			198 ^e		101 ^e	67	34	25	51%	37%	49	37	30	75%	61%

639 ^a CR- Critically Endangered; EN- Endangered; VU- Vulnerable; NT- Near Threatened

640 ^b population count data is unavailable for IBS for some island groups, therefore there may be more IBS for this species that hold >5% of the population

641 ^c includes three island groups where the individual IBS counts are unavailable, however the total island counts are >5% of the population

642 ^d samples collected at-sea over numerous years and pooled together for analysis, this is the final year of collection, however only one sample per year.

643 ^e Three studies have used a combination of both morphological and biochemical methods and are included in both columns.

644 **Table 3:** Key dietary monitoring sites. These sites have had at least two full morphological diet
 645 studies carried out.

Breeding Site	Breeding Population	Species
Albatross Island	Tasmania	Shy ^c
Bird Island	South Georgia	Black-browed ^{a,c}
		Grey-headed ^c
		Wandering ^c
Campbell Island	Campbell Island	Grey-headed
Falaise d'Entrecasteaux	Amsterdam Island	Indian yellow-nosed
French Frigate Shoals	Hawaii	Black-footed ^b
		Laysan ^a
Isla Gonzalo	Diego Ramírez	Grey-headed ^c
		Black-browed ^{a,c}
Île de la Possession	Crozet Island	Sooty ^a
		Wandering ^{a,c}
Isla Espanola	Galapagos Islands	Waved ^b
Jeanne d'Arc Peninsula	Kerguelen	Black-browed ^a
Kure Atoll	Hawaii	Black-footed ^b
		Laysan ^b
Laysan Island	Hawaii	Black-footed ^b
		Laysan ^b
Marion Island	Prince Edward Islands	Grey-headed ^c
		Light-mantled ^a
		Sooty
		Wandering ^c

Midway Atoll	Hawaii	Black-footed ^b
		Laysan ^b
North-East Island	Snares Island	Buller's
Taiaroa Head	New Zealand	Northern royal ^a
The Little (Middle) Sister	Chatham Islands	Northern royal
		Buller's ^a

646 ^a Contain less than 5% of the breeding population.

647 ^b Most recent morphological diet study > 35 years ago.

648 ^c Species/sites with *greater* than two full morphological diet studies < 35 years ago.

649 Table 4: Dietary methods used to assess albatross diet, with requirements, associated biases, disturbance and additional information obtained.

Method	Sample period	Taxonomic Resolution	Prey database required	Relative Disturbance	Key limitations	Unit of Measure	Additional Information
Regurgitation	Days (flesh remains) Weeks (hard-part remains)	Species/group	Prey hard-parts	Medium	Over-estimation of prey with hard parts, under-estimation of soft-bodied prey, provisioning diet only for many species, potentially only partial stomach contents obtained.	FOC, Mass, proportion of items	Prey size, reconstituted meal mass
Stomach flushing	Days (flesh remains) Weeks (hard-part remains)	Species/group	Prey hard-parts	High	Over-estimation of prey with hard parts, under-estimation of soft-bodied prey.	FOC, Mass, proportion of items	Prey size, reconstituted meal mass
Stomach content of dead birds	Days (flesh remains) Weeks (hard-part remains)	Species/group	Prey hard-parts	Low	Over-estimation of prey with hard parts, under-estimation of soft-bodied prey, potentially confounded by cause of mortality.	FOC, Mass, proportion of items	Prey size, reconstituted meal mass
Pellets (boluses)	Weeks (hard-part remains)	Species with hard parts	Prey hard-parts	Low	Only identifies prey with hard-parts.	FOC, Proportion of items	Prey size
SIA	Days (using blood) Months (using feathers)	Trophic level	Prey stable isotope signatures	Medium-High	Low taxonomic resolution (potentially improved using multi-source isotope mixing model).	FOC, relative proportions from mixing models	Foraging habitat (carbon source)
DNA	Days (faeces)	Species/Genus and broad diet	Prey genetic sequences	Low	Lacks mass and size information of prey, semi-quantitative.	FOC, proportion of sequences	Bird sex, parasites

Fatty Acids	Days (using blood) Months (using muscle or fat)	Trophic level	Prey fatty acid signatures	High	Low taxonomic resolution.	FOC, relative proportions from mixing models	Foraging habitat
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650 FOC= Frequency of co-occurrence

651 **Table 5:** Summary of key findings, recommendations and actions for ongoing albatross dietary monitoring.

Key Findings	Recommendation	Proposed Action
<p>Knowledge gaps</p> <p>Significant gaps in prey information exist for: Amsterdam, Chatham, Salvin’s, and white-capped albatross, with limited information for Tristan and short-tailed albatross.</p> <p>Prey information mostly restricted to chick rearing</p> <p>Reduction in resolution of information on prey items consumed due to changes in</p>	<p>Prioritise filling the gaps for the species and sites where such information is needed to make a difference to conservation and management.</p> <p>Increase monitoring to incorporate other stages of the breeding and non-breeding seasons. This may potentially be facilitated by a combination of SIA and the utilisation of new techniques such as DNA dietary analysis.</p> <p>Continue to progress the application of DNA and other forensic dietary analyses for albatross.</p> <p>DNA analysis may allow some of these gaps to be filled as it is logistically straightforward to collect</p>	<p>ACAP/Birdlife International to facilitate the prioritisation of species and IBS to investigate diet. Potentially use tracking databases and existing stable isotope and prey data to determine monitoring priorities.</p> <p>Incorporate appropriate dietary studies as an integral component of species recovery and management plans.</p> <p>Elevate the importance of dietary studies in long term monitoring plans to link observed demographic parameters to ecological drivers.</p> <p>Undertake trials to check the feasibility of DNA and other forensic methods for albatross.</p>

<p>methodology</p>	<p>and provides detailed prey information.</p> <p>Resume collection of prey information either using morphological examination of hard parts or DNA dietary techniques, to complement SIA.</p>	
<p>Detecting change</p> <p>Difficulty in detecting change due to limited long-term data collection.</p>	<p>Maintain long-term research at key sites to enable robust longitudinal diet assessment and maximise the outputs from past investment in such studies.</p> <p>Compile diet data including prey and SIA at a centralised location to enable detection of changes over time</p> <p>To achieve consistency in data collection, adopt</p>	<p>Use the key dietary monitoring sites (Table 3) as a basis for an implementation plan to enable longer time-series data to be collected.</p> <p>Develop a centralised top-predator database of diet information to facilitate quantification of changes in prey over temporal and spatial scales. Such a database could include similar information from other marine predators to allow evaluation of impacts of climate and fisheries changes at an ecosystem level. Co-ordination</p>

	<p>standardised methods of collecting and reporting dietary data that enables comparisons over time.</p> <p>These should likely be based on existing protocols such as the CCAMLR Ecosystem Monitoring Program Standard Methods (SC-CCAMR 1997).</p>	<p>with EGBAMM within SCAR* who have begun a similar database for SI data.</p> <p>Work with organisations such as ACAP to encourage signatories to improve diet monitoring.</p> <p>Repeat SIA studies at the same sites to identify any major shifts in prey or habitat use.</p>
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652 *EGBAMM – expert group on birds and marine mammals within the Scientific Committee on Antarctic Research (SCAR)

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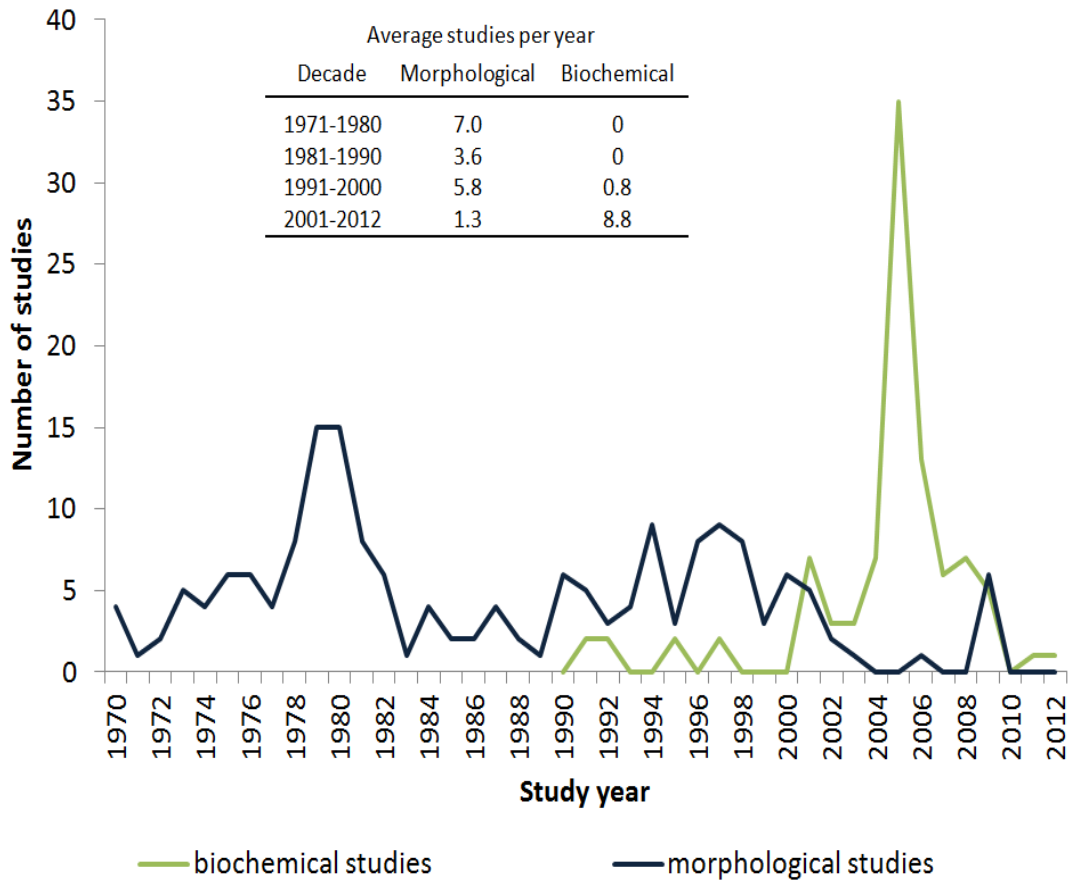


Fig. 1: The number of diet studies of albatrosses over time using different methods. Morphological - prey identified from physical characteristics (including analysis of regurgitations, stomach contents and pellets). Biochemical - predominantly stable isotope analysis, with one fatty acid study. Ten morphological studies and five biochemical studies were excluded from this graph as the study year was unspecified (Nine morphological studies excluded were published before 1999, and one in 2015).

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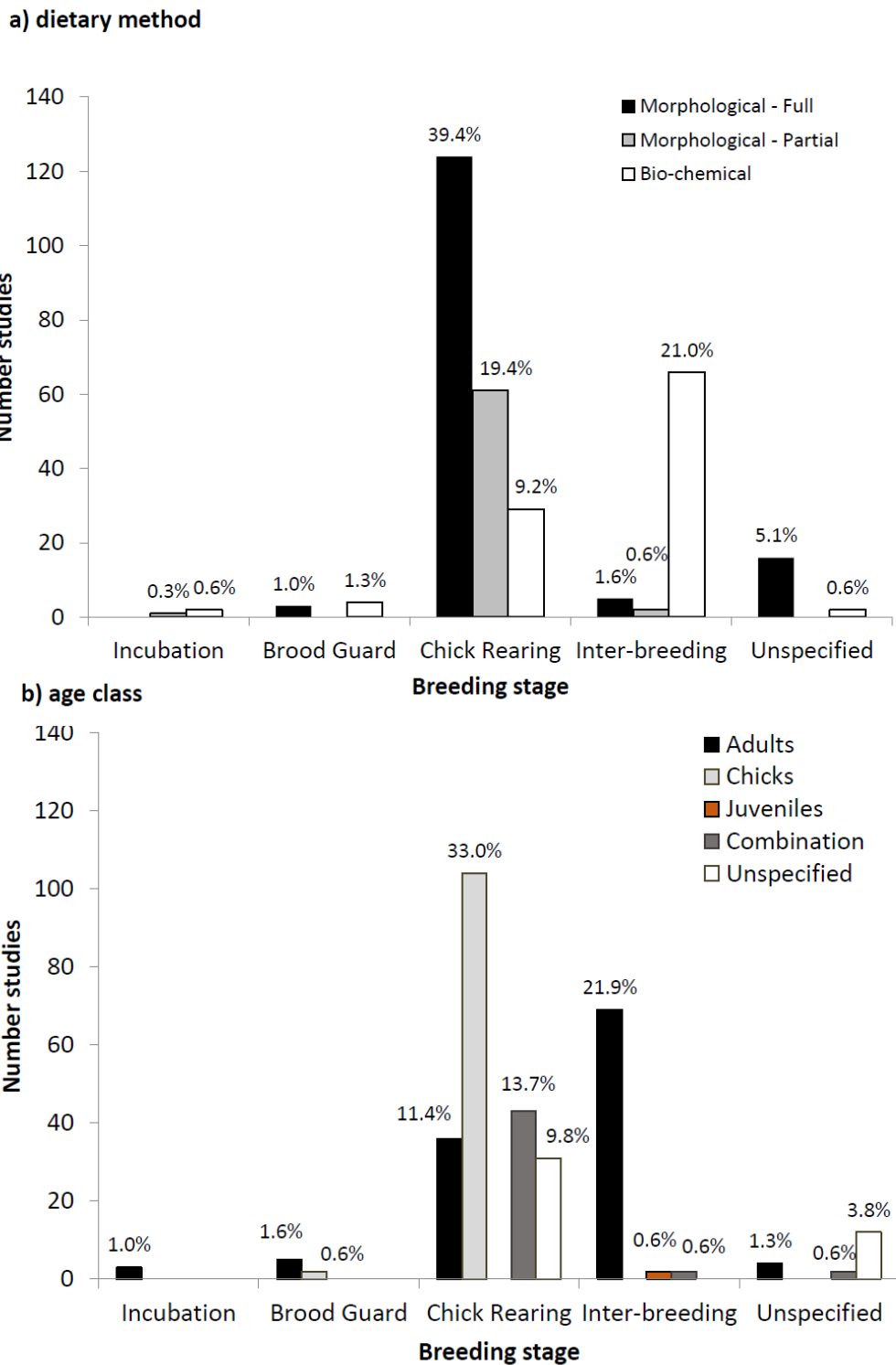
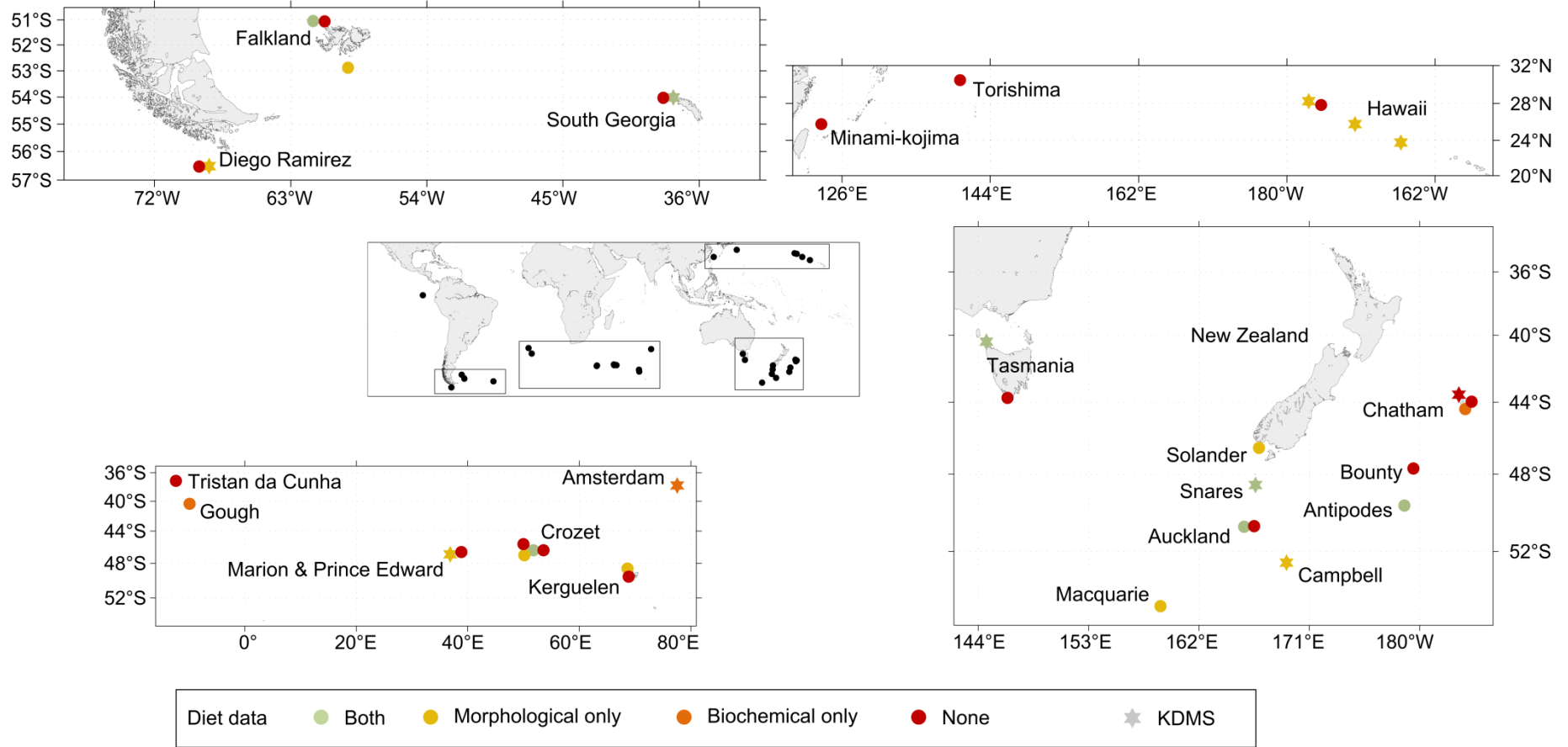


Fig. 2: Summary of the number of albatross diet studies conducted during each major breeding phase, grouped by (a) investigation method (i.e. morphological or bio-chemical analysis) and (b) age class of sampled birds. Each morphological study was categorised as either full or partial, depending on whether multiple prey groups or a single prey group (e.g. cephalopods or fish) were identified.



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703 **Fig. 3:** Gaps in albatross dietary information at important breeding sites (sites with >5% of the population) and key dietary monitoring sites for ongoing

704 monitoring. Coloured points represent the species at the site with the least dietary information. A star represents a key dietary monitoring site (KDMS),

705 where diet information of high taxonomic resolution has been collected and ongoing monitoring to detect change would be highly beneficial. Not shown in

706 detail on the figure is Isla Espanola in the Galapagos, which is a key dietary monitoring site for waved albatross with both biochemical and morphological
707 dietary information.