Feeding ecology of wintering Great Northern Divers *Gavia immer* in Argyll, Scotland

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Abstract

I investigated the role of tide and time of day on feeding success and prey species of the Great Northern Diver *Gavia immer* at its wintering grounds in Argyll, Scotland. Focal animal sampling was used on solitary divers to determine their activity during different tidal states and at different times across four main sites. When a bird performed ten successive dives, feeding success was recorded and inferred. Divers spent more time feeding early in the morning in comparison to other periods of the day. Less time was spent feeding at high tide, but this difference was not statistically significant. Divers spent 55% of the daylight period feeding, with most of this feeding time spent underwater. Prey was brought to the surface during 15% of dives and birds drank (thought to indicate ingestion of prey underwater) following 33% of dives. Crabs and flatfish were the main observed prey items, with 61% of the prey brought to the surface estimated to have a mass of less than 5 g, although items up to 80 g were consumed on occasion. The composition of prey brought to the surface varied between sites, with more crab prey items seen on sites with rocky substrates. I investigated differences in the feeding behaviour of adult and first-winter Divers at one site, but observed few differences. The importance of high-quality feeding sites for Great Northern Divers, and the implications of time spent underwater within current census techniques are discussed.

Introduction

The Great Northern Diver *Gavia immer* (hereafter 'Diver') is a member of the Gaviidae family that commonly breeds throughout northern North America, Greenland and Iceland. In the eastern Atlantic, its wintering range spans Iceland to the Faroe Islands, Norway and Sweden, Spain and Switzerland, the Republic of Ireland and the United Kingdom (Svensson *et al.* 2009; BirdLife International 2015). The wintering population of Divers in Scotland (based on the biometric measurement of skins in the National Museum of Scotland) is thought to comprise birds from Iceland (45%), Greenland and Baffin Island (45%) and mainland Canada (10%; Weir *et al*. 1997).

Furness (2015), recognising that there was moderate uncertainty in the size of the Diver population wintering in the waters around Britain, suggested a figure of 4,000 (adults and immatures), of which 3,000 were around Scotland. Lawson *et al*. (2015, revised in 2018) used a variety of survey techniques to provide a mean peak population estimate of 4,689 wintering Divers in inshore areas around Scotland. The latest land-based survey (Non-Estuarine Waterbird Survey III) provided an estimate of 4,326 for the UK, of which 4,065 were around Scotland (95% confidence interval = 3,388–4,805; Austin *et al*. 2017; Frost *et al*. 2019). Estimating wintering populations of Divers is not straightforward; several techniques are used, including aerial surveys, land-based counts and boat surveys, each of which has limitations. Notably, a key UK review of Diver numbers using aerial surveys did not include a correction factor for birds which were underwater during the survey periods (Lawson *et al*. 2015, revised in 2018). However, a correction factor has been developed for Great Northern Divers wintering off eastern north America (Winiarski *et al*. 2014).

Scotland, therefore, holds the bulk of the wintering European Great Northern Diver population (estimated at around 6,000 birds; Pennington *et al*. 2004). It is reported that around 20% of the European wintering population of Divers occur in the waters around Argyll, Scotland (ap Rheinallt *et al*. 2007), and recently the areas around the Sound of Gigha, and Coll and Tiree have been designated as Special Protection Areas (SPAs) for nonbreeding birds of this species, along with Eider Ducks *Somateria mollissima*, Slavonian Grebes *Podiceps auratus* and Red-breasted Mergansers *Mergus serrator* at the Sound of Gigha (NatureScot 2022, 2022). The seas around Argyll are not immune to development pressures such as expansions in aquaculture, changes in fishery practices, and the development of offshore renewable projects (Aitchison 2021; NatureScot 2022). Consequently, a better understanding of the ecology of these species is required to help inform conservation decisions. However, the detailed information on Diver feeding ecology (e.g. time spent feeding and their diet) required to make informed assessment of the risks associated with these threats is currently limited.

Previously, studies of the feeding behaviour and prey of Divers in their wintering habitats around the coastlines of Great Britain have been based mainly on timed dives and some observational studies of their prey. These studies are often based on small sample sizes with limited geographic detail (Collinge 1924; Robinson 1924; King 1976; Kinnear 1978). The duration of Diver dives is influenced by water depth (Kenow *et al*. 2018) and turbidity (Thompson & Price 2006), as well as choice of available prey and the abundance of prey items (Alvo & Berrill 1999; Gingras & Paszkowski 2006). Studies of the activity cycles of wintering Divers in the western Atlantic found variation in the influence of time of day on feeding activity. For example, at Assateague Island, Virginia, USA, where there is a large tidal range, McIntyre (1978) found an association between Diver feeding and both the time of day and the stage of the tidal cycle. However, at Weekapaug, Rhode Island, USA, where there is a low tidal range, both Daub (1989) and Ford & Gieg (1995) found no association between feeding activity and the tidal cycle or time of day. These studies also found differences in the time that birds spent foraging, with Divers foraging for 55% of daylight hours in Virginia and 30-40% of daylight hours in Rhode Island (McIntyre 1978; Daub 1989; Ford & Geig 1995). In southwest Norway, Byrkjedal (2011), using 30-minute observations of focal birds, found differences between the time spent feeding by Divers of different social/age classes. Adults feeding with juveniles spent less time feeding than the juveniles they accompanied, and solitary juveniles spent most time feeding (Byrkjedal, 2011). McIntyre (1978) found that all birds in the study area fed in the early morning, mid-morning and mid-afternoon, and that they showed a final burst of feeding intensity in the late afternoon and stopped feeding around sunset (occasionally earlier) before rafting 10–20 minutes after sundown.

Divers ingest most of their prey underwater (Barr 1966; King 1976; Evers *et al*. 2020), with larger prey items, that are difficult to swallow, being brought to the surface. Observing their head movements can help distinguish prey items: crustaceans are flailed against the water surface to dismember them before swallowing the carapace (King 1976; Evers *et al*. 2020), while large flatfish (*Pleuronectiformes*) are struck with powerful bill-open stabs before being swallowed (D. C. Jardine pers. obs.). After ingesting large prey items, Divers normally take one or more short drinks, presumably to assist swallowing, and occasionally they will stand and flap their wings, which also has the potential to assist swallowing (Byrkjedal 2011).

Identifying Diver prey items can be difficult when most are consumed underwater. The stomach contents of 38 adult Divers (20 male and 18 females) were sampled by Collinge (1924) in his study on economic ornithology, and while his account provides quantitative monthly information, it does not provide information of the geographical source of the samples. Overall, Collinge (1924) found fish remains in 32 Diver stomachs (84%) and identified species including Gurnard *Triglidae* sp., Haddock *Melanogrammus aeglefinus*, Herring *Clupea harengus*, Sprat *Sprattus sprattus*, Whiting *Merlangius merlangus*, Sandeels *Ammodytes* sp., Trout *Salmo trutta* and Flatfish *Pleuronectiformes*. Collinge (1924) adjudged that 55.3%

of Diver prey was fish, 24% was crustacea and annelids, 18.5% marine molluscs, 2.1% unidentified animal matter and 0.1% algae. Furthermore, 55.3% of fishes eaten were prey species of commercial interest, with the remaining 44.7% of the diet neutral to the interests of humans. Collinge (1924) did not indicate the size of the prey items found in the Divers' stomachs. More modern studies of diet from necropsied Divers indicate that Shore Crab *Carcinus maenas*, Squat Lobster *Galathea squamifera*, unidentified molluscs, and Whiting *Pollachius virens* or Haddock *Melanogrammus aeglefinus* (as determined from otoliths) form part of their diet (Heubeck *et al.* 1993), while Weir *et al*. (1997) found bivalve species and Norway Lobster *Nephrops norvegicus* within the stomachs of dead Divers. Leopold *et al*. (2000) found, in a drowned but apparently healthy second calendar year individual recovered in The Netherlands, remains of gobies (mainly Sand Gobies *Pomatoschistus minutus*, lengths: 3.5–7.3 cm; weights: 0.4–3.7 g), one Brill *Scophthamlus rhombus* (8.5 cm; 8.45 g), five 0-group Flounders *Platichthys flesus* (5.9–8.5 cm; 2.1–8.5 g) and four shrimp *Crangon crangon* (0.5 g). See Supplementary Materials for details of all prey recorded in the United Kingdom and Ireland.

While the studies listed above provide some insight into the foraging ecology of Divers, there is little contemporary evidence of this important aspect of their ecology in their wintering stronghold in Western Scotland. Therefore this study aimed to investigate the composition of their diet and the factors which influenced their feeding patterns. This evidence will inform assessment of developments that may impact on their wintering foraging habitats and the conservation management of protected areas for Great Northern Divers.

Methods

Fieldwork was conducted from 2018–21 at inshore sites in Argyll, Scotland (55^0 40’ to 56^o 12’ N; Figure 1) in areas where Divers were usually foraging in water depths of less than 10 m. The tidal range in this region of Scotland is around 0.5–1 m during neap tides and 0.9–2.2 m during spring tides (UK Hydrographic Office). The study used focal-animal sampling (Altmann 1974) of solitary feeders; detailed observations of group feeders was not attempted as identification of individual birds can be difficult. Observations were largely carried out in calm weather (sea state 0–3; wave height ranging from calm, 0 m, to slight, 0.5–1.25 m) to ensure that the positions of birds could be tracked throughout the sampling period. When more than one Diver was present, plumage and bill characteristics were used to distinguish between individuals.

Observations of Diver activity

To determine Diver feeding times, studies were conducted at two main sites, one within the Sound of Gigha SPA (32% of observations) and the other at Craobh Haven-Asknish Bay (62%); the remaining 6% of observations were opportunistic from two sites each on the islands of Gigha and Kerrera, and at the mouth of West Loch Tarbert, Loch Stornoway and at Toberonochy on the Isle of Luing. Activity observations were carried out either side of the winter solstice (19 November 2021 to 19 January 2022) using the instantaneous sampling technique (Ford & Geig 1995). In short, Divers were observed from the shore using binoculars or a spotting scope and activity was recorded once a minute over a five-minute period. Observations were conducted throughout the tidal cycle during low tide (± 1.5 hours), high tide (± 1.5 hours) and the flood tide and ebb tide intervening periods. Observations were conducted throughout the day from pre-dawn to post-dusk, and divided into nine periods comprising before sunrise, one, two and three hours after sunrise, an intervening period in the middle of the day, and three, two and one hours before sunset and after sunset. This resulted in a total of 36 tide-time categories. The sites used were chosen to suit the tide-time observations required.

Wherever possible attempts were made to observe both Divers close to the shore and those further offshore; observations of the former were greater as it was easier to ensure that the same bird was tracked throughout the five-minute sampling period. Unlike similar North American studies, no birds were observed sleeping during this study, so five activities were used in the analysis: (1) feeding (underwater and manipulating large items on the surface); (2) peering/‘snorkeling’ (actively looking for prey); (3) loafing/drifting/on the surface between dives; (4) preening/maintenance; and (5) other (including flying and other underwater swimming, e.g. avoidance of marine mammals or attacking other birds).

I aimed to make ten five-minute observation periods for each tide-time category (36 in total). This was not achieved for two of the tide-time categories. A total of 385 five-minute observation periods were made across the tide-time categories, representing 1,925 instantaneous observations. Therefore, to recognise the small differences in sampling rate between tide-time categories, the data for each tide-time category were transformed by dividing the activity total for each tide-time category by the number of samples and multiplying by ten. The frequency of feeding activity between tidal states and time of day was statistically examined using chi-squared tests.

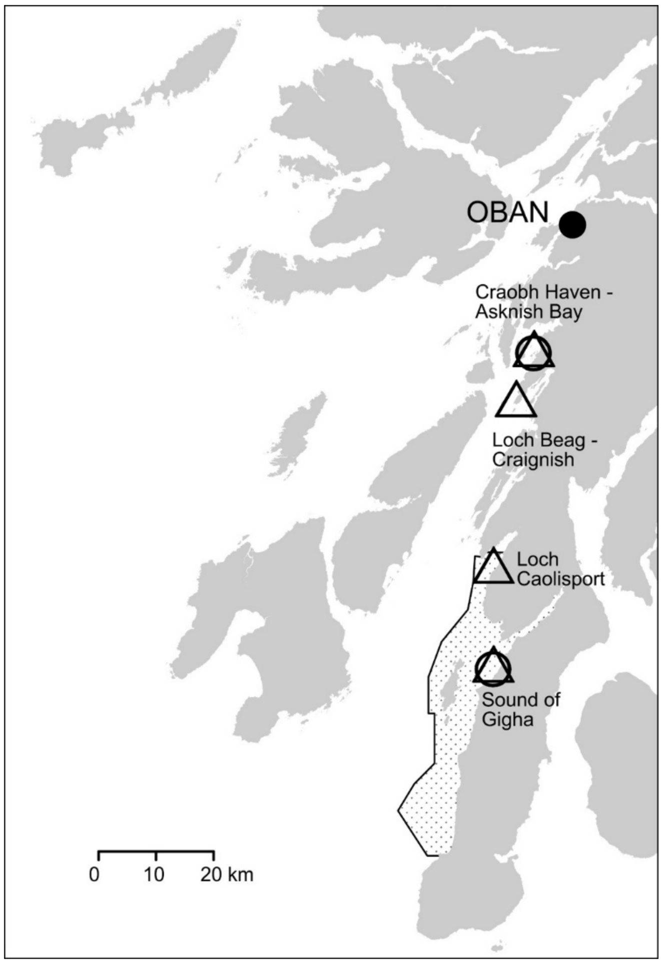

Figure 1. Location of the study area: Argyll, Scotland. Circles show the location of the two main activity observation points and triangles the location of the feeding success and diet studies. The Sound of Gigha SPA is stippled.

Observations of Diver foraging success and diet

To determine Diver foraging success and prey items, four main inshore study sites were used: Sound of Gigha (SPA), Loch Caolisport (SPA), Loch Beag-Craignish, Craobh Haven-Asknish Bay, with opportunistic observations occurring at another 34 locations within the study area (Figure 1). All observations were made from the shore using binoculars, spotting telescope and a bridge camera (Nikon P900, x83 zoom), except for those made at Scalasaig, Colonsay, where they were made from the pier which allowed closer observation of birds feeding further from shore. Observations were made from several locations within each study site and were aggregated for each area. Observations set out to establish how often Divers brought prey samples to the surface and the number of times they drank between dives. The size and composition of prey items was also noted. Group feeding was only noted at four sites (Colonsay, A' Chleit, Ronachan and North Gigha; suggesting that shoaling fish may not be a major prey resource in the study area) and so, while recognising an introduced bias, I therefore conducted focal-animal sampling (Altmann 1974) of solitary feeders only (and very occasionally when two birds were feeding alongside one another).

To determine foraging success, sequences of ten dives were observed and the outcome of each dive was recorded along with the total time taken to perform the ten dives (i.e. time from entry of first dive to entry of eleventh dive). Sequences of fewer than ten dives, where the bird was 'lost' from observation, stopped feeding, or could not be distinguished from another individual were excluded from the analysis, but prey items and size were recorded. When a bird surfaced it was noted whether it carried prey in its bill, and if it did not, whether it took a drink before diving again. For the purposes of analysis, birds which took a drink upon surfacing were assumed to have ingested a prey item before surfacing. Where possible the age of the bird (adult vs juvenile) was noted and the distance from the shore estimated and differences in these were explored using standard statistical tests. Analyses of dive times and foraging success were completed with Microsoft XLSTAT 2023.1.1 using chi-square, Levene's, Kruskal-Wallis and t-tests.

Other reasons which affected foraging success e.g. attempted kleptoparasitic attacks by gulls (*Laridae*) were noted.

Prey items brought to the surface were identified to species level by observation and/or photography and behaviour) (Wheeler 1978). However, this was not always possible, e.g. if a bird fed facing away from the observer, if a prey item was swallowed before identification could be confirmed, or due to sea swell. As species identification was not always possible, prey was split into eight groups for analysis (Supplementary Materials). The size of prey items was estimated against Diver bill length (culmen; Figure 2) and the mass of fish was calculated via length:mass equations for the principal prey items (Froese & Pauly 2023). To estimate Diver bill length, undamaged specimens of adult Divers at the National Museum of Scotland were used. While a small difference was found between the culmen lengths of females (mean = 78 $\pm$ 2 mm 95% confidence interval, N = 37) and males (mean = 80 $\pm$ 2 mm 95% confidence interval, N = 24), it was not possible to sex individuals in the field, so a combined mean bill-length (including unsexed individuals) of 79 mm (95% confidence interval = 78–80 mm; N = 66) was used in the estimation of prey size (and mass). The mass of crabs was estimated from a sample of 30 Shore Crabs *Carcinus maenas* caught and measured in Argyll in June 2022. All observations of prey items brought to the surface during activity studies and foraging success studies were used in the analysis of prey size (mass).

Figure 2. Example of fish measuring technique: Plaice *Pleuronectes platessa* measured at 1.7 times the length of the Great Northern Diver *Gavia immer* culmen (135 mm). Photograph taken in West Tarbert, Gigha, Argyll, November 2021. © *David C Jardine.*

Results

Diver activity

Overall, Divers spent a mean of 55% of daylight hours engaged in feeding. Feeding activity was lower at high-tide (50% of instantaneous observations) than during other tidal states: ebb (57%), flow (59%) and flood (56%; X^2 = 0.358, 3 df, N = 1800, P = 0.20; Figure 3). However, at high-tide they spent a greater proportion of time looking for food/snorkelling (7%) than during other states of tide (ebb = 4%, low = 3%, flood = 2%), resulting in differences in the overall proportion of time spent both feeding and looking for food varying little between the state of the tide (range 57–61%).

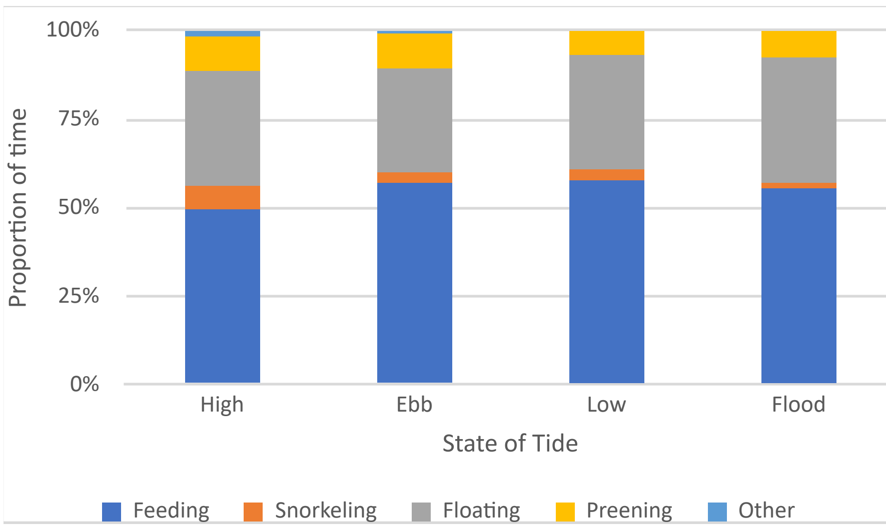

Figure 3. Activity budgets of Great Northern Divers *Gavia immer* in Argyll during different stages of the tidal cycle, November 2021 to January 2022. From bottom to top, feeding, snorkelling, floating, preening and other behaviours (see text for details).

The earliest Diver feeding dives were recorded 40 minutes before sunrise (on a moonlit morning) on 30 December 2020 (when no prey was brought to the surface) and 38 minutes before sunrise on 12 January 2021 (when prey was brought to the surface). The latest feeding dive noted was 42 minutes after sunset on 5 January 2021, and whilst this bird was lost to view, it brought prey to the surface to feed earlier (at 35 minutes after sunset).

During the day, the proportion of time Divers spent feeding varied between 46–62%. When feeding and snorkelling was combined, activity peaked just before sunrise (Figure 4). After this early morning feeding period, Divers spent more time preening before feeding then increased in the late morning (Figure 4). The proportion of time spent feeding declined in the middle of the day and early afternoon, the period when the highest proportion of time was instead spent preening (Figure 4). In the late afternoon, feeding increased again before dipping slightly as birds moved off to roost. (X^2 = 0.444, 8 df, N = 1,800, P < 0.01).

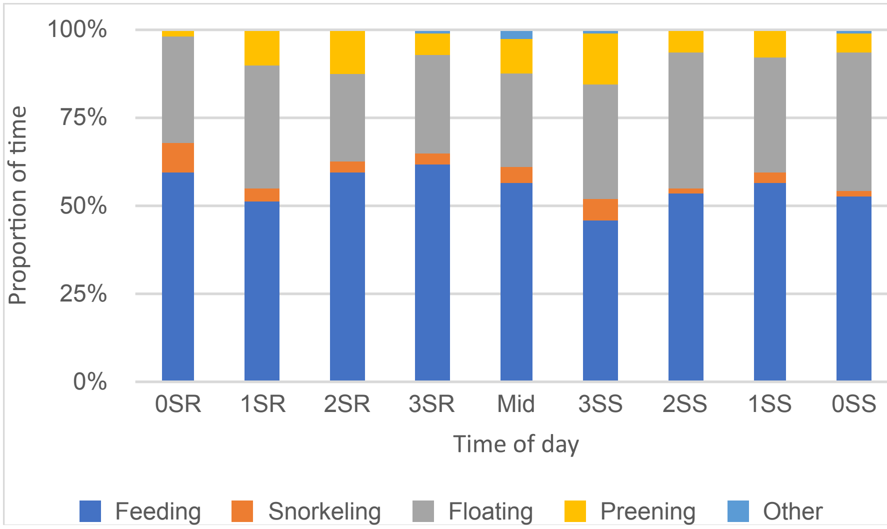

Figure 4. Activity of Great Northern Divers *Gavia immer* in Argyll during November 2020 to January 2021, during different times of the day. Activity was sampled instantaneously at one-minute intervals during ten five-minute samples per time-tide category. Different time periods: 0SR (before sunrise), SR1 (up to one hour after sunrise), SR2 (between one and two hours after sunrise), SR3 (between two and three hours after sunrise), Mid (after three hours after sunrise and over 3 hours before sunset), 3SS (between two and three hours before sunset), 2SS (between one and two hours before sunset), 1SS (between one hour before sunset and sunset), and 0SS (after sunset). From bottom to top, feeding, snorkelling, floating, preening and other behaviours (see text for details).

Diver foraging success and diet

A total of 373 ten-dive feeding sequences were observed (3,730 dives, encompassing 5,124 minutes). Dives lasted of a mean of 81 seconds, including dive recovery and/or surface feeding. There were slight differences between sites, with shorter dive cycles noted at the Sound of Gigha (74 seconds, N = 1,260 dives) and Loch Caolisport (74 seconds, N = 470 dives), than at Loch Beag, Craignish (97 seconds, N = 680 dives), Asknish-Craobh (84 seconds, N = 670 dives) and the other sites (80 seconds, N = 650 dives; F = 9.93, 4 df, P < 0.01).

Prey was brought to the surface on 549 occasions (15% of dives). On 195 occasions (36% of dives) the prey item could not be identified because it was obscured or swallowed too quickly. Birds always drank water after swallowing prey brought to the surface. On 38% of the dives when no prey was seen, the Diver took a drink before diving again (1,217 dives). Most prey items brought to the surface were ingested; only two items out of the 549 brought to the surface during the ten-dive observations were lost (both were fish which were dropped during handling and escaped).

In all observations, which included occasions when the full sequence of ten dives were not observed, nine or ten food items out of the 1,065 prey items brought to the surface were not ingested (one may have been ingested underwater when the bird re-dived). During 18 kleptoparasitic attacks by Herring Gulls *Larus argentatus* and Great Black-backed Gulls *L. marinus*, prey was retained by the Diver on 15 occasions. There were some differences in the dive outcomes between sites (Figure 5), with birds at Asknish-Craobh Haven surfacing more frequently with prey items and fewer of the dives were followed by a drink (K = 8.98, 3 df, P = 0.03).

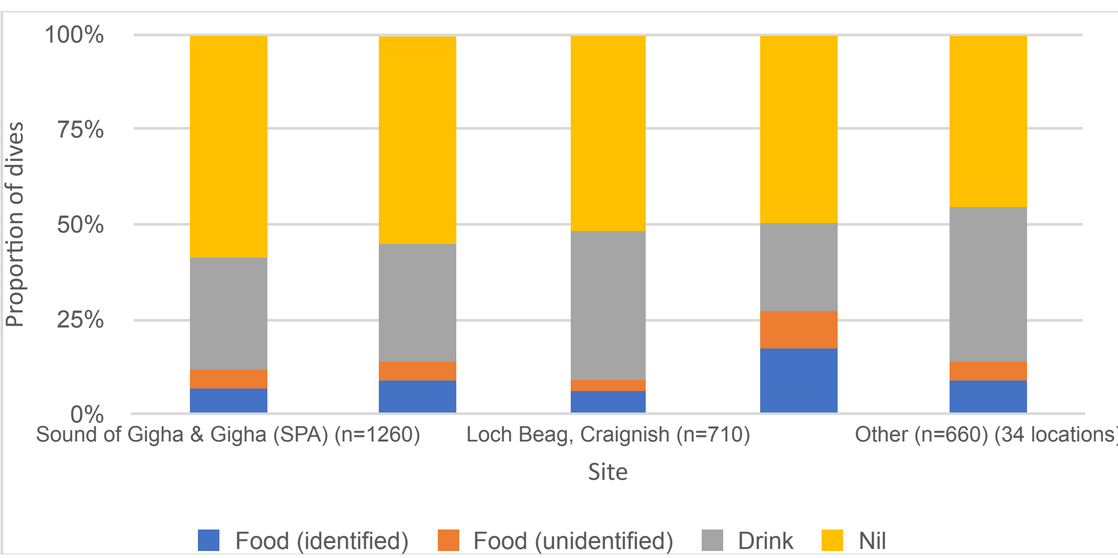

Figure 5. Proportion of Great Northern Diver *Gavia immer* dives with different outcomes (i.e., indices of foraging success) at four main sites and at 34 locations ('Other') in the study area (Figure 1) in Argyll,

Scotland. From bottom to top, identified food items, unidentified food items, instances where a drink was taken and assumed failed feeding attempts.

Crabs were the most common prey item brought to the surface, followed by flatfish (Table 1), although the proportion of these varied between sites, with flatfish almost equalling crabs at Loch Beag, Craignish. From a visual comparison it appears more flatfish were caught at sites where there were large areas with sandy or muddy substrates, while those sites where more crabs were caught had rocky or cobbly sea-beds (Marine Scotland, 2023).

Table 1. Number of identified prey items (%) observed being consumed by Great Northern Divers *Gavia immer* at different sites within Argyll, Scotland during 2018–21. For details of the species that comprise the eight prey groups, see Supplementary Materials.

	Number of prey items identified					
Prey group	Sound of Gigha & Gigha	Loch Caolisport	Loch Beag, Craignish	Asknish-Craobh	Other sites	Total
Demersal fish	8 (4.0)	1 (1.2)	3 (3.6)	5 (1.7)	9 (4.7)	26 (3.0)
Pipefish	-	-	1 (1.2)	5 (1.7)	6 (3.1)	12 (1.4)
Benthic fish	15 (7.5)	7 (8.5)	12 (14.5)	4 (1.3)	17 (8.8)	55 (6.4)
Butterfish	2 (1.0)	3 (3.7)	2 (2.4)	4 (1.3)	7 (3.6)	18 (2.1)
Flatfish	47 (23.6)	8 (9.8)	28 (33.7)	3 (1.0)	19 (9.8)	105 (12.3)
Crab	120 (60.3)	60 (73.2)	29 (34.9)	269 (90.0)	132 (68.4)	610 (71.3)
Other Crustaceans	6 (3.0)	3 (3.7)	1 (1.2)	6 (2.0)	1 (0.5)	17 (2.0)
Other	1 (0.5)	-	7 (8.4)	3 (1.0)	2 (1.0)	13 (1.5)
Total	199 (100)	82 (100)	83 (100)	299 (100)	193 (100)	856 (100)

The mass was estimated for 815 (95.2%) prey items identified to prey group at the surface. It was not possible to estimate the mass for some bivalves, octopus, some species of crabs and other crustaceans as size:mass correlations were not readily available for these groups. The distribution of prey size was skewed towards small prey items, with modal mass of 3.75 g. Of these, 74.6% were estimated to be less than 5 g (Figure 6). However, there was variation in average weight of the different food groups brought to the surface and some very large flatfish, benthic fish and crab were caught, providing a significant contribution to the required daily intake (See Discussion).

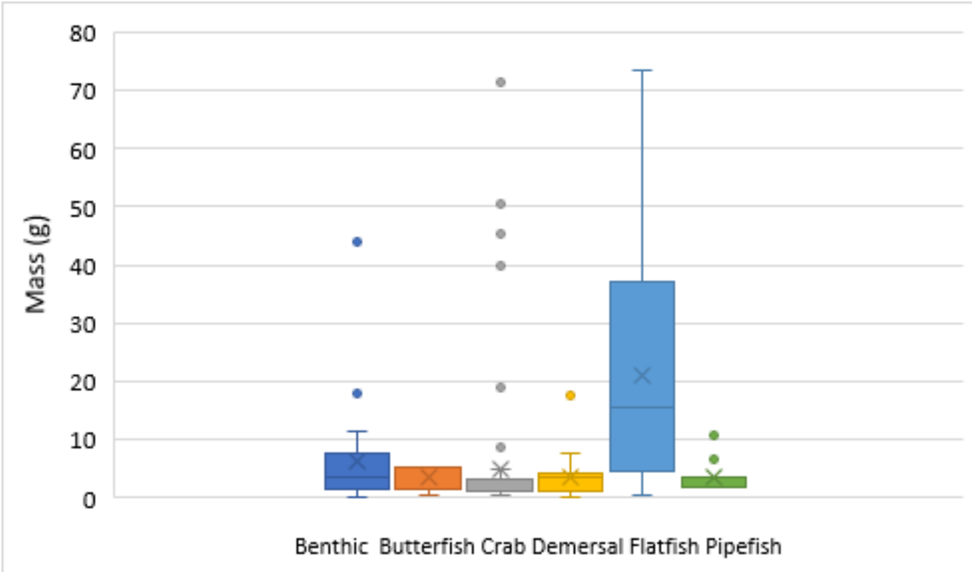

Figure 6. Distribution of estimated mass (g) of prey items, by prey group (for details of the species that comprise the eight prey groups, see Supplementary Materials), of Great Northern Divers *Gavia immer* brought to the surface in Argyll, Scotland. Excludes the groups 'other crustacean' and 'other' for which estimating prey mass was difficult e.g. octopus, spider crabs (total 41 items, 4.8%).

Comparison of adult and first-winter Diver foraging

At Asknish-Craobh, the number of observations was large enough to allow comparison between Divers of different age classes. First-winter birds were watched for 37 feeding sequences (370 dives) and had a shorter dive and dive recovery cycle (75 seconds) than adult birds (96 seconds, N = 20 dive sequences), but this difference was just significant (t-test, P = 0.05). First-winter birds surfaced more often with prey (29.1% of dives) than adults (21.0%), but not significantly so (t-test, P = 0.13). However, young birds did not drink (21.1% of dives) as often as adults (32.5%) after a feeding attempt (t-test, P = 0.03). Combining these it appears, based on the assumption that a drink after a dive indicates ingestion underwater, there is little difference in the feeding success of adults (53.5%) and first-year birds (50.3%; t-test, P = 0.52).

There was no difference in overall prey composition between adults and young birds ($X^2 = 8.72$, 7 df, P = 0.27; Table 2). However, first year birds caught a greater proportion of small crabs than adults; 25% of the catches of the first-year birds had an estimated carapace width of 4–12 mm (cf. 16% in adults), 53% were between 12–20 mm (cf. 38% in adults) and 18% were between 20–28 mm (cf. 42% in adults; $X^2 = 11.93$, 3 df, P < 0.01).

Table 2. Number of identified prey items (%) by prey group (See Supplementary Materials for details of species contained in each prey group) of adult and first-winter Great Northern Divers *Gavia immer* at Asknish-Craobh, Argyll, Scotland.

Prey group	Age class	
	Adult	First-winter
Demersal fish	2 (3.3)	2 (1.3)
Pipefish	2 (3.3)	1 (0.6)
Benthic fish	-	3 (1.9)
Butterfish	2 (3.3)	2 (1.3)
Flatfish	1 (1.7)	1 (0.6)
Crab	50 (83.3)	144 (91.1)
Other Crustaceans	1 (1.7)	4 (2.5)
Other	2 (3.3)	1 (0.6)
Total	60 (100)	158 (100)

Discussion

Overall, the diurnal feeding patterns of Great Northern Divers in Argyll were similar to those of birds in North America (McIntyre 1978; Daub 1989; Ford & Geig 1995) and Norway (Byrkjedal 2011), with over 50% of daylight hours in winter being spent feeding. As with birds wintering off the coast of Virgina, USA, I observed a strong temporal feeding pattern, with the greatest activity early in the morning (McIntyre, 1978). Differences in methodology may account for the different proportions of time spent diving between different sites, however, this study used the same methodology as Ford & Geig (1995) off Rhode Island, USA. The difference between birds spending 55% of their time feeding in this study and the 30–40% reported off Rhode Island by Daub (1989) and Ford & Geig (1995) may be due the shorter daylengths experienced in mid-winter in Argyll, or because the North American studies were carried out between January and April during the period of lengthening daylight. This study, like Daub (1989) and Ford & Geig (1995), did not find strong evidence of the state of the tide influencing feeding patterns. This contrasts with the findings of McIntyre (1978) whose study was based in an area with a high tidal range (6 m). As both this study and that of Ford & Geig (1995) were based in areas with low tidal range, it would appear that the impact of tides on the feeding habits of Divers may be related to the tidal ranges of their wintering sites. Divers in Argyll appeared to surface more often with prey (14.7%) than those in other studies. For example, Grant (1996) found that in North Carolina USA, Divers only brought prey to the surface on 4.6% of dives (N = 303 dives). Higher rates of prey capture may be reflective of prey being more readily available at the Argyll study sites.

Daylength is an important factor in the winter foraging ecology of some Divers (Byrkjedal, 2011). However, Divers have been caught in nets set at 60 m (Schorger 1947), suggesting that they can forage in very low light levels. The high proportion of time that Divers spent feeding and snorkelling in shallow water before sunrise observed during this study supports this hypothesis. The observation of a Diver feeding 40 minutes before sunrise under strong moonlight raises the question whether they have the potential to feed at night during winter in northern latitudes, although this was not recorded by Paruk (2008) at freshwater sites at the end of the breeding season. However, a few Divers overwinter north of the Arctic Circle in north Norway and north Iceland (del Hoyo *et al*. 1992); these birds presumably feed very low light intensity conditions.

Argyll is an important area for Divers, hosting up to 20% or more of the European wintering population, with large aggregations found off Islay, Tiree, Mull and the southern Kintyre peninsula as well as at Sound of Gigha (ap Rheinallt *et al*. 2007). It is unclear how many of these birds are adults and how many are juveniles or immatures. In mid-winter, the high proportion of daylight hours spent foraging suggests that these birds require a large caloric intake to survive the winter months. Divers need areas that have abundant food because their foraging strategy, while highly efficient, is energetically expensive (Norberg

2021). This means that Divers may be vulnerable to threats and pressures that could increase their energy budgets or reduce their foraging success. However, it is unclear whether Divers wintering elsewhere around the British Isles spend as much time foraging as those observed in Argyll. Since foraging effort is higher in juveniles than in adults (Byrkjedal 2011), any constraints on foraging ability may be especially important for overwintering juveniles. These could, for example, relate to issues such as reduction in the abundance of crustacean prey in areas around salmon cages where chemical treatments are used to kill sea lice, or disturbance of birds by vessel traffic (Aitchison 2021). The importance of larger prey items such as large flatfish and crabs should also not be underestimated as one individual prey item (caught on one of around an estimated 425 dives made per day in mid-winter by Divers in the study area) may provide 4–8% of an individual's daily intake (see below). Conservation measures which prevent the depletion or availability of these prey resources should be a priority for Diver conservation in Argyll.

The high proportion of time spent underwater by Divers has important implications for the assessment of the sizes of wintering populations of Divers. Counting inshore birds is relatively straightforward if time is taken during surveys to allow for birds to surface and be counted; however, these methods are not able to assess those birds feeding more than 2 km offshore (Webb & Reid 2004). Roost counts conducted from the shore have often provided some of the highest population estimates in some areas, but these can suffer from failing light and the inability to count roosts that are distant from open shores (Shackleton 2012). Increasingly, aerial surveys have been used to overcome these issues, but these do not always account for birds which are underwater, nor do they count all areas close to shoreline cliffs (Lawson *et al*. 2015) where Divers often feed. Therefore, there is a high possibility that current assessments of wintering populations of this species in Scotland are underestimates. It is recommended that in future aerial surveys of this species also include water close to the shoreline, and that corrections are made for the proportion of birds underwater at the time of the survey. Consideration should also be given to testing the use of thermal imaging with drones for roosting birds, both for counting and to identify the location of offshore roosts (Seymour *et al* 2017).

This study has a number of limitations and biases which must be recognised when interpreting the results. Firstly, it does not include analysis of group feeding events, when Divers are thought to feed on shoaling fish. However, in over 200 hours of close observation, group feeding was only observed on five occasions in the study areas and much less frequently than the Black-throated Divers *G. arctica* present in the study area. This suggests this this may be a minor bias, but it should be noted that the importance of shoaling fish may be underestimated in these results. Vliestra (2000) suggested that solitary feeding Divers were feeding on prey that was distributed throughout their foraging habitats, suggesting that individual prey samples may be independent; however, if some clustering of prey occurs (e.g. crabs around their food) then this may not be the case.

Using information on the mid-winter activity of Divers in Argyll, along with the length of their dives, it can be estimated that Divers make around 425 dives per day. My results suggest that they would bring prey to the surface on around 62 of these dives, and on a further 137 occasions they would drink when they surfaced, suggesting that they had ingested prey underwater. Thus, the estimated total mass of observed prey consumed each day (434 g; 7 g for each of the 62 dives) is just less than half the daily intake calculated in other studies during the breeding season (900-960 g; Barr 1996; Evers *et al*. 2020). This suggests that the mass of prey ingested underwater was around 500 g, which, based on an assumption that dives where the bird drinks on surfacing have been successful, suggests that the average underwater catch is around 3.6 g per dive, close to the observed modal weight of surfaced prey (3.75 g). While this is higher than the average prey mass observed by Leopold *et al*. (2000) in an apparently healthy second calendar year bird (1.2 g), it still comprises small individual prey items which are shorter than the bill length of a Diver (i.e. benthic fish and flatfish that are c. 75 mm and 109 mm demersal fish).

At any site it needs to be recognised that observed diet may reflect prey availability; this study suggests that prey availability may vary with benthic habitat, but as no sampling of prey was undertaken this cannot be stated with certainty. Similarly, current and past management activities (e.g. fisheries practices) will impact the food resources available to Divers. Therefore, while this study has found that much of the prey brought to the surface by solitary feeding Divers in Argyll during winter is benthic, this may be a consequence of a depleted pelagic resource.

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Supplementary Materials

The marine prey of Great Northern Divers *Gavia immer* in the United Kingdom and Ireland and the prey categories that they were assigned to for this study. Prey species were identified from the literature, photographs taken during this study and other published sources.

Species	Literature (ref)	Photographs (Birdguides,	Prey category
Spurdog *Squalus acanthias*		X	
Common (Flapper) Skate *Dipterus*		X	
Herring *Clupea harengus*	Collinge (1924); Cramp (1977)		
Sprat *Sprattus sprattus*	Collinge (1924); Cramp (1977)		Demersal
Trout *Salmo trutta*	Collinge (1924); Cramp (1977)		
Whiting/Haddock	Heubeck *et al*. (1993)		
Haddock *Melanogrammus*	Collinge (1924); Cramp (1977)		
Whiting *Merlangius merlangus*	Collinge (1924); Cramp (1977)		
Pipefish sp *Syngnathus sp.*	Cramp (1977)	X	Pipefish
Greater Pipefish *Syngnathus acus*		X	Pipefish
Scorpion-fish *Scorpaena scrofa*		X	Benthic fish
Gurnard sp. *Triglidae*	Collinge (1924); Cramp (1977)	X	Benthic fish
Bull-rout *Myoxocephalus scorpius*	Cramp (1977)		Benthic fish
Grey Mullet sp. *Chelon labrosus/ Liza ramada/ Liza aurata*			Demersal fish
Wrasse sp. *Labrus sp.*			Demersal
Ballan Wrasse *Labrus bergylta*			Demersal
Greater Weever *Trachinus draco*		X	
Shanny *Lipophrys photis*		X	
Butterfish *Pholius gunellus*		X	Butterfish
Sandeel sp. *Ammodytes/Hyperoplus*	Cramp (1977)		Benthic fish
Goby sp. *Gobius/Potatoschistus sp.*	Cramp (1977)		
Common Goby *Pomatoschistus*			Benthic fish
Sand Goby *Pomatoschistus minutus*			Benthic fish
Flatfish sp. *Pleuronectiformes*	Collinge (1924); Cramp (1977)		Flatfish
Plaice *Pleuronectes platesa*		X	Flatfish

Flounder *Platichthys flesus*		X	Flatfish
Dab *Limanda limanda*		X	Flatfish
Crustacea	Collinge (1924)		
Shore Crab *Carcinus maenas*	Heubeck *et al*. (1993); Cramp	X	Crab
Velvet Crab *Necora puber*		X	Crab
Swimming crab *Portunidae*	Cramp (1977)	X	
Edible Crab *Cancer parugus*			Crab
Spider Crab *Hyas Araneus*			Crab
Squat Lobster *Galathea squamifera*	Heubeck *et al*. (1993)		Other
Norway Lobster *Nephrops*	Weir *et al.* (1997)	X	Other
Shrimp	Cramp (1977)		
Prawn	Cramp (1977)		
Mollusca	Collinge (1924); Cramp (1977); Heubeck *et al*. (1993)		
Razorshell *Solen sp.*	Cramp (1977)		
Razor *Ensis magnus*			Other
Bivalve sp.	Furness (1994); Weir *et al.*		
Whelk *Gastropoda*			Other
Cephalopoda	Cramp (1977)		
Curled Octopus *Eledone cirrhosa*			Other
Annelida	Cramp (1977)		
Polychaete worms	Cramp (1977)		