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ORIGINAL ARTICLE

Combining stable hydrogen (δ^2H) isotopes and geolocation to assign Scaly-sided Mergansers to moult river catchments

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Abstract Scaly-sided Mergansers *Mergus squamatus* breed on freshwater rivers in Far East Russia, Korea, and China, wintering on similar habitat in China and Korea, but information on their post-breeding moulting habitats remains elusive. We combined analysis of stable hydrogen isotope ratios (δ^2H) in flight feathers from nesting females equipped with geolocators to test whether we could correctly identify their use of moulting rivers (which show a strong north–south gradient in river water δ^2H characteristics) based on feather δ^2H values. The results are the first ever to demonstrate a strong positive correlation ($r^2 = 0.91$) between measured river catchment water δ^2H and feather δ^2H from birds of known moulting location (from geolocation) in an avian piscivorous species. Furthermore, our δ^2H results overwhelmingly supported previous determinations based on feather δ^{13}C and δ^{15}N measurements from the same individuals confirming that most Scaly-sided Mergansers of both sexes moulted on freshwater, although four non-breeding and failed breeding females (out of 21) and one male (out of six) apparently undertook moult migration to brackish and marine waters. The single case where the δ^2H results contradicted previous isotopic evidence was likely due to birds eating migratory fish of marine provenance that migrate up freshwater rivers. These results confirm the potential power of feather δ^2H to assign piscivorous birds to specific river catchment moult sites and the utility of using multiple stable isotopes to assign birds to moult habitat and location in potentially complex estuarine and brackish situations or where migratory prey may be used by birds in freshwater habitats.

Keywords Habitat use · Primorye · Remigial moult · Deuterium · Carbon-13 · Nitrogen-15

Zusammenfassung

Kombination von stabilen Wasserstoff-Isotopen (δ2H) und Geolokation zur Bestimmung der Mauserhabitate des Schuppensägers *Mergus squamatus* in Flusseinzugsgebieten

Schuppensäger (*Mergus squamatus*) brüten auf Süßwasserflüssen im fernen Osten Russlands, in Korea und China, und sie überwintern in ähnlichen Habitaten in China und Korea, aber Informationen über das Mauser-Habitat nach der Brut sind nur schwer zu erlangen. Wir kombinierten die Analyse von Isotopenverhältnissen stabiler Wasserstoff-

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Isotopen (δ2H) in Flugfedern nistender Weibchen mit Daten aus von den Weibchen getragenen Geolokatoren, um festzustellen, ob wir ihre Nutzung von Mauser-Flüssen anhand der δ2H-Werte aus den Federn korrekt identifizieren können (die Flüsse zeigen einen starken Nord-Süd-Gradienten in der δ2H-Charakteristik des Wassers). Die Ergebnisse zeigen erstmalig für eine piscivore Vogelart eine stark positive Korrelation zwischen dem δ2H des gemessenen Flusswassers und dem δ2H von Vögeln mit aufgrund der Geolokation bekanntem Mauser-Gebiet. Darüber hinaus bestätigen unsere δ2H-Ergebnisse hervorragend frühere Analysen auf Grundlage von δ13C- und δ15 N-Messungen aus Federn derselben Individuen, die bestätigen, dass die meisten Schuppensäger beiderlei Geschlechts auf Süßwasser mauserten, wobei allerdings vier nicht oder erfolglos brütende Weibchen (von 21) und ein Männchen (von 6) offenbar einen Mauserzug zu Brack- oder Seewasser unternommen haben. Der einzige Fall, in dem die δ2H-Ergebnisse früheren Isotopenbestimmungen widersprachen, hatte wahrscheinlich damit zu tun, dass die Vögel wandernde Seefische fraßen, die Süßwasserflüsse hinaufwandern. Diese Ergebnisse unterstreichen den möglichen Nutzen von δ2H-Messungen aus Federn, um piscivore Vögel einem bestimmten Flusseinzugsgebiet als Mauser-Habitat zuzuordnen, und sie bestätigen die Nützlichkeit des Gebrauchs mehrerer stabiler Isotope, um Vögel einem Mauserhabitat und einem Ort in möglicherweise komplexen estuarinen und brackigen Gegebenheiten zuzuordnen oder wenn wandernde Beute von Vögeln in Süßwasser-Habitaten gefressen wird.

Introduction

The Scaly-sided Merganser *Mergus squamatus* is an endangered species restricted to small breeding populations in the Russian and Chinese Far East (Solovyeva et al. 2014a). An important component in the management of this poorly known species is to ascertain the importance of post-breeding habitat where birds are especially vulnerable due to flightlessness during moult. Establishing linkages among various components of the annual cycle of migratory species is essential to full avian life-cycle modelling (Marra et al. 1998; Gunnarsson et al. 2005). Such research approaches to management have become more viable in recent decades due to the development of more miniaturized and less intrusive tracking devices such as light-level geolocators (Stutchbury et al. 2009) and the forensic use of naturally occurring endogenous markers utilizing stable isotope geochemistry and genetics (Hobson and Wassenaar 2008; Ruegg et al. 2014).

Stable isotope analyses in feathers offer the potential to identify the nature of the isotopic landscape or "isoscape" to which individual migratory birds were exposed during feather growth (reviewed by Hobson 2008). Unless produced by endogenous reserves previously accumulated in contrasting isoscapes (Morrison and Hobson 2004; Fox et al. 2009), feather isotope ratios reflect those of the local diet, and since food-webs in turn reflect isoscape patterns, geographic information on moult locations is often possible. Analyses of feather stable hydrogen isotope ratios (δ^2H_f) in particular has proven useful in assigning origins of individuals due to the strong continental patterns in precipitation δ^2H (δ^2H_p). This principle has been successfully applied to identifying migratory connectivity and movement patterns of several bird species in Europe (Hobson et al. 2004a; Bearhop et al. 2005; Newton et al. 2006; Yohannes et al. 2007; Procházka et al. 2008, 2013; Hobson et al. 2012a) and North America (Hobson et al. 2004b; Hobson 2008; Hobson et al. 2014). Continental patterns of hydrogen isotopes in precipitation (δ^2H_p) are generally well-known and once the relationship between long-term weighted mean δ^2H_p and δ^2H_f is established through a rescaling function (Wunder 2010; Hobson et al. 2012b), a δ^2H_f isoscape can be created to infer moult origins. This approach has been successfully applied to a number of studies aimed at delineating origins of waterbirds, especially ducks (Clark et al. 2006; Hobson et al. 2009; Ashley et al. 2010; Gunnarsson et al. 2012; Guillemain et al. 2014). However, waterfowl that use river systems for moulting will experience water δ^2H values that may be derived from distant sources (e.g. snow melt) or may integrate precipitation patterns over broad drainages within catchments. In these cases, it would be better to use actual river water δ^2H values (Kendall and Coplen 2001), but to date, no studies have been able to link moult origins to riverine systems in this fashion. In marine systems, we do not expect much spatial structure in water δ^2H values because seawater, the source of hydrogen to marine food-webs, is fairly constant over large expanses with the exception of polar regions and areas affected by the outflows of large river systems (Friedman 1953). However, for waterbirds that may moult in freshwater, brackish or marine biomes, the measurement of δ^2H_f, in combination with other isotopes (e.g. $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) may be informative.

In an earlier isotopic ($\delta^{13}C$, $\delta^{15}N$) analysis of feathers from Scaly-sided Mergansers (Solovyeva et al. 2014b), we provided evidence that birds moulted in freshwater rivers, brackish and marine waters in Primorye, Far Eastern Russia (Solovyeva et al. 2012). However, although $\delta^{13}C$ and $\delta^{15}N$ feather determinations were helpful in confirming the use of these sites for some individuals, both isotope ratios are affected by a range of other abiotic and biotic factors which introduced considerable variation that hindered the interpretation of the moult provenance. It is well known that δ^2H_p values show strong latitudinal patterns across continents (Dansgaard 1964; Bowen et al. 2005) and this is the case in the Russian Far East, where there is a strong north–south gradient in δ^2H_p (see Fig. S1 in supporting information). Hence, we had good reason to suspect that river waters may be sufficiently distinctive to enable discrete catchment assignment to individual moulting Scaly-sided Mergansers on the basis of δ^2H_f. Here, we used the same feather material (from the same individuals used in the earlier study) for δ^2H_f together with geolocator tracks to confirm moult origins in this species. In general, while we recognized that little is known about the behaviour of hydrogen isotopes in marine food webs, we anticipated that feathers grown in a fully marine biome would be enriched in ^2H compared to freshwater or brackish systems (Hobson et al. 2000). Specifically, we attempt to verify whether we can use δ^2H_f to identify the catchments where Scaly-sided Mergansers underwent wing moult based on distinctive differences in δ^2H in river waters (δ^2H_w) between catchments in their Primorye breeding areas (Kharitonova et al. 2012), as confirmed by tracking of individual mergansers using geolocation and our earlier $\delta^{13}C$, $\delta^{15}N$ analysis.

Methods

Free-flying Scaly-sided Mergansers were captured using 70-mm mesh, 4-shelf mist nets (3.2 × 21 m) along the Kievka River, near Lazo (43°23′N 133°54′E) during March–May. Breeding females were also captured in nest cavities during 2006–2013 on rivers of the western and eastern slope of Sikhote-Alin mountain range in Primorye, Far Eastern Russia (see Fig. 1 in Solovyeva et al. 2012). We fitted eight of the breeding Scaly-sided Merganser females (at least 2 years old) with British Antarctic Survey Mk9 (2.5 g) or with Mk11 (1.5 g) light-level geolocators, which were subsequently retrieved and data downloaded (Solovyeva et al. 2012). Geolocators were attached to engraved plastic tarsus rings by two cable ties and secured through drilled holes (Solovyeva et al. 2012). Feather isotope compositions derived from feather samples taken from these individuals at subsequent recapture could, therefore, be calibrated with known positions during their previous moult season based on geolocation histories. Because males cannot be readily recaptured to retrieve devices, these were not fitted with geolocators. Mean positions for brood-rearing females during the summer were on average within 61.9 km of the nest site (Solovyeva et al. 2012), suggesting reasonable device accuracy for subsequent location of moulting quarters and assignment to discrete river catchments, although we cannot be confident that changes in behaviour during moult could affect the accuracy of geolocation (as demonstrated for other species, Lisovski et al. 2012). Captured birds were assigned to after hatch-year (AHY), after second-year (ASY) or after third-year (ad) based on the extent of the black stripe on the speculum (D. Solovyeva unpubl. data) to retrospectively determine the age at the time of new growth of feathers analysed for stable isotope composition. We assumed mid-July to late August to be the female moult period, which corresponds to periods without major movement during the moulting flightless period (Kolomiytsev 1992) confirmed by the evident lack of movement based on sunrise/sunset data from geolocation. Immersion of geolocator electrodes in water enabled post hoc analysis of when the bird was on saline versus freshwater based on differential logged conductivity measurements.

Feather samples were clipped from the lowest secondary under-wing coverts for analysis from a larger sample of 21 females (four of which were re-sampled in consecutive years) and six males of all age classes (see below). Feathers from all these individuals had been previously analysed for $\delta^{13}C$ and $\delta^{15}N$ (Solovyeva et al. 2014b). Feather samples were washed in 0.25 M NaOH solution to remove surface contamination, rinsed in distilled water, dried in an oven at 50 °C to constant weight, and ground to fine powder using a liquid nitrogen cooled impactor mill and analysed for δ^2H using the methodology previously described in Hobson et al. (2004a). Briefly, 0.35 mg of feather material was weighed into silver capsules and combusted under helium flow in a Hekatek oven at 1350 °C interfaced with a Carlo-Erba (Milan, Italy) elemental analyser. The resultant H_2 gas was measured for δ^2H using the comparative equilibration technique of Wassenaar and Hobson (2003) using three keratin calibrated standards Caribou Hoof Standard (CBS −197 ‰), Commercial Keratin Standard (SPK −121.6 ‰) and Kudu Horn Standard (KHS −54 ‰). All measurements are reported in δ-notation in parts per thousand (‰) relative to the Vienna Standard Mean Ocean Water (VSMOW)—Standard Light Antarctic Precipitation (SLAP) scale. Measurement error was estimated to be ±2 ‰. Water samples were taken systematically from most of the river catchments throughout the Sikhote-Alin Mountain Range as part of widespread investigation of river water stable isotopes in southern Far East Russia (see Figure 1 in Kharitonova et al. 2012). For measurement of δ^2H in river water, samples were injected into a Thermo Finnigan TC/EA (Temperature Conversion Elemental Analyzer) and combusted using pyrolysis at 1450 °C. H_2 gas was subsequently separated by chromatographic column and interfaced via helium flow to a Finnigan MAT253 mass spectrometer. The analytical precision was ±0.8 ‰ for water δ^2H measurements and reported relative to VSMOW-SLAP. We compared measured δ^2H_f values from birds which were (1) known from geolocation data or (2) from a known nest site which were known to have hatched young and to have moulted on a specific catchment with published values from river water in that catchment from another study (δ^2H_w, Kharitonova et al. 2012), as far as possible in the same study season. In a further three cases, where females were known to have raised broods on the Avvakumovka River (43°48′N 134°52′E) for which no water samples were available). Their δ^2H_f values were compared with samples from the adjacent Margaritovka River (43°45′N 134°37′E), which share a common watershed and, therefore, raise their waters very close to each other.

Results

Four successfully breeding females (i.e. those which raised their broods and simultaneously moulted on adjacent stretches of the same river) provided good geolocation data from five different years on the Kievka River. The mean latitude and longitude for these bird/years (±SE) during the moult period are shown in Fig. 1. This shows that despite the variation in the positions generated from geolocation analysis, we can be reasonably confident of assigning moulting birds to river catchment from such data in the other cases.

Birds known to have moulted on freshwater had δ^2H_f values ranging from −121.3 to −60.2 ‰, which corresponds to water values of −114.2 to −69.6 ‰. For the females known from geolocation data to moult in specific catchments either side of the Sikhote-Alin Mountain Range, there was a high correspondence between measures of river water δ^2H and female feather δ^2H_f ($H_f = 1.211\ H_w + 13.603$, $r^2 = 0.91$, $F_{1,9} = 81.5$, $P < 0.0001$, Fig. 2). Note that this model excludes the females from the Avvakumovka River because of the lack of δ^2H_w samples from that particular catchment. However, δ^2H_w values from the adjacent Margaritovka River, the watershed of which abuts this catchment, fits the same general pattern (Fig. 2).

Amongst the other samples from untracked birds, the much more ^2H-enriched values for those birds inhabiting brackish regions (e.g. −41.6 to −0.7 ‰) was intuitively consistent with what we might expect due to a marine influence. These results were also overwhelmingly supported by the results from our earlier $\delta^{13}C$ and $\delta^{15}N$ analyses of the same feathers where we assumed a freshwater threshold to be −20 ‰ for feather $\delta^{13}C$ and 14 ‰ for feather $\delta^{15}N$ (Fig. 3, Table S1 and see Solovyeva et al. 2014b). However, a single bird showed a feather enriched

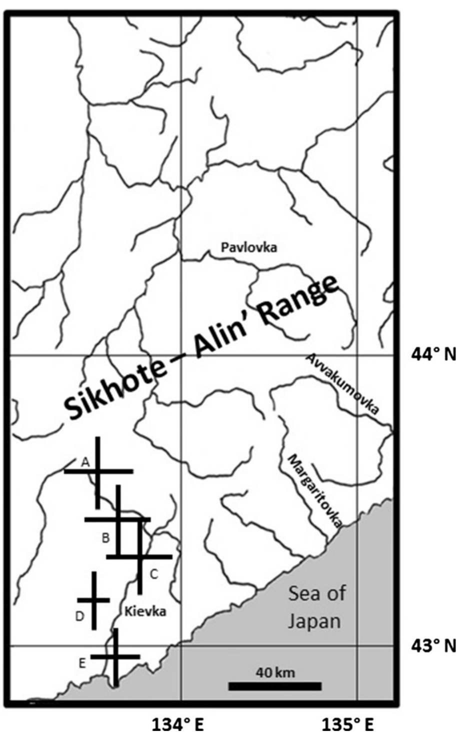

Fig. 1 Map showing the mean moulting period positions of Scaly-sided Merganser females nesting on the Kievka River fitted with geolocators as calculated post hoc from geolocation to provide an indication of the level of accuracy associated with assigning birds to particular moult catchments (for reference to water quality measurements) based on such measurements. *Crosses* indicate the mean longitude and latitude for each individual female/year combination, with associated standard errors for each. *Letters* indicate individual females in different years as identified by their geolocator codes (as shown in Table S1) as follows: A—8549 (2008), B—7856 (2007), C—6371 (2008), D—7851 (2008) and E—7851 (2007). Other river catchments named in the text are identified accordingly

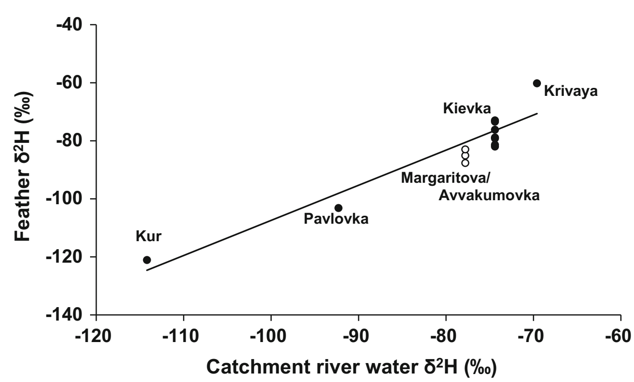

Fig. 2 Relationship between Scaly-sided Merganser feather δ^2H_f and the river water δ^2H_w on which these individuals moulted (confirmed for these individuals by geolocation) identified by river catchment. δ^2H_w determinations are based on measurements reported in Kharitonova et al. (2012 and unpubl.). Fitted regression has formula $H_f = 1.211\ H_w + 13.603$ ($r^2 = 0.91$, $F_{1,9} = 81.5$, $P < 0.0001$). Also shown (*unfilled symbols*), but not included in the regression analysis, are three females that moulted on the Avvakumovka River but plotted in relation to δ^2H_w determinations from the nearby Margaritovka River

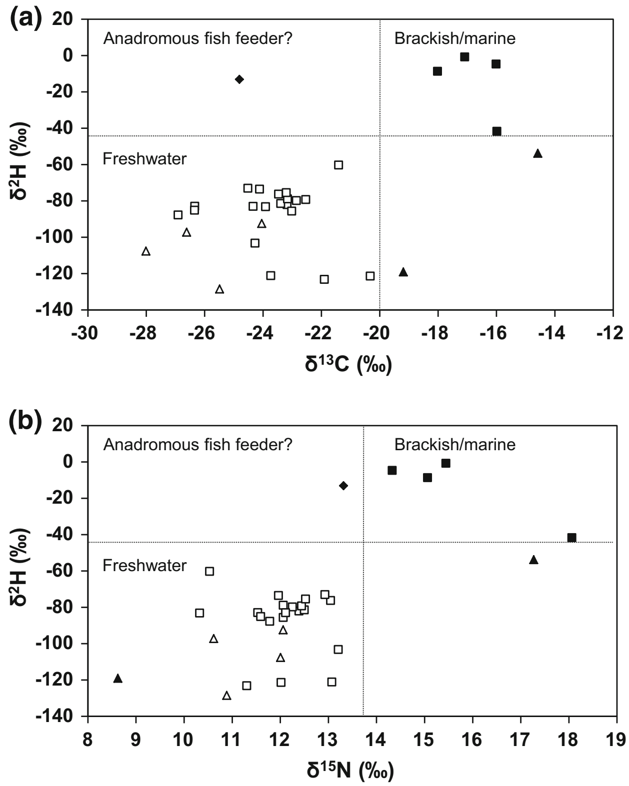

Fig. 3 Relationship between **a** feather δ^2H and δ^{13}C and **b** feather δ^2H and δ^{15}N for Scaly-sided Mergansers examined in this study. Feather δ^{13}C and δ^{15}N determinations for the same individuals are taken from Solovyeva et al. (2014b). *Squares* and *diamond* represent data for females and *triangles* for males. *Filled triangles* indicate situations where the δ^2H data from male feathers were consistent with a possible freshwater input in contrast to the δ^{13}C and δ^{15}N data. *Filled squares* show confirmed brackish/marine moulting sites confirmed across isotopes and the *filled diamond* shows female potentially feeding on anadromous fish

in ^{2}H (bird 8529: −13.1 ‰), but with a δ^{13}C (−24.8 ‰) and δ^{15}N (13.3 ‰) value more consistent with a freshwater biome. Here, the hydrogen budget of the individual was dominated by marine sources, but the carbon and (to a lesser extent) the nitrogen budget more dominated by freshwater sources. It is not clear what mechanisms may be driving the decoupling of the isotopes in this case. Our threshold approach for interpretation of the δ^{13}C, δ^{15}N and δ^2H feather data has limitations (Yerkes et al. 2008) and more extensive food-web sampling at these sites would be required to examine this question further.

Based on δ^2H_f determinations, all males used different moulting sites and or had different diets within the species' breeding range in Russia (and probably China, see the breeding range in Solovyeva et al. 2014a) and all moulted on freshwater sites except a museum specimen with a δ^2H_f value of −25.4 ‰ which suggested some brackish water influence or to have moulted on freshwater close to wintering grounds in South/Central China.

Discussion

These are the first analyses to demonstrate a sufficiently strong relationship between δ^2H_f and δ^2H_w in a piscivorous bird to enable the assignment of an individual to its previous moulting catchment based on feather samples. Using feather samples from known moult sites based on geolocation of the individual birds, our results showed that δ^2H_f analyses may be a useful means of distinguishing between female Scaly-sided Mergansers that moulted on different river catchments, as well as differentiating between marine, freshwater, and brackish habitats used by birds of both sexes during this period. The use of δ^2H extends the isotopic toolbox in deciphering moult origins in general and supported our earlier contention that only a small percentage of Scaly-sided Mergansers moulted in marine and brackish sites. These results are in keeping with previous studies (e.g. Hobson et al. 2000), but it is still not clear what may account for a large isotopic range in δ^2H values in feathers of marine birds (e.g. Knoche et al. 2007; Ostrom et al. 2014) or keratins in marine mammals (Hobson et al. 2010). Importantly, our analysis showed an extremely good correlation between δ^2H_f and δ^2H_w for freshwater locations where our geolocators confirmed moulting origins, confirming our interpretations of δ^2H_f values in assigning birds to moulting biome. The results of geolocation from the Kievka River breeding females also give confidence that these results, despite the variance in positions, are of sufficient accuracy to assign moulting birds to river catchments in such an analysis. This result also provides strong evidence that the approach can be used to assign moult origins to other waterbirds that use riverine food webs and reveals an important application of continent-wide river δ^2H_w isoscapes (Kendall and Coplen 2001).

All three adult males captured on their breeding river (the Kievka δ^2H_w = −74.4 ‰) were shown to have grown the sampled feathers during the previous year's moult on rivers situated to the north and east of the Kievka River according to their δ^2H_f determinations (−97.2, −107.6, and −128.5 ‰, see Table S1). The known north-eastern margin of the breeding range of Scaly-sided Mergansers is the Kur River, with a δ^2H_w value of −114.2 ‰. The δ^2H_f determinations of a female known from geolocation to have moulted on the Kur River were −121.1 and −121.3 ‰ in two consecutive years. Thus, the male with a δ^2H_f determination of −128.5 ‰ may have undertaken a moult migration to river systems outside of the current known breeding range. Males generally depart from breeding areas in early to mid-May, and no moulting males have ever been recorded on the Kievka River during the entire course of our study. The analysis of feather material from the unringed male obtained from the Malinovka River (a tributary of the Ussuri River on the western slope of the Sikhote-Alin range, so lacking migratory marine fish) suggest a marine diet during moult (based on $\delta^{13}C_f$ and $\delta^{15}N_f$ see Table S1). The δ^2H_f values suggest marine waters to the far north, perhaps in northern Kamchatka, from where there have been indications of males occurring during moult. All these records suggest that there is a tendency in males to undertake moult migration to areas far from the breeding grounds, generally to the north and west to remote rivers or to the north and east to the marine waters of the Sea of Okhotsk.

A potential confounding factor in our analysis is that the birds can eat migratory fish species during the moult period and that both diet and drinking water contribute differentially to feather δ^2H values (Hobson et al. 1999). Several species of marine fish migrate upstream in the rivers of Primorye to breed. Male Scaly-sided Mergansers have been witnessed feeding on the migratory Pacific Redfin *Tribolodon brandtii* on the Kievka River where the species lives offshore and migrates up river to spawn during May–September (Reshetnikov et al. 1997). These fish would make a marine contribution to an otherwise freshwater tissue signal in mergansers, depending how long those fish have been in freshwater (see for example Graham et al. 2014). Feeding on a mixed diet of freshwater and marine migratory fish whilst foraging and drinking in a freshwater environment might help explain the single anomalous isotopic composition of feathers of the AHY male which showed $\delta^2H_f = -119.1$ ‰ (i.e. strongly freshwater), $\delta^{13}C = -19.2$ ‰ (marine), but $\delta^{15}N = 8.62$ ‰ (freshwater, see Solovyeva et al. 2014b) if this individual received a large component of its H from drinking water and especially if fish tissue equilibration times vary for C, N, and H which is likely (Soto et al. 2013). Similarly we might expect the opposite effect for a merganser deriving a large component of its H budget by drinking in brackish waters while feeding primarily on freshwater origin (anadromous) fish that are returning to the sea as we saw in our sample of a single individual. Several species of salmon (but predominantly the Chum Salmon *Oncorhynchus keta*) migrate down the rivers of Primorye to the sea, from early May until early August. Young salmon gather in shallow marine waters, especially in river estuaries where they reach extremely high densities (L. Bachevskaya, pers. comm.) and such aggregations could serve as a rich food supply for moulting mergansers. Nevertheless, this combined analysis confirms that only three females and one male likely moulted their flight feathers in a marine environment compared to 14 females and five males that did so clearly on freshwater systems. The combined use of δ^2H_w determinations from river systems and δ^2H_f from geolocated females of know moulting provenance also establishes the possibility of differentiating the moulting river provenance of non-instrumented birds using only feather samples.

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