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Trophic ecology of Yellow-billed Loons *Gavia adamsii* and Common Loons *G. immer* during the non-breeding season

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Abstract
Diet and aspects of feeding behaviour of Yellow-billed Loons *Gavia adamsii* and Common Loons *G. immer* were compared during the non-breeding season in coastal Norway. Stomach contents from 14 Common Loons and 13 Yellow-billed Loons showed that fishes constituted the main prey of both species. However, saithe *Pollachius virens* constituted a major component of the diet of the Yellow-billed Loon, whereas wrasses (Labridae), flatfish (Pleuronectidae), and sandeel *Ammodytes tobianus* were important prey for Common Loons. Common Loons also frequently included crustaceans and sometimes molluscs in their diet. We tested the hypothesis that the Yellow-billed Loon, with its more upturned bill, feed more on bottom-living prey than the Common Loon. Contrary to the hypothesis, stomach contents indicated that more bottom-living prey were taken by Common Loons, and Yellow-billed Loons seemed to prey more on pelagic fish. A difference in prey selection was consistent with field observations that Yellow-billed Loons often fed in water judged too deep for bottom-feeding, social groups were often synchronized when feeding, and their stomach contents contained only a few gastroliths compared to Common Loons. Species differences in number of gastroliths indicate that Yellow-billed Loons are feeding on softer food such as pelagic fish, whereas Common Loons are feeding on crustaceans and the more armoured and spiny fishes occurring in bottom habitats.

INTRODUCTION

Loons (Gaviidae) are primarily piscivorous year round, although other aquatic vertebrates as well as invertebrates may be included in their diet. The two largest species, the Yellow-billed Loon *Gavia adamsii* and the Common Loon *G. immer* are geographically separated during the breeding season, with the Yellow-billed Loon primarily found in the tundra zone and the Common Loon in the boreal forest zone (Cramp & Simmons 1977, North 1994, McIntyre & Barr 1997, Evers et al. 2010, Uher-Koch et al. 2020, Paruk et al. 2021). Both species mainly spend the non-breeding season in marine areas, feeding on small as well as large fish and to a lesser extent crustaceans and other marine invertebrates. The main wintering areas are on the east and west coast of North America, on the coast of northern Asia, and along the coasts of Europe. Yellow-billed Loons generally winter north of Common Loons, but the two species overlap considerably in their West Palearctic and the West Nearctic wintering ranges (Cramp & Simmons 1977, Il'ičev & Flint 1982, North 1994, McIntyre & Barr 1997, Byrkjedal et al. 2000). The two species are structurally similar with overlap in body mass, Common Loon weighing 3.6–4.5 kg and Yellow-billed Loon 4.1–6.4 kg (Cramp & Simmons 1977), and could be expected to be food competitors during the non-breeding season.

In the Yellow-billed Loon, the gonys is usually more angular and the upper mandible is less curved than in the Common Loon giving the bill of the Yellow-billed Loon a more "upturned" profile. Given the difference in bill morphology, Jehl (1970) and Storer (1978) hypothesised that Yellow-billed Loons would feed more on bottom-living prey while the Common Loons would feed more on free-swimming organisms. The hypothesis was based on early dietary studies comparing grebes (Podicipedidae) with upturned versus straight bills. Information in the literature on the diet of the two loon species from marine habitat in the non-breeding season is summarized in Appendix 1. Quantification of the diet in the referred sources is often unclear, but compared by taxa, only Common Loons have been reported to include pelagic prey in their diet, yet only marginally so.

According to North (1994) and Uher-Koch (2020), the food resources used by the Yellow-billed Loon during the non-breeding season remain poorly known. From a study of birds in captivity, Barr (1996) concluded that Common Loons prefer fusiform fishes but will opportunistically feed on prey species that are most readily available.

Present study presents new data on the food and on aspects of feeding behaviour of Yellow-billed and Common Loons obtained in the non-breeding season on the Norwegian coast, where their distributions largely overlap. The food and feeding of the two species are reviewed in relation to Jehl's (1970) hypothesis that Yellow-billed Loon should be the one most prone to feed on bottom-living organisms.

MATERIAL AND METHODS

Stomach examinations

Thirteen Yellow-billed Loons and fourteen Common Loons were brought to the Natural History Collections of the University Museum of Bergen from different sites in the species' wintering area on the Norwegian coast. The geographical distribution of the examined specimens is given in Figure 1, with details in Appendix 2.

The stomach contents of salvaged birds were examined and described during preparation of study specimens for museum collections. Three of the Yellow-billed Loons included in our study were from 1909 and the stomach contents, while remaining unpublished, were listed in the museum's bird specimen catalogue. The stomach contents of these birds were most likely examined and identified by Dr. Sigurd Johnsen, the curator of vertebrates at that time who was a notable ichthyologist (Brinkmann 1949). The remaining loons were salvaged during the 36-year period of 1987–2022, and we examined these birds ourselves.

The Yellow-billed Loons were salvaged during October–May, and the Common Loons from November–April with one specimen each from June and July. Being from the nonbreeding range on the coast, the June and July specimens were included despite being salvaged during the summer. Both species arrive on the Norwegian wintering grounds in September–October and leave in late April–early May (Jonsson & Tysse 1992), but a few, chiefly immature birds, may over-summer on the wintering grounds. Most of the salvaged birds with a known cause of death had drowned in gill nets (Appendix 2), which was also probably the case for most of the specimens where no information on cause of death was reported.

Except the three birds from 1909, all specimens were stored at deep-freeze temperatures before dissection took place. No information was recorded about their handling before the specimens were frozen, and thus material in the digestive tract presumably had been subject to postmortal digestion to varying degree. Processes after death could affect soft tissues, whereas hard bony, calcareous, and chitinous material should remain undigested.

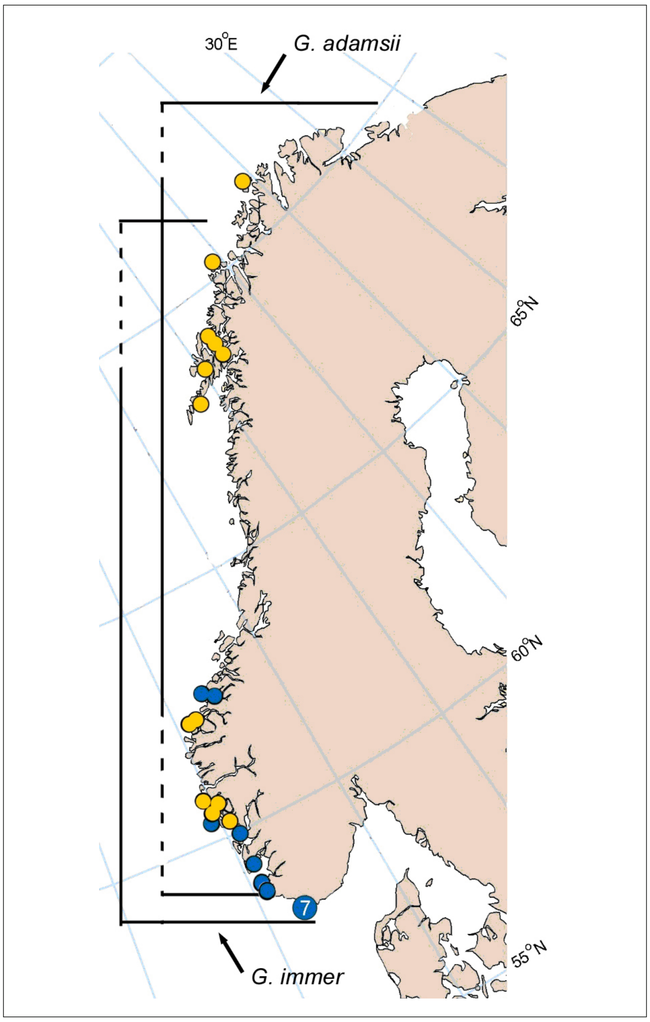

Figure 1. Location of the individuals of Yellow-billed Loons (yellow dots) and Common Loons (blue dots). The stretches of the Norwegian coast inhabited by the two species during the non-breeding season are indicated by solid black lines, stretches with sparse occurrences are indicated with dotted lines. Seven Common Loons in the southernmost part of the range were from sites close enough to be represented by a single dot.

We examined oesophagi as well as gizzards for presence of food items. Prey remains were transferred to petri dishes and the stomach and oesophagus were flushed in a basin of water to recover any prey remains that might be lodged in tissue folds. All food items were preserved in 75% ethanol, and identified to lowest taxon possible. Where necessary, we compared prey remains with reference specimens in the extensive osteological fish collection at the museum. For details, the remains were examined in a dissection microscope (6.4–40× magnification). With extensive experience from examining bone fragments from archaeological excavations one of the authors (OFB) was able to identify fishes to species level from even tiny bone fragments.

Table 1. Stomach contents of Yellow-billed and Common Loons from birds salvaged in the non-breeding range along the Norwegian Coast.

Prey			YELLOW-BILLED LOON N birds (13)	YELLOW-BILLED LOON N prey (37)	COMMON LOON N birds (14)	COMMON LOON N prey (156)
Bottom-living*						
Malacostraca:	Decapoda					
		Galathea nexa			2	2
		Galathea strigosa			4	18
		Cancer pagurus			2	4
		Carcinus maenas			1	1
		Liocarcinus depurator			1	14
		Hyas coarctatus			1	1
Gastropoda:	Trochidae					
		Steromphala cineraria			1	8
Bivalvia:	Myidae					
		Mya truncata			1	1
Actinopterygii:	Anguillidae					
		Anguilla anguilla			1	1
	Gadidae					
		Gadus morhua	1	2	1	1
	Gobiidae					
		Gobiidae indet.			1	1
	Syngnathidae					
		Syngnathus acus			1	1
	Cottidae					
		Myoxocephalus scorpius			1	2
	Labridae					
		Symphodus melops	1	1	2	2
		Ctenolabrus rupestris			4	8
	Pholidae					
		Pholis gunnellus			2	2
	Ammodytidae					
		Ammodytes tobianus			2	76
	Blennidae					
		Lipophrys pholis			1	1
Callionymidae						
		Callionymus lyra	1	3	2	2
Cyclopteridae						
		*Cyclopterus lumpus***	1	1		
Pleuronectidae						
		Limanda limanda			1	1
		Pleuronectes platessa	1	1	1	2
		Microstomus kitt			2	2
		Hippoglossoides platessoides			1	1
Pelagic*						
Actinopterygii:	Clupeidae					
	Clupea harengus		3	3	1	1
Salmonidae						
	Salmo trutta		1	1	2	3
Gadidae						
	Pollachius virens		8	25		

* Bottom-living organisms include benthic and demersal species. Classification of fish according to Whitehead et al (1986), Muus & Nielsen (1998), Mecklenburg et al. (2014). *Ammodytes tobianus* is a bottom-living species submersed in sandy substrate in winter and for predator avoidance (Reay et al. 1986; Muus & Nielsen 1998)

**Demersal on coastal spawning grounds but otherwise pelagic (Blacker 1983; Holst 1993; Eriksen et al. 2014)

Prey remains in gizzards were more or less fragmented but we quantified the minimum number of individuals per species, judged from variation of size of bones or other structures, and from number of right-hand vs. left-hand structures of the same type. Prey individuals in oesophagus were whole or only little fragmented and could readily be counted. In the following sections, the combined contents of oesophagus and gizzard are referred to as stomach contents.

When possible, the size of individual prey was estimated from proportions of prey fragments, for fish bones by comparison to material in the osteological reference collections at the museum. Otolith lengths were converted to fish standard length based on formulae reported by Breiby (1985). Crustacean carapace sizes were calculated from measurements of rostral structures or claws of chelipeds related to proportions measured on photos of whole specimens. Diameter of gastropod shells was measured across the aperture side of the shells.

Field observations

During the winter seasons of 1996–2010, one of the authors (IB) conducted field observations of Common Loon behaviour along the coast of Jæren, Rogaland County (Byrkjedal 2017), and similar observations were collected in 2013 for foraging Yellow-billed Loons during a couple of short visits to Balsfjord, Troms County, which is a well-known locality for migrating and wintering Yellow-billed Loons (Byrkjedal et al. 2000).

The field observations provided information on prey species brought to the surface for handling, the number of dives with no fish brought to surface, and the duration of dives in relation to bottom depth. Dives without prey handling at the surface could have been unsuccessful or might be predation of small-bodied fusiform fish (Barr 1996, McIntyre & Barr 1997, Evers et al. 2010). Field observations were conducted using 8–10× binoculars and 20–60× spotting scopes.

Data on bottom depth where loons were observed feeding were extracted from the original data of Byrkjedal et al. (2000), which were collected by observers for that project. Additional data were collected during subsequent field observations by IB. The depth data were selected for present use when the coordinates of bird locations were reported accurately enough by the observer(s) to be classified to depth based on the 5 m contour intervals of the Electronic Navigational Charts for coastal Norway (2022 update, Kartverket.no).

RESULTS

Prey found in stomach samples

All of the 27 stomach samples from both species of loon contained fish, but in addition 10 of 14 stomach samples from Common Loons contained marine invertebrates (snails, bivalves, crabs; Table 1). Of the 156 individual prey items found in the stomachs of Common Loons, a total of 152 (97.4%) were bottom-living organisms and only 4 (2.6%) were pelagic. In contrast, 8 (21.6%) of the 37 prey items were bottom-living and 29 (78.4%) were pelagic in Yellow-billed Loons (Figure 2). The difference between the two species was statistically significant (Likelihood Ratio = 103.4, $p < 0.001$) with a higher proportion of bottom-living organisms in the diet of the Common Loon. In the Common Loon samples, sandeel *Ammodytes tobianus* made up 76 of the prey, which were recovered from two of the loon specimens. According to McIntyre (1988), Common Loons can ingest aggregated small fish "with the speed of a swimming-pool vacuum cleaner", and the two individuals could have been foraging on sandeel aggregations. This, however, did not skew the frequency distribution of bottom-living vs pelagic prey, as excluding these two loons gave 49 (96.1%) vs 2 (3.9%) prey, respectively, per cent frequencies practically identical to the frequencies above.

Nine stomachs of the Yellow-billed Loon (69.2%) contained only pelagic prey, 3 (23.1%) had a mixture of pelagic and bottom-living prey, and 1 (7.7%) had only bottom-living prey. None of the Common Loon stomachs contained only pelagic prey, 3 (21.4%) contained both pelagic and bottom-living prey, and the remaining 11 stomachs (78.6%) contained only bottom-living prey.

The two species of loons were recovered from somewhat different regions, with 7 of the 13 Yellow-billed Loon samples north of the Common Loon samples, and 10 of the 14 Common Loon samples south of the Yellow-billed Loon samples (Figure 1). Nevertheless, the proportion of pelagic prey of individual birds did not correlate with degrees of latitude (Spearman R = 0.07, p = 0.8 for Yellow-billed Loon and R = -0.39, p = 0.2 for Common Loon). Samples from both species were obtained in the overlapping region of 60–63° N, but here Yellow-billed Loons had a total of 60% pelagic prey (n = 10) whereas Common Loons had none (n = 41). The difference between species in the proportion of pelagic vs bottom-living prey was still upheld in the zone of overlap (Likelihood Ratio = 25.759, $p < 0.001$).

Marine invertebrates comprised 49 of the prey items (31.4 % by numbers) of Common Loons but none of the prey items in Yellow-billed Loons. The difference in favour of piscivory in Yellow-billed Loon is statistically significant (Fisher's Test, $p < 0.001$).

In the present material, saithe *Pollachius virens* was a staple part of the diet for Yellow-billed Loons occurring in 61.5% of the birds and constituting 67.6% of the total number of prey. The diet of Common Loons was more varied, but wrasses (Labridae) occurred in 42.9% of the birds and squat lobsters *Galathea* spp. constituted 12.8% of the prey items by numbers. The number of individual prey per stomach varied from 1 to 6 in Yellow-billed Loons and from 1 to as many as 75 in the Common Loons. The high number in the latter was due to one of the two birds that had preyed upon sandeel

Table 2. Number of prey items in different size groups from the stomachs of Yellow-billed and Common Loons. Measurements of fish are given in total length (cm) where NM = not measurable.

	Yellow-billed Loon								**Common Loon**							
	6–10	11–15	16–20	21–25	26–30	31–35	36–40	NM	6–10	11–15	16–20	21–25	26–30	31–35	36–40	NM
Clupea harengus								3								1
Salmo trutta					1					1				1		1
Anguilla anguilla																1
Gadus morhua			1				1								1	
Pollachius virens	2	16	1	3	1	2										
Gobiidae indet.									1							
Syngnathus acus											1					
Myoxocephalus scorpius																2
Symphodus melops								1		1						1
Ctenolabrus rupestris									1	6		1				
Labridae indet.																1
Pholis gunnellus									1		1					
Ammodytes tobianus										76						
Lipophrys pholis										1						
Callionymus lyra								3		1						1
Cyclopterus lumpus																eggs
Limanda limanda												1				
Pleuronectes platessa	1									2						
Microstomus kitt										1						
Hippoglossoides platessoides										1						
Sum fish	3	16	2	3	2	2	1	7	3	90	2	2	0	1	1	8

Invertebrates (only in Common Loons, n = numbers with measurements)	
Galathea nexa	carapax length: avg. 3.0 cm; range 2.6–3.8 cm; n = 2
Galathea strigosa	carapax length: avg. 3.4 cm; SD 0.7; range 1.8–4.5 cm; n = 16
Cancer pagurus	carapax width: avg. 2.7 cm; range 1.5–4.4 cm; n = 4
Carcinus maenas	carapax width: 5.0 cm; n = 1
Liocarcinus depurator	carapax width: avg 4.9 cm; SD 1.1; range 2.3–6.4 cm; n = 13
Hyas coarctatus	carapax width: 4.5 cm; n = 1
Steromphala cineraria	largest diameter: avg. 8.2 mm; SD 0.6; range 7.1–8.9 mm; n = 8
Mya truncata	siphon: length 64.4 mm; width 6.7 mm, n = 1

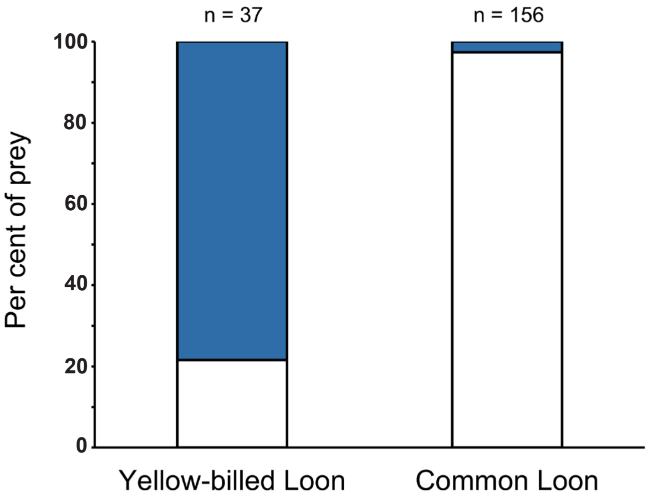

Figure 2. Proportions of pelagic (blue) and bottom-living (white) prey, found in stomachs of Yellow-billed and Common Loons summed up from Table 1.

(cf. above). When excluding these two individuals, an average of 4.3 prey items were found in the stomachs of Common Loons, comparable to the average of 2.8 prey items in Yellow-billed Loons.

Some prey were fragmented to an extent that no exact size measurements or reasonably accurate size estimates could be made (Table 2). Clearly, however, most of the prey animals were 20 cm or less in length, with most invertebrates, including crabs, being only a few centimetres. The largest fish in the material was an Atlantic cod *Gadus morhua*, with one specimen estimated to have had a total length of ca. 40 cm recorded in either of the loon species.

One of the Yellow-billed Loons contained a lump of skin fragments from a lumpsucker *Cyclopterus lumpus* along with six lumpsucker eggs, but without any bones. The species may have occurred in the bird's stomach because the fish had been torn open by the loon to get access to the soft interior, which was an action also seen during the field observations (see below).

Surprisingly, one of the Common Loons had eaten a bivalve, which could be identified as a well-grown example of a blunt gaper *Mya truncata*. The item found in the digestive tract was an intact siphon of 6 cm length (Table 2). No bivalve shell remains were found in the stomach, so presumably the loon had bitten off and swallowed the siphon and whatever soft clam tissue that was attached.

Gastroliths

Pea-sized pebbles were found in the gizzards of all the Common Loons, an average of 10.4 ± 5.4 SD gastroliths per bird (range: 2 to 21). In contrast, the ten Yellow-billed Loons that we dissected had an average of 2.2 ± 2.0 SD gastroliths per bird (range: 0–6 gastroliths). The difference between the two loon species in gastrolith numbers is statistically different ($t = 4.5$, $p < 0.001$). Eight pea-sized shells from top snails *Stermophala cineraria* were found in the stomach of one of the Common Loons (Table 1) and could have been swallowed as gastroliths instead of as food items. However, the same loon also had 11 ordinary gastroliths in its stomach, and thus the snails were most likely ingested as food.

Other items

One of the Common Loon stomachs contained a thin piece of clear plastic, about 13 x 13 mm in size and 0.2 mm thick.

Field observations of prey

Field observations from a total of 77 Common Loons and 8 Yellow-billed Loons comprised 955 dives of the first species and 52 dives of the second. Of the dive cycles, Common Loons surfaced with fish in 133 cases (14%) and Yellow-billed Loons in 3 (6%). Since the number of dives observed differed for individual loons, the 10 first dives of each bird were extracted for statistical comparisons. The totals included 22 Common Loons and 3 Yellow-billed Loons, with 21 and 1 prey, respectively, which did not differ statistically (Fisher exact test, $p = 0.284$). The Yellow-billed Loons surfaced with a flatfish Pleuronectiformes in two of the cases and a lumpsucker in the third. In the case of the lumpsucker, the loon only fed from the interior of the fish and discarded the tough integument. Common Loons brought seven types of fish to the surface for handling, including flatfish in 111 cases, sculpins (Cottidae) in five cases, pipefish (Syngnathidae) in five cases, eelpouts (Zoarcidae) in four cases, Atlantic cod in two cases, unidentified codfish (Gadidae) in two cases, and unidentified fish in three cases. All of the identified types of fish were benthic or demersal species associated with bottom habitats.

Bottom depth at feeding, dive duration vs. depth, and feeding dispersion

Field observations for 135 Common Loons showed feeding over bottom depths from the 1–5 m interval up to the 25–30 m interval, whereas in 92 Yellow-billed Loons the deepest categories extended down to the 165–170 m depth interval (Figure 3). The distribution of depths differed significantly between the two species (Kolmogorov-Smirnov Goodness of Fit for Continuous Data, $D = 0.4808$, $p < 0.005$). Median values were 1–5 m for Common Loons and 10–15 m for Yellow-billed Loons. In Yellow-billed Loons, 12.0% of the birds dived over bottom depths in the interval 30–170 m.

Diving durations were accurately recorded for two Yellow-billed Loons foraging over deep bottom depths, one of them, diving over 70 m bottom depth spent 47 seconds under water in one dive, while the other one, diving over a bottom depth of 170 m, spent 63 seconds in a single dive. Dive durations in deep water were within the diving times recorded for three individuals of Yellow-billed Loons foraging over a bottom depth of 5–6 m, for which 36 dives gave an average 63 ± 24 SD seconds per dive (range: 10–107 seconds). In comparison, 33 dives of 7 Common Loons fishing over

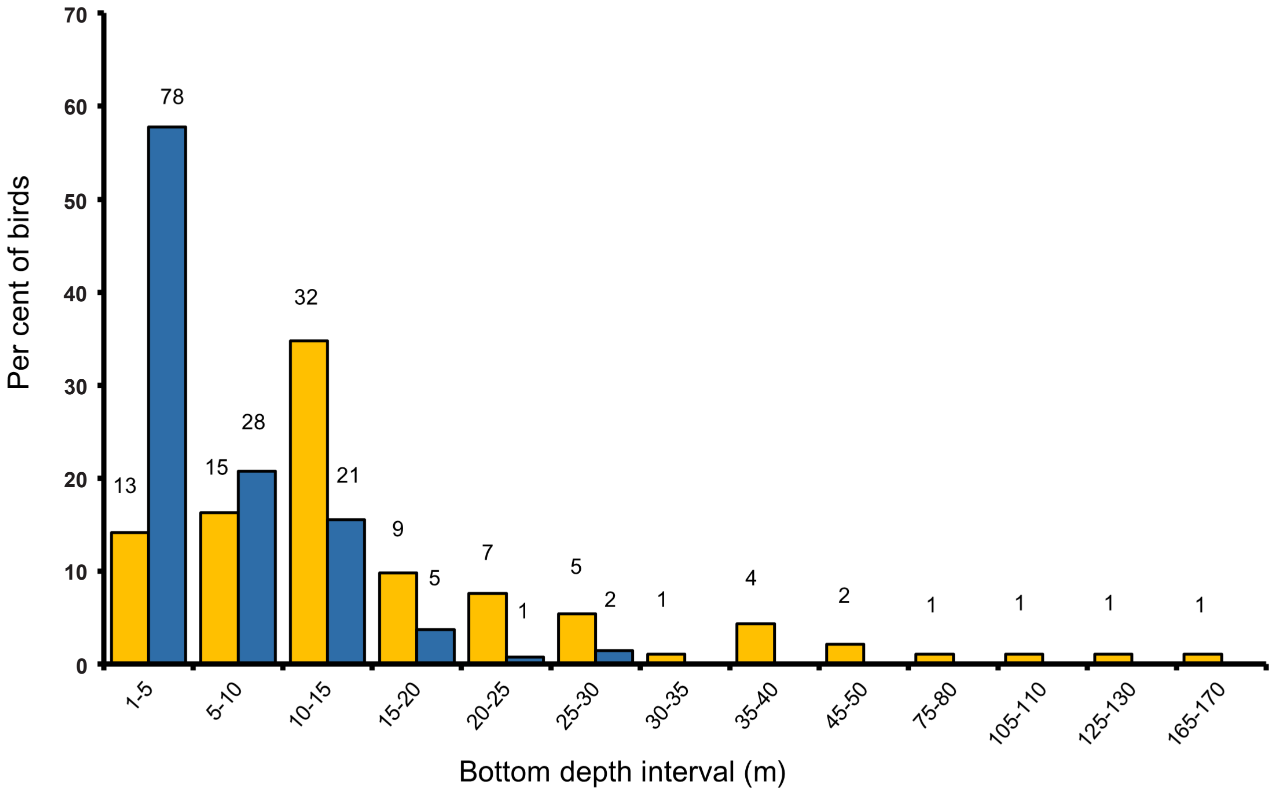

Figure 3. Bottom depth categories where foraging birds were first observed in field observations of Yellow-billed Loons (92 birds, yellow columns) and Common Loons (135 birds, blue columns). Number of birds given above each column.

a bottom depth of 1–5 m had an average duration of 72 ± 31 SD seconds (range: 11–150 sec).

Notes were made on estimated dispersion distances and timing in pairs or groups of feeding loons. The observations were made in flat sea and with the use of a speech recorder to avoid interrupted view while taking notes, giving full confidence that the same individuals were observed. Two cases of two Yellow-billed Loons that were probably pairs were observed 2 October 2013, showed that both pair members made food-searching dives while following close to one another. Estimated distances between the birds in 16 successive dives were median 2 m (0.5–45 m) for the one pair and in five successive dives of the other pair were 6 m (3–50 m). The birds also made their dives in synchrony, timed exactly for six dives gave 0–13 seconds between their start of dive (average 2.7 ± 4.7 SD) and 0–11 seconds between their surfacing (average 5.0 ± 5.1 SD). In cases where Common Loons were observed swimming close together (a metre or so apart) when not feeding, the birds separated from each other before they started to dive and forage for food. In 13 different cases of two adults together that were presumably paired, the birds started and then continued diving for food after they had moved a median of 100 m apart (range 13–200 m). For 20 different cases of adults with juvenile(s) that were presumably family groups (Byrkjedal 2011), the corresponding figures were 50 m (range 20–100 m). The Common Loons carried on their foraging independent of each other without any synchrony of their dives.

DISCUSSION

The salvaged specimens of loons had a north-south distribution with more Yellow-billed Loons in the north and Common Loons in the south. However, none of the prey species identified in the stomach contents are restricted to areas of the Norwegian coast inhabited by only one of the two loon species (Moen & Svensen 2000, Pethon 2019). Thus, diet comparisons were unlikely to be biased by geographical variation in the distribution of their prey. Similarly, the proportion of pelagic vs. bottom-living prey in the stomachs was not related to latitude.

Previously published data indicated that Yellow-billed Loons and Common Loons feed on similar type of organisms in the non-breeding season. Fish constituted the main prey category, although invertebrates, such as crustaceans, clams, snails, and polychaetes were taken. In contrast, the present study found notable differences between the two loon species in the species of fishes that were preyed upon, and only Common Loons included invertebrates in their diet.

The available data do not support Jehl's (1970) hypothesis of Yellow-billed Loons feeding more on bottom-living organisms than Common Loons. While previously published information from stomach examinations failed to indicate a difference in bottom-living and pelagic prey in the two species (Appendix 1), the present study from Norwegian waters actually shows results contrary to Jehl's (1970) hypothesis, as

Common Loons were found to feed much more often on bottom-living organisms that did Yellow-billed Loons, the latter almost exclusively feeding on pelagic fish. The differences in diet observed in the stomach contents were consistent with field observations that Yellow-billed Loons routinely foraged in far deeper waters than Common Loons. Common Loons were mostly observed feeding in coastal waters that were only a few metres depth, which was consistent with previous studies (Guðmundsson 1952, Haney 1990, Ford & Gieg 1995, McIntyre & Barr 1997, Evers et al. 2010). In contrast, Yellow-billed Loons were found actively feeding in deep waters with bottom depths down to 170 m (Byrkjedal et al. 2000, and present study). Information on diving depth has not been reported for Yellow-billed Loons (Uher-Koch et al. 2020), but three salvaged birds were recovered from gill nets at depths of 25–30 m (Appendix 2). Common Loons have been reported to be able to dive down to 60 m (Schorger 1947). It seems unlikely that Yellow-billed Loons are diving for bottom-living prey when feeding over depths that are almost three times greater. The two recorded diving times above 70 and 170 m bottom depth do not deviate from the diving times recorded in shallow waters, indicating that the birds did not dive all the way to the bottom.

Foraging activity differed between the species with large distances among social groups of Common Loons versus close distances and synchronized diving of Yellow-billed Loons. The difference indicates that Common Loons were likely feeding on dispersed bottom-living prey, while the coordinated behaviour of Yellow-billed Loons indicated that shoaling pelagic prey were targeted (cf. Evers et al. 2010).

Yellow-billed Loons and Common Loons surfaced without prey in 94.2% and 86.0% of their dives, respectively. No prey brought to the surface may either be due to an unsuccessful dive where no prey were capture or the prey may have been swallowed under water. According to e.g. McIntyre and Barr (1997), small fusiform prey are swallowed whole by Common Loons while they are still under water, and when not surfacing with prey the loons might have been catching shoaling fish, which are typically of fusiform shape. However, the difference between the species in surfacing without prey was not statistically different.

Both species of loons ingest pebbles to aid breaking up food in their gizzards (Collett 1894a,b, Cottham & Knappen 1939, Jehl 1970, Portenko 1981, Heubeck et al. 1993, Barr 1996, McIntyre & Barr 1997). The number of gastroliths found in the Common Loons matches what has been reported elsewhere, as does that of Yellow-billed Loon, although the latter refers to only a single breeding season bird (Portenko 1981). The low number of gastroliths found in the stomachs of Yellow-billed Loons was on average only a fifth of that found in Common Loons. The difference is suggestive because a diet of the more armoured organisms found among bottom-living species would be expected to require more gastroliths than a diet on fusiform pelagic shoaling type of fish. A higher number of gastroliths may thus be linked to a higher proportion of bottom-living organisms in the diet of Common Loons.

A previous comparison of habitat characteristics of the two species of loons wintering along the Norwegian coast found that Yellow-billed Loons were reported more often over soft bottom substrates than Common Loons, which tended to occur where bottoms were rocky (Byrkjedal et al. 2000). Rocky bottoms harbour a higher diversity of epifauna than soft substrate consisting of mud (e.g. Friedrich 1969), while shoals of fish and other pelagic organisms may depend on hydrology rather than bottom structure. The habitat differences of the two loons in relation to bottom substrate may be explained by their different tendencies to feed on bottom-living versus pelagic organisms.

On the western coast of Norway, Folvik and Mjøs (1995) found that Yellow-billed Loons were more numerous during spring migration than expected from the low number of birds known to winter along the North Sea coasts. The authors suggested that the species could have a wider winter distribution at sea where they have not been detected by observers. From the pelagic diet of the Yellow-billed Loon this seems reasonable. In summary, the present study does not support Jehl's (1970) hypothesis that Yellow-billed Loons forage more on bottom-dwelling organisms than Common Loons. Instead, new evidence from stomach contents and field observations of feeding behaviour indicates that Yellow-billed Loons forage primarily on a diet of pelagic fish during the nonbreeding season.

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Appendix 1. Taxa of invertebrates and fish reported (x) in the non-breeding season diet of Yellow-billed and Common Loons according to published literature.

Habitats and taxa			Yellow-billed Loon	Common Loon	Source
Bottom-living (benthic, demersal)					
Invertebrates					
	Polychaeta	*Nereis* sp.	x		c
		indet.		x	d
	Mollusca	*Protothaca staminea*		x	e
		Planorbis sp.		x	d
		Cephalopoda		x	d
		indet.	x	x	c; f
	Echinodermata	Asteroidea		x	j
	Amphipoda	*Ochromonella* sp.	x		c
		Anonyx nugax	x		c
		indet.		x	d
	Isopoda	*Idothea* sp.	x		c
	Natantia	*Pandalus danae*	x		c
		Spirontocaris ochotensis	x		c
		Crangon crangon		x	g
		indet.		x	d
	Reptantia	*Cancer pagurus*	x		c
		Carcinus maenas		x	f
		indet.		x	d; i; j
Fish					
	Anguillidae	*Anguilla anguilla*		x	d; k
	Ammodytidae	*Ammodytes americanus*		x	k
		Ammodytes sp.		x	d
	Sciaenidae	*Cynoscion regalis*		x	k
	Embiotocidae	*Cymatogaster aggregate*		x	k
	Gasterosteidae	*Gasterosteus aculeatus*		x	d
	Syngnathidae	*Syngnathus* sp.		x	k
	Gadidae	*Microgadus proximus*	x		c
		Gadus morhua		x	d
		Melanogrammus aeglefinus		x	d; k
		Merlangius merlangus		x	d; k
		M. aeglefinus/ Pollachius virens		x	f
	Gobiidae	*Pomatoschistus minutus*		x	g
		indet.		x	d
	Zoarcidae	*Zoarces viviparus*		x	d; k
	Triglidae	*Eutrigla gurnardus*		x	d
	Scorpaenidae	*Sebastes alutus*	x		a
	Cottidae	*Myoxocephalus scorpius*	x	x	b
		Myoxocephalus cf. joak	*x*		c
		Leptocottus armatus	*x*		c
		Hemilepidotus hemilepidotus		x	k
		indet.	x		c
	Scophthalmidae	*Scophthalmus rhombus*		x	g
	Cyclopsettidae	Citharichtyys sordidus	x		h
	Pleuronectidae	Platichthys flesus		x	d; g
		Platichthys stellatus		x	e
		Pseudopleuronectes americanus		x	j
		indet.		x	d

Appendix 1. *Continued*.

Habitats and taxa			Yellow-billed Loon	Common Loon	Source
Pelagic					
	Fish				
	Clupeidae	*Clupea harengus*		x	d; k
		Sprattus sprattus		x	d; k
		Brevoortia tyrannus		x	k

Sources: a. Bailey (1922); b. Collett (1894a,b); c. Cottham & Knappen (1932); d. Madsen (1957); e. Paulson (1988); f. Heubeck (1993); g. Leopold et al. (2000); h. Jehl (1970); i. Daub (1989); j. Ford & Gieg (1995); k. McIntyre & Barr (1997)

Appendix 2. Details of the 27 individual loons examined in this project, with dates sorted by winter phenology. Collection acronyms for prepared specimens: LNM Lista naturmuseum; AU, The Arctic University Museum of Norway; ZMUB, ZU, VA The University Museum of Bergen.

Species	ID Number	Sex	Age	Date (dd.mm.yyyy)	Locality	Cause of death
Yellow-billed Loon						
	ZMUB 3950	f		17.10.1909	Geitanger, Hordaland	
	AU 13/2002	m	ad	31.10.2001	Sommerøy, Tromsø, Troms	gillnet, 30 m depth
	ZMUB 3955	m	juv	20.11.1909	Herdla, Hordaland	
	AU 72/1990	m		06.12.1990	Stokmarknes, Hadsel, Nordland	gillnet, 30 m depth
	ZMUB 3962	f	juv	18.12.1909	Solsvik, Hordaland	
	ZU 7910	m?	juv	02.02.2014	Osøyro, Hordaland	
	AU 3/2002	m	juv	01.03.2000	Hadsel, Nordland	
	AU 27/1987	f	ad	09.03.1987	Rogla, Harstad, Troms	entangled in longline
	ZMUB 15518	f	juv	22.03.1992	Havøy, Sandøy, Møre og Romsdal	oil slick
	ZMUB 15512	m	ad	02.04.1990	Gursken, Møre og Romsdal	
	AU 216/2016		juv	07.04.2016	Stamsund, Vestvågøy, Nordland	gillnet, 25-30 m depth
	AU 64/1998	f	ad	00.05.1996	Dverberg, Andøy, Nordland	
	AU 65/1998	m	ad	00.05.1996	Ingøy, Måsøy, Finnmark	
Common Loon						
	ZMUB 15525	m	juv	13.11.1996	Våge, Tysnes, Hordaland	gillnet
	ZMUB 16228	m	ad	Winter 2008/09	Molde, Møre og Romsdal	
	ZMUB 16227	f	juv	Winter 2008/09	Molde, Møre og Romsdal	gillnet
	LNM 15644	f	ad	09.01.2003	Lista, Agder	gillnet
	LNM 15645	m	juv	09.01.2003	Lista, Agder	gillnet
	LNM 15656	f	ad	Jan.-March 2003	Lista, Agder	gillnet
	ZMUB 16094	f	ad	12.02.2018	Hellestø, Klepp, Rogaland	found shot
	(no number)	m	juv	15.03.2011	Boknafjorden, Rogaland	gillnet
	LNM 14328	m	juv	20.03.2022	Straumen, Lista, Agder	
	LNM 15654	f	ad	25.03.2003	Lista, Agder	gillnet
	LNM 14349	m	juv	10.04.2022	Verevågen, Lista, Agder	gillnet
	(no number)	juv		02.06.2019	Hjartøysundet, Alvheim, Hordaland	gillnet
	LNM 15655	m	ad	01.07.2007	Lista, Agder	gillnet
	VA-128/25	f	ad	25.02.2025	Ølberg, Sola, Rogaland	

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